Development and Application of a Classification System for Undisturbed and Disturbed Tropical Montane Forests Based on Vegetation Structure

Dissertation Thesis

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Summary

Classification of the vegetation was a central part of a DFG-financed analysis of undisturbed and disturbed montane rain forest ecosystems in Southern Ecuador. The aim of the study presented here was the development and application of a classification system based on structural characters for both, undisturbed and disturbed forests.

In an altitude between 1570 m a.s.l. and 3100 m a.s.l. 139 plots of 20 m x 20 m were established and the abundance of 151 structural parameters was quantified per tree stratum. Cluster analysis allowed grouping of the 139 plots into 14 groups, called structural forest types. These types were: Secondary growth after road construction, Secondary growth after landslide, Plantation of *Pinus patula*, Forest on edges of natural gaps, Secondary ravine forest, Ravine forest under human influence, Primary ravine forest at lower altitude, Primary ravine forest at higher altitude, Microphyll ridge forest, Mesophyll ridge forest, Macrophyll ridge forest, and megaphyll ridge forest. Two forest types were investigated outside the closer investigation area and were classified as Secondary forest in Mindo and Primary forest in Cajanuma.

Primary forest types were only found south of the Rio San Francisco, whereas on the northern side in a matrix of pastures and farmland only plantations and secondary vegetation along ravines could be detected. In the area of primary forest, a primary ravine forest type of lower altitudes turned into a type of higher altitudes around 2100 m a.s.l. in ravines. Both types were characterised by comparably great tree heights and wide stem diameters. On ridges, three types of ridge forest coexisted in the lower part until microphyll ridge forest dominated in altitudes above 2200 m a.s.l.. Timberline was reached at 2650 m a.s.l. on the eastern side of the cordillera, at approximately 3000 m a.s.l. on the western side in Cajanuma. Decreasing canopy height on ridges could be explained by water stress in wind exposed sites and unfavourable N-mineralisation conditions (due to decreasing pH, profile depth, raising C/N-values, and water stagnation with increasing altitude). Secondary forest types were characterised by human influence (felling of emergent trees), pioneer vegetation and high abundance of connecting elements like lianas and bamboo.

The structural forest types could be integrated into accepted schemes of altitudinal zonation of the Andean vegetation without contradiction, but allowing a further distinction of the zone under investigation.

Frequency analysis and calculation of correlation between variables allowed the reduction of the catalogue from 151 to 104 structural parameters

by excluding variables that did not contribute to the clustering. This exclusion did not alter the result of the cluster analysis. On the basis of the reduced catalogue a key to the 14 structural forest types was developed. This key was applied to 100 plots of 10 m x 10 m in a parallel study of other project participants investigating the distribution of hummingbird-visited plants. Distribution patterns of this functional group could be related to the structural forest types. Recent investigations of bird and moth communities will also be tested for functional relationships.

Zusammenfassung

Die Klassifikation der Vegetation war zentraler Bestandteil einer von der DFG geförderten Untersuchung ökosystemarer Kenngrößen eines tropischen Bergwaldes in Südecuador. Ziel meiner Studie war die Entwicklung und Anwendung eines Systems zur Klassifizierung ungestörter und gestörter Bergwaldvegetation auf der Basis struktureller Vegetationsmerkmale.

Auf 139 Plots von 20 m x 20 m in Meereshöhen zwischen 1570 m ü.NN und 3100 m ü.NN wurde pro Baumschicht das Vorkommen von 151 ausgewählten Merkmalen quantitativ erfaßt. Mittels Clusteranalyse konnten die 139 Plots in 14 Gruppen gegliedert werden, die als Waldstrukturtypen bezeichnet wurden. Es wurden unterschieden: Sekundärvegetation an Straßenböschungen, Sekundärvegetation auf Rutschungen oder Lichtungen, Aufforstungen mit *Pinus patula*, Natürliche Waldränder, Sekundärer Schluchtwald, Schluchtwald mit Anzeichen menschlicher Einflußnahme, Primärer Schluchtwald tieferer Lagen, Primärer Schluchtwald höherer Lagen, Mikrophyller Gratwald, Mesophyller Gratwald, Macrophyller Gratwald und Megaphyller Gratwald. Dazu kamen die zu Testzwecken aufgenommenen Waldstrukturtypen Sekundärwald in Mindo und Primärwald in Cajanuma außerhalb des engeren Untersuchungsgebietes.

Die primären Waldstrukturtypen fanden sich ausschließlich südlich des Rio San Francisco, während nördlich des Flusses im landwirtschaftlich genutzten Umland nur Aufforstungen und sekundäre Vegetation entlang von Tiefenlinien und an Böschungen gefunden werden konnten. In den Schluchten des Primärwaldbereiches ging in einer Höhe von 2100 m ü.NN der Schluchtwald tieferer Lagen in den höherer Lagen über. Beide Waldtypen zeigten im Vergleich zu den Gratwäldern deutlich höheren Wuchs und größere Stammdurchmesser. Im unteren Bereich der Grate bis 2200 m ü.NN koexistierten drei Gratwaldtypen, bevor darüber der microphylle Gratwald bis zur Waldgrenze bei 2650 m ü.NN dominierte. Die verminderte Wuchsleistung der Gratwälder könnte durch Trockenstreß bei Windexposition sowie schlechte N-Versorgung durch ungünstige Mineralisierungsbedingungen (mit zunehmender Meereshöhe sinkender pH, sich weitendes C/N-Verhältnis und zunehmende Staunässe) verursacht sein. In den Sekundärwäldern fanden sich Anzeichen menschlicher Einflußnahme (Einzelstammnutzung von Werthölzern), außerdem Pinoierbäume, sowie Lianen und Bambus als vernetzende Elemente.

Die Waldstrukturtypen konnten in anerkannte Schemata der Höhengliederung der Andenvegetation eingegliedert werden. Dabei widersprechen sie

der Unterteilung nicht, verfeinern diese aber für den untersuchten Höhenbereich.

Untersuchungen der Frequenz des Auftretens einzelner Merkmale und Korrelationsanalysen erlaubten durch Ausschluß von Variablen, die nicht zur Gruppenbildung beitrugen, den Merkmalskatalog auf 104 Variablen zu kürzen, ohne die Gruppenbildung zu beeinflussen. Der hieraus entwickelte Bestimmungsschlüssel zum Auffinden der Waldstrukturtypen wurde im gleichen Untersuchungsgebiet für 100 Plots von 10 m x 10 m angewandt, auf denen von anderen Projektteilnehmern die Abundanz kolibribesuchter Pflanzen untersucht wurde. Eine vergleichende Analyse ergab, daß sich die Muster der Verteilung dieser funktionalen Pflanzengruppe in der Einteilung der Waldstrukturtypen wiederfinden. In laufendenStudien zur Verteilung von Nachtfalter- und Vogelgemeinschaften wird untersucht, ob sich ebenfalls funktionale Zusammenhänge finden lassen.

Resumen

La clasificación de la vegetation fue parte central de una investigación financiada por la DFG sobre los parámetros ecosistemáticos de un bosque tropical perturbado y no perturbado en el Sur de Ecuador. El objetivo de mis estudios fue el desarollo y la aplicación de un sistema de clasificación de la vegetación perturbada y no perturbada de bosques montanos a base de características estructurales de vegetación.

En 139 plots de 20 m por 20 m ubicados entre los 1570 m s.n.m. y 3100 m s.n.m. fueron alistados 151 características seleccionadas por cada estrato de arboles.

Por medio de análisis de cluster los 139 plots se pudieron clasificar en 14 grupos, los cuales fueron designados como tipos de estructura de bosque. Lo siguiente fue diferenciado: vegetación secundaria en repecho de carreteras, vegetación secundaria en deslizamientos o claros, plantación de *Pinus patula*, bordes de bosque naturales, bosque de quebrada secundario, bosque de quebrada con indicios de influencia humana, bosque de quebrada primario en altitudes bajas, bosque de quebrada primario en altitudes mayores, bosque microfilo de cresta, bosque mesofilo de cresta, bosque macrofilo de cresta, y bosque megafilo de cresta. A esto se añadieron el bosque secundario en Mindo y el bosque primario en Cajanuma, dos tipos de estructura de bosque determinados como prueba, los cuales se encuentran fuera del area inmediata de investigación.

Los tipos de estructura de bosque primarios se encontraron exclusivamente al sur del Rio San Francisco, mientras que al norte del rio, en un area de uso agricola, solamente se encontraron plantaciones y vegetación secundaria a lo largo de quebradas y repecho.

En las quebradas del area del bosque primario se manifiesta en una altura de 2100 m s.n.m. una transición de bosque de quebradas de altitudes bajas a altitudes mayores. Estos dos tipos de bosque demostraron en comparación con los bosques de cresta un crecimiento claramente más alto y un diámetro de tronco más grande. En la parte baja de las crestas, hasta los 2200 m s.n.m., coexisten 3 tipos de bosque de cresta, encima de los cuales domina el bosque de crestas microfilo hasta el limite de bosque en 2650 m s.n.m.. El crecimiento reducido de los bosques de cresta podrian originarse por sequedad dado a una exposición de viento, asi como mal suministro de N por condiciones desfavorables de mineralización (con creciente altura sobre el mar, baja el pH, se extiende la relación C/N y aumenta el estancamiento de agua). En los bosques secundarios se encontraron indicios de influencia humana (utiliza-

ción de troncos singulares de maderas utiles valiosas), asi como árboles pioneros, al igual que lianas y bambœ como elementos de conexión.

Los tipos de estructura de bosque pudieron ser incorporados en esquemas reconocidos de clasificaciones de la vegetación andina por alturas, sin contradecir la subdivision de estos esquemas, más bien refinando la misma para cada sección de altura investigada.

Excluyendo variables no contribuyentes a la formación de grupos, investigaciones sobre la frequencia de la aparición de características singulares y los análisis de corelación permitieron reducir el catalogo de características a 104 variables, sin influir en la formación de grupos. La asi desarollada clave de identificación para tipos de estructura de bosques fué aplicada en el mismo area de investigación para 100 plots de 10 m por 10 m, en los cuales la abundancia de plantas visitadas por colibríes fue investigada por otros miembros del projecto. Un análisis comparativo demostró, que los modelos de distribución de este grupo funcional de plantas se reencuentran en la clasificación de los tipos de estructura de bosque. En investigaciones actuales sobre la distribución de comunidades de mariposas nocturnas y de aves se estudia, si también aquí se pueden encontrar relaciones funcionales.

Zusammenfassende Übersicht

A Einleitung

Tropische Wälder gehören zu den Ökosystemen mit der höchsten Diversität pflanzlicher und tierischer Lebenwesen weltweit. Insbesondere die Bergwälder der Neotropis gelten als ein Hotspot pflanzlicher Biodiversität (Barthlott et al. 1996), der trotz seiner Bedeutung für den Erhalt der Artenvielfalt einer noch höheren Zerstörungsrate ausgesetzt ist, als tropische Tieflandwälder. Die Anden Ecuadors haben bereits 90% ihrer ehemaligen Bergwälder verloren (Hamilton et al. 1995, Henderson et al. 1991), müßten aber aufgrund ihrer enormen Artenfülle verstärkten Schutz erfahren (Myers et al. 2000). Um das Bestehen der letzten verbliebenen Bergregenwälder zu sichern, ist ein besseres Verständnis des Funktionierens und Zusammenwirkens ihrer Ökosystemkomponenten unabdingbar (Orians et al. 1996). Ein von der Deutschen Forschungsgemeinschaft (DFG) seit 1997 finanziertes Gemeinschaftsprojekt geowissenschaftlicher und biologischer Disziplinen versucht eine integrierte Systemanalyse des Bergwaldökosystems in Südecuador (Beck & Müller-Hohenstein 2001). Die beschreibende Erfassung und Klassifizierung der Vegetation ist dabei ein zentraler Bestandteil. Die hier vorgestellte Studie hat das Ziel, ein Klassifikationssystem als Grundlage für weitergehende Untersuchungen funktionaler Zusammenhänge bereitzustellen.

Ansätze zur Klassifizierung von Vegetation lassen sich in zwei Gruppen gliedern (Beard 1973): floristische Ansätze basieren auf dem Bestimmen von Pflanzenarten und deren Zusammensetzung zu Pflanzengemeinschaften, die z.B. in ein pflanzensoziologisches Konzept eingegliedert werden können. Strukturelle Ansätze hingegen gliedern Vegetation nach der Architektur, dem Aufbau und dem Lebensformenspektrum, um physiognomische Einheiten ausweisen zu können.

Die meisten floristischen Ansätze wurden für die Vegetation der gemäßigten Breiten erarbeitet (Cajander 1909, Du Rietz 1930, Braun-Blanquet 1964) und sind kaum auf die der Tropen übertragbar, wo pro Flächeneinheit eine enorm hohe Zahl von Arten, aber meist nur eine jeweils geringe Dichte von Individuen jeder Art zu finden ist. Eine Systematisierung nach dominanten Arten ist daher schwierig und verlangt, wenn überhaupt möglich, die Expertise von Spezialisten für verschiedene taxonomische Gruppen (Vareschi 1980). Eine floristische Bearbeitung bietet daher für die hochdiversen ecuadorianischen Bergregenwälder nicht den effektivsten Weg, um für Ver-

gleiche mit den Ergebnissen anderer Arbeitsgruppen des Gemeinschaftsprojektes eine schnelle und nachvollziehbare Klassifikation zu liefern.

Auch strukturelle Ansätze sind nicht alle gleichermaßen sinnvoll auf tropische Vegetation anzuwenden. So basiert z.B. das klassische Konzept der Lebensformen von RAUNKIEAR (1934) auf dem Vorhandensein einer kalten Jahreszeit (BEARD 1973). Die Erweiterung dieses Systems nach MUELLER-DOMBOIS & ELLENBERG (1974) sowie das Lebenszonen-Konzept von HOLDRIDGE et al. (1971) gestatten zwar die weltweite Anwendung, erlauben aber aufgrund des globalen Maßstabes keine kleinräumige Untergliederung.

Einen Überblick über die geschichtliche Entstehung der wichtigsten Konzepte zur Beschreibung von Vegetationsstrukturen (beginnend mit SCHIMPER 1898 und WARMING 1909) liefert BEARD (1973), während PAULSCH & CZIMCZIK (2001) neuere Ansätze referieren, die sowohl floristische als auch strukturelle Merkmale zur Kennzeichnung von Vegetation heranziehen. In vielen Fällen beschränkt sich die Beschreibung der Struktur auf die forstwirtschaftlich wichtigen Parameter Baumhöhe, Brusthöhendurchmesser (dbh) und Stammzahl, manchmal bereichert durch Blattcharaktersitika (CONDIT 1998, GARCIA 1998, KORNING et al. 1990, POPMA et al. 1988, PROCTER et al. 1988, VALENCIA 1995, VALENCIA & JORGENSEN 1992, VALENCIA et al. 1998, YOUNG 1998, ZOMER et al. 2001). Innerhalb der Ansätze, die einen längeren Katalog struktureller Merkmale zur Vegetationsbeschreibung heranziehen, ist für viele die Bestimmung der Pflanzenarten weiterhin grundlegend (PARSONS 1975, HOHEISEL 1976, VARESCHI 1980, ORSHAN 1986, TOMLINSON 1983). Nur einige wenige entwickeln ein von der Artbestimmung unabhängiges Klassifikationssystem und können dann Ergebnisse einer strukturellen Klassifizierung mit floristischen Erhebungen vergleichen (WEBB et al. 1970, WERGER & SPRANGERS 1982, LUX et al. 1994, LE BROCQUE & BUCKNEY 1997). Alle Autoren, die diesen Vergleich anstellen, schließen aus ihren Ergebnissen, daß beide Wege zu vergleichbaren Gliederungen führen, die Untersuchung der Struktur aber die bei weitem effektivere Lösung darstellt.

Der Schluß, daß für die Kennzeichnung der Bergregenwälder Ecuadors eine strukturelle Klassifizierung am erfolgversprechendsten ist, basiert nicht allein auf Zeitgründen. Untersuchungen der Vegetationsstruktur können Zusammenhänge aufdecken, die einer rein floristischen Bearbeitung verborgen bleiben (GENTRY 1988), z.B. die Auswirkungen des Hurricane Gilbert auf die Waldvegetation Mexicos, in deren Folge die Artenzusammensetzung nahezu unverändert blieb, während sich die Struktur der Wälder (durch Kronen- und Astbruch, Baumfall und Entlaubung) maßgeblich änderte (SANCHEZ & ISLEBE 1999). Untersuchungen von Tier-Pflanze-Interaktion haben ebenfalls die Bedeutung der Vegetationsstruktur gezeigt. So sind z.B.

Vogelgemeinschaften tropischer Wälder auf bestimmte Straten beschränkt (Preleuthner et al. 1998), während bestimmte Papageienarten Emergenten mit waagrechten Ästen als Plätze zum Fressen herangetragener Früchte benötigen (Roth 1982). Zur Untersuchung solcher ökosystemaren Zusammenhänge ist die Beschreibung der Vegetationsstruktur unabdingbar.

Aus verschiedenen Gründen ist keines der struktur-basierten Klassifikationssysteme ohne weiteres auf tropische Bergwälder anwendbar (zu globaler Maßstab bei Mueller-Dombois & Ellenberg 1974 und Holdridge et al. 1971, nicht für Wälder entwickelt bei Halloy 1990 und Lux et al. 1994, Ausgraben des Wurzelsystems nötig bei Orshan 1986, Überbetonung von Blattmerkmalen bei Vareschi 1980 und Le Brocque & Buckney 1997).

Ziel der hier vorgestellten Untersuchung war daher die Entwicklung und Anwendung eines eigenen Systems zur Klassifizierung der Bergwaldvegetation auf der Basis struktureller Merkmale. Unter „Struktur" wurde dabei die horizontale und vertikale Anordnung von Vegetation (Barkmann 1979) verstanden. Aus der potentiell unendlichen Fülle möglicher zu beschreibender Merkmale mußte eine Auswahl getroffen, und die Quantität des Auftretens der gewählten Parameter dokumentiert werden. Diese Quantifizierung sollte zu einer nachvollziehbaren Gruppierung der Untersuchungseinheiten zu Vegetationseinheiten führen, wobei die Variation zwischen den Einheiten möglichst groß, innerhalb der Einheiten jedoch möglichst gering sein sollte. Falls solche Vegetationseinheiten existierten, sollte ihre räumliche Verteilung beschrieben und mit abiotischen Standortfaktoren und anthropogenen Einflüssen in Beziehung gesetzt werden. Aus den untersuchten Merkmalen sollten diejenigen bestimmt werden, die das höchste Potential haben, zwischen den Einheiten zu unterscheiden.

Diese Merkmale sollten zu einem einfach zu handhabenden Schlüssel zur Bestimmung der Vegetationseinheiten kombiniert werden, der als Basis für weitergehende Ökosystemstudien auch von Nicht-Botanikern angewendet werden kann.

B Material und Methoden

B.1 Untersuchungsgebiet

Das Untersuchungsgebiet für die vorliegende Studie liegt an der Ostabdachung der ecuadorianischen Andenkordilliere (4° 00' Süd und 79° 05' West) auf dem Gebiet der Estación Científica San Francisco (ECSF). Es umfaßt einen Höhengradienten von 1800 m ü.NN bis 3100 m ü.NN. Trotz saisona-

ler Schwankungen der Monatsniederschläge ist das Klima des Untersuchungsgebietes perhumid. Niederschlagsmessungen der Jahre 1998-2000 auf 1900 m ü.NN ergaben einen durchschnittlichen Jahresniederschlag von 2220 mm (YASIN 2001). Hohe Wassersättigung der Böden und ein bis zu 60° steiles Relief machen Hangrutschungen zu einem weitverbreiteten Phänomen, selbst in anthropogen ungestörten Bereichen (STOYAN 2000). Nach SCHRUMPF et al. (2001) sind im Untersuchungsgebiet Böden mit hohem Anteil an organischem Material auf Phylliten und Sandsteinen entwickelt. Aufgrund sinkender pH-Werte und steigender C/N-Verhältnisse wird die N-Versorgung mit zunehmender Meereshöhe schlechter und könnte im Zusammenwirken mit Staunässe wachstumslimitierend auf Pflanzen wirken (SCHRUMPF et al. 2001).

Obwohl die Besiedlungsgeschichte der Anden bis zur letzten Eiszeit zurückreicht (ELLENBERG 1979, DOLLFUSS 1982, RUTHSATZ 1983), ist die Umgebung des Untersuchungsgebietes erst seit etwa 60 Jahren großflächig menschlichem Einfluß ausgesetzt. Seit Ende der 80er Jahre der Zugang durch den Bau einer Straße zwischen den Städten Loja und Zamora erleichtert wurde, folgten größere Umwandlungen von Primärwäldern in Weideland.

B.2 Überblickskartierung

Um einen Überblick über die Verteilung von Wäldern, Waldresten und genutzten Landschaftsbereichen zu gewinnen, wurde eine Landnutzungskartierung im Maßstab 1:25000 beiderseits der Verbindungsstraße Loja-Zamora durchgeführt. Als Kartiergrundlage dienten Luftbilder (Instituto Geográfico Militar 1998) und topographische Karten (Instituto Geográfico Militar, Loja Norte 1981, Zamora 1994, Loja Sur 1996, 1:50 000).

B.3 Parzellenscharfe Strukturkartierung genutzter Bereiche

Innerhalb der in der Überblickskartierung ausgewiesenen landwirtschaftlich genutzten Bereiche wurden entlang des Höhengradienten (1000-2000 m ü.NN) 12 Wirtschaftsbetriebe (Fincas) ausgesucht, auf denen für jede abgrenzbare Parzelle Strukturmerkmale kartiert wurden. Darunter fielen, neben der Art der Nutzung, die Größe und Form der Parzelle, die Art der Abgrenzung zu benachbarten Parzellen (Zaun, Hecke, Waldrand), die Zahl angrenzender Parzellen, die Vegetationsbedeckung, das Vorkommen von

Bäumen oder Waldresten, der Totholzanteil, Viehgangeln, die Bearbeitungsintensität und die Entfernung zum Wohnhaus des jeweiligen Bauern. Mittels einer Clusteranalyse wurden die Parzellen dann zu Struktureinheiten gruppiert, deren Verteilung für jede der 12 Fincas in einer Karte dargestellt wurde. Gezielte Gespräche mit den Bauern lieferten Auskunft über Besitzverhältnisse, die Dauer der Bewirtschaftung, den Einsatz von Maschinen und Düngemitteln.

B.4 Plotscharfe Strukturkartierung von Waldbereichen

In den bei der Überblickskartierung ausgewiesenen Waldbereichen wurde die Vegetationsstruktur auf Plots von 20 m x 20 m kartiert. Zunächst wurden bestehende Klassifikationsansätze auf ihre Anwendbarkeit im Bergregenwald vergleichend getestet. Dies waren insbesondere die Ansätze von Mueller-Dombois & Ellenberg (1974), Beard (1955), Richards et al. (1940), Webb et al. (1970), Parsons (1975), Orshan (1986) und Werger & Sprangers (1982), die auf 15 Plots für alle verholzenden Baumindividuen mit einem dbh > 2 cm angewandt wurden. Um die Systeme zu vergleichen, wurde die Zahl der vorkommenden Parameter und die Frequenz ihres Auftretens ausgewertet (Axmacher 1998). Die Ergebnisse dieser Voruntersuchung dienten als Basis für die Entwicklung eines eigenen Klassifikationssystems, das für jede Baumschicht separat angewandt wurde. Dazu wurden pro Baumschicht acht Klassen metrischer Parameter aufgenommen, die den Bestand des Plot insgesamt beschrieben (z.B. durchschnittlicher Stamm- bzw. Kronenabstand, Höhe der Baumschicht). Ein Katalog von 143 Strukturparametern wurde in einer vierstufigen Ordinalskala aufgenommen, die in Anlehnung an Webb et al. (1970) eingeteilt wurde:

0 = fehlend (kein Mitglied der betrachteten Baumschicht zeigt dieses Merkmal)
1 = selten (weniger als ein Drittel der Mitglieder der betrachteten Baumschicht zeigen dieses Merkmal)
2 = häufig (mehr als ein Drittel, aber weniger als zwei Drittel der Mitglieder der betrachteten Baumschicht zeigen dieses Merkmal)
3 = dominant (mehr als zwei Drittel der Mitglieder der betrachteten Baumschicht zeigen dieses Merkmal).

Die 143 Parameter beschrieben Kronenform, Blattform, -stellung und -größe, Borkenbeschaffenheit, Verholzungsgrad und Verzweigungsmuster nach

Vorschlägen verschiedener getesteter Systeme. Zusätzlich wurden Parameter aufgenommen, die den Epiphytenbesatz und die Verteilung vaskulärer Epiphyten sowie den Grad der Vernetzung benachbarter Baumindividuen durch Lianen oder Bambus dokumentierten. Der gesamte Katalog von somit 151 Strukturparametern wurde auf 139 Plots zur Anwendung gebracht. Diese Plots wurden entlang des Höhengradienten mindestens alle 50 Höhenmeter verteilt. Eine randomisierte Verteilung war aufgrund der Unzugänglichkeit und Steilheit des Geländes nicht durchführbar.

Im eigentlichen Untersuchungsgebiet lagen 119 Plots. Um das Aufnahmesystem zu testen, wurden 12 Plots auf der Westseite des Podocarpus-Nationalparks in einem Berwald vergleichbarer Höhenlage (Cajanuma) eingerichtet, acht weitere nördlich von Quito in einem sekundären Bergwald (Mindo).

B.5 Statistische Auswertung

Zur statistischen Auswertung wurde eine Clusteranalyse mit SPSS durchgeführt. Nach der Eliminierung von Ausreißern mit der "single-linkage"-Methode wurde der Ward-Algorhythmus mit quadrierter euklidischer Distanz benutzt (BACKHAUS et al. 1996, EVERITT 1995). Da die Custeranalyse nur Objekte (hier Plots) gruppiert, aber nicht erklären kann, welche Variablen für die Gruppierung maßgeblich waren, wurde als Interpretationshilfe ein T-Wert (BACKHAUS et al. 1996) für jede Variable in allen Clustergruppen nach folgender Formel berechnet:

$$\mathbf{T} = \frac{\bar{X}(J,G) - \bar{X}(J)}{S(J)}$$

mit: $\bar{X}(J, G)$ = Mittelwert der Variable J (d.h. des Strukturmerkmals) über alle Objekte in Gruppe G (d.h. alle Plots einer Gruppe der Clusterung)

$\bar{X}(J)$ = Mittelwert der Variable J über alle Objekte (d.h. alle Plots)

$S(J)$ = Standardabweichung der Variable J über alle Objekte (d.h. alle Plots).

Ist der T-Wert positiv, dann ist das Strukturmerkmal in der entsprechenden Clustergruppe im Vergleich zur Grundgesamtheit aller Plots überrepräsentiert. Bei negativem T-Wert ist das Strukturmerkmal in der Gruppe unterrepräsentiert.

Um Variablen ausgliedern zu können, die so selten oder so gleichmäßig auftreten, daß sie nicht zur Unterscheidung der Gruppen beitragen, wurde die Frequenz aller möglichen Ausprägungen aller Variablen berechnet. Gleichzeitig wurde die Korrelation jeder Variablen mit jeder anderen berechnet (Spearman Correlation Coefficient), um zu untersuchen, ob Paare korrelierender Variablen ein und dieselbe Struktur beschreiben und daher auf eine von beiden verzichtet werde kann (beispielsweise könnte das Auftreten megaphyller Blätter mit dem Vorkommen trichterförmiger Kronen korrelieren, da beide bei Baumfarnen und Palmen jeweils gemeinsam erscheinen). Der auf diese Weise reduzierte Merkmalskatalog wurde als Grundlage einer erneuten Clusterung benutzt, um zu testen, ob die Gruppenbildung stabil bleibt.

Die Verteilung der Clustergruppen im Gelände wurde interpretiert und in einer Karte dargestellt. Die Datenaufnahme für alle Plots erfolgte zwischen Juni 1997 und Januar 2000.

C Ergebnisse und Interpretation

C.1 Übersichtskartierung

In der im Maßstab 1:25000 gehaltenen Übersichtskartierung (Schneider 2000, Paulsch et al. 2001) wurde zwischen folgenden Landschaftselementen unterschieden: Wälder, Aufforstungen (zumeist mit *Pinus patula*), Gebüsche, Weiden, Äcker, ältere und jüngere Rodungen (einschließlich abgebrannter Flächen), farndominierte Areale, Rutschungen, Straßen und Wege, Häuser sowie Masten einer Starkstromleitung. Die für den Bau der Stromleitung 1997 geschlagene Schneise war 2000 noch deutlich sichtbar. Aus der Verteilung der Flächenanteile der einzelnen Landschaftselemente konnte geschlossen werden, daß Weidewirtschaft die hauptsächliche Form der Landnutzung darstellte, wohingegen ackerbauliche Nutzung nur auf kleinen Flächen in direkter Umgebung der Häuser betrieben wurde. Wälder fanden sich insbesondere in höheren Lagen fernab der Straße. Jüngere Rodungen wurden hauptsächlich im jeweils höchstgelegenen Bereich einer Finca angetroffen. Die Interpretation dieses Musters, nämlich die immer weiter selbst in unzugängliche Hochlagen fortschreitende Brandrodung und Umwandlung von Wäldern in Weiden, wurde durch die Befragung der Bauern bestätigt.

Aufforstungen waren selten und wurden nicht von subsistenzorientierten Bauern betrieben, denen nach eigener Auskunft die Investitionsmittel fehl-

ten. Bereiche, die schon über längere Zeiträume als Weiden genutzt wurden, wiesen einen hohen Bedeckungsgrad durch Adlerfarn (*Pteridium aquilinum*) auf (PAULSCH et al. 2001). Diese invasive Farnart wird vom Weidevieh gemieden und übersteht Abbrennen der oberirdischen Teile durch sofortigen Neuaustrieb aus den unbeschädigten Rhizomen. Das Ausgraben der Rhizome ist nach Auskunft der Befragten zu aufwendig, sodaß die Weiden aufgegeben werden und durch neuerliche Rodung von Primärwaldbereichen der Verlust von Weideflächen ersetzt wird.

Rutschungen fanden sich insbesondere entlang der Straße und waren während des gesamten Untersuchungszeitraumes aktiv. STOYAN (2000), der die Dynamik dieser Rutschungen untersuchte, geht davon aus, daß die durch den Straßenbau entstandenen Rutschungen Jahrzehnte bis zu ihrer Stabilisierung benötigen.

C.2 Parzellenscharfe Strukturkartierung genutzter Bereiche

Die 12 ausgewählten Fincas ließen sich in 245 Parzellen untergliedern, die 716 Grenzen untereinander oder mit angrenzenden Flächen außerhalb der kartierten Fincas ausbildeten (SCHNEIDER 2000). Die Außengrenzen der Fincas folgten zumeist kleinen Bachläufen, Graten oder der Straße.

Der hohe Anteil von Weideparzellen (61) bestätigte das schon in der Übersichtskartierung gefundene Vorherrschen der Weidewirtschaft gegenüber anderen Formen der Landnutzung. Dennoch verfügte jeder untersuchte Betrieb mindestens über drei noch unberührte Parzellen mit Primärwald, die als Reserve bei weiterem Rodungsbedarf angesehen wurden. 41% aller Grenzen von Waldparzellen waren Grenzen zu Weideparzellen, was belegt, daß gerodete Flächen sofort in Weiden umgewandelt wurden (zum Teil durch Auspflanzen von Grashorsten), ohne daß eine längere Zwischennutzung durch Fruchtanbau erfolgte.

Nur 2% der untersuchten Grenzen zeigten einen abrupten Wechsel in der Zahl der Vegetationsschichten oder den dominierenden Lebensformen und wurden als „scharfe“ Grenzen klassifiziert. Das Fehlen solcher scharfen Grenzen weist auf die erst junge Besiedlungsgeschichte des Untersuchungsgebietes hin, in dem Besitzgrenzen noch nicht lange etabliert sind. Geringer technischer Einsatz und unspezifische Maßnahmen wie Abbrennen einzelner Bereiche verhindern ebenfalls die Ausbildung klarer Grenzen.

Für alle 245 Parzellen wurden die im Methodenteil genannten Strukturparameter aufgenommen. Ein Clusteranalyse führte zu 14 Struktureinheiten, die sich hinsichtlich der Flächenformen und –größen, der dominierenden

Lebensformen, der Vegetationshöhe und –schichtung, der Vegetationsbedeckung sowie der Entfernung zum Hofgebäude unterschieden. Für jede Finca wurden zwei Karten erarbeitet: eine zeigt die Nutzung jeder Parzelle, die andere die Zugehörigkeit jeder Parzelle zu einer Struktureinheit. Die vergleichende Interpretation beider Kartensätze zeigt, daß die Kartierung der Struktur eine feinere Untergliederung von Nutzungseinheiten erlaubt. Flächen ähnlicher Nutzung können sich in ihrer Struktur stark voneinander unterscheiden und somit beispielsweise eine ganz unterschiedliche Rolle als Ausgangspunkte einer Sukzession bilden (z.B. baumlose Weiden im Vergleich zu Weiden mit erhaltenen Baumgruppen).

Insgesamt zeigt sich ein kleinräumiges Mosaik verschiedener Einheiten in einer strukturreichen, durch Brandrodung und Weidewirtschaft geprägten Landschaft.

C.3 Plotscharfe Strukturkartierung von Waldbereichen

In den in der Übersichtskartierung als Wald ausgewiesenen Bereichen wurden zunächst die Ansätze von Mueller-Dombois & Ellenberg (1974), Beard (1955), Richards et al. (1940), Webb et al. (1970), Parsons (1975), Orshan (1986) und Werger & Sprangers (1982) auf 15 Plots auf ihre Anwendbarkeit für Bergwald überprüft (Axmacher 1998). Die global skalierten und auf ungestörte Vegetation bezogenen Systeme von Mueller-Dombois & Ellenberg (1974), und Beard (1955) erlaubten keine kleinräumige Differenzierung. Aus dem Ansatz von Orshan (1986) konnten zwar 91 Parameter im Untersuchungsgebiet gefunden werden, dies sind aber weniger als 40% der vorgeschlagenen Merkmale dieses Ansatzes. Die beste Relation von tatsächlich vorkommenden zu vorgeschlagenen Merkmalen wies mit 73% der Ansatz von Werger & Sprangers (1982) auf. Eine vergleichende Clusteranalyse ergab, daß alle Systeme stark gestörte Plots (mit Sekundärvegetation) von Primärwald trennen konnten, aber die weitere Untergliederung des ungestörten Waldes schwierig war.

Das aus Parametern verschiedener Ansätze und eigenen Ergänzungen neu entwickelte Aufnahmesystem von 151 Merkmalen wurde auf 139 Plots für jede Baumschicht angewendet. Dabei wurden auf 9 Plots nur eine, auf 72 Plots zwei und auf 58 Plots drei Baumschichten festgestellt. Eine Clusteranalyse über alle 453 Merkmale (151 pro Schicht) liefert nur eine Trennung nach Anzahl der Schichten. Im Folgenden wurden daher die einschichtigen Plots separat ausgewertet. Um die zwei- bzw. dreischichtigen Plots gemeinsam auswerten zu können, wurde die mittlere Baumschicht der dreischichti-

gen Plots zunächst vernachlässigt. Dies gewährleistete, daß jeweils Kronenschicht mit Kronenschicht und Unterwuchs mit Unterwuchs verglichen werden konnte.

Die gemeinsame Clusterung der mehrschichtigen Plots lieferte ein Dendrogramm, an dessen Ende sechs Plots kettenartig angehängt waren, die keiner Gruppe zugeordnet werden konnten. Daraufhin wurde der Datensatz nach folgenden Kriterien durchsucht: Plots, in denen die oberste Baumschicht nur von einem einzigen Emergenten gebildet wurde, oder Plots, in denen zwar mehr als ein aber weniger als fünf Bäume die oberste Baumschicht bilden, diese nicht mehr als 30% deckt und der Stammabstand mindestens 3 m beträgt. In den so ausgegliederten 11 Plots waren alle sechs vorher nicht zuordenbaren Plots vertreten. Da hier die oberste Baumschicht geringe Deckung hatte und zumeist nur die Merkmale eines einzigen Baumes abbildete, wurde die eigentliche Kronenschicht erst von den als mittlere Baumschicht erfaßten Bäumen gebildet. Für diese Plots wurden daher die Daten der mittleren Baumschicht für die Clusteranalyse verwendet, woraufhin sich alle Plots in Gruppen gliedern ließen.

Die 9 einschichtigen Plots konnten in zwei Gruppen zu jeweils drei Plots gegliedert werden, ein Plot wurde aufgrund seiner Lage einer Gruppe ansonsten mehrschichtiger Plots zugeordnet, zwei Plots bildeten Sonderfälle. Einer von ihnen war durch Holzeinschlag seines Unterwuches vollständig beraubt, der andere war der höchstgelegene aller Plots und leitete bereits zum Buschpáramo über.

Die 130 mehrschichtigen Plots konnten in 12 Gruppen gegliedert werden. So führte die Gliederung sämtlicher 139 Plots zu 14 Gruppen, die als Waldstrukturtypen bezeichnet wurden. Für jede dieser Gruppen wurden für alle Merkmale T-Werte berechnet und die Werte >/0,7/ zur Interpretation herangezogen. Im Folgenden werden die 14 Waldstrukturtypen beschrieben:

C.3.1 Sekundärvegetation an Straßenböschungen (Cluster I a)

Die drei Plots dieser Gruppe lagen an der oberen Straßenböschung der Verbindungsstraße Loja-Zamora zwischen 1800 m ü.NN und 2060 m ü.NN. Die 25-50 Individuen der einzigen Baumschicht waren nicht über 10 m hoch und ihre Stämme nicht dicker als 10 cm. Der Abstand der unregelmäßigen oder schirmförmigen Kronen war kleiner als 1 m. Die zumeist weichlaubigen Pflanzen hatten keine Epiphyten, waren aber durch Lianen und Bambus vernetzt. Die geringe Wuchshöhe, das Fehlen alter Bäume und die Lage am Straßenrand ließen den Schluß zu, daß es sich hier um Sekundärvegetation auf durch den Straßenbau stark gestörten Standorten handelte.

C.3.2 Sekundärvegetation auf Rutschungen oder Lichtungen (Cluster I b)
Die Vegetation der drei Plots dieses Clusters war niedriger, aber individuenreicher und dichter als die der vorher beschriebenen Gruppe, sonst aber sehr ähnlich und in gleicher Höhenlage. Die Unterschiede mögen darin begründet liegen, daß die maßgebliche Störung jüngeren Datums war (Schlagen der Stromschneise 1997). Beide Gruppen können nicht als „Waldtypen" im engeren Sinne bezeichnet werden, da keine eigentliche Waldvegetation vorhanden war. Dennoch besitzen sie das Potential, wieder zu Sekundärwald aufzuwachsen.

C.3.3 Aufforstung mit Pinus patula *(Cluster II)*
Die obere Baumschicht der fünf Plots dieses Clusters bestand ausschließlich aus *Pinus patula* in einer Pflanzdichte von 25-50 Individuen pro Plot, die bei 20-30 cm dbh 15 m Höhe und 90% Deckung erreichten. Die Pflanzung lag auf etwa 1950 m ü.NN. Der Unterwuchs war spärlich ausgebildet und deckte nur 10-20%. Epiphyten oder verbindende Elemente fehlten fast völlig. Die hohe Pflanzdichte und die Uniformität einer Monokultur (aus exotischen Gymnospermen) führten dazu, daß eine ganze Reihe von Variablen im Vergleich zur Gesamtheit der Plots über- bzw. unterrepräsentiert waren: Konische Kronenform, waagrechte Äste, Beastung bis in das untere Stammdrittel und nadelförmige Blätter waren stark überrepräsentiert, während sämtliche das Auftreten von Epiphyten beschreibenden Merkmale fehlten und aufgrund des kaum vorhandenen Unterwuchses in dieser Schicht viele Merkmale ebenfalls nicht vorkamen. Damit war dieses Cluster sehr klar von allen anderen Waldtypen abgrenzbar.

C.3.4 Sekundärwald in Mindo (Cluster III)
In einem 18 Jahre alten Sekundärwald nördlich von Quito wurden 8 Plots fernab des eigentlichen Untersuchungsgebietes in einer Höhe von 1570-1620 m ü.NN angelegt, um zu testen, ob das Klassifizierungssystem diesen sicherlich andersartigen Wald ausgliedern konnte. Sieben dieser Testplots bildeten das separate Cluster III, nur einer wurde in Cluster VI c gestellt. Die bis zu 25 m hohe Kronenschicht zeichnete sich durch schirmförmige Kronen weichlaubiger Bäume mit großen, gefingerten Blättern aus, die viele Kletterpflanzen (insbesondere Araceen) beherbergten. Alle diese Merkmale treffen auf Vertreter der Gattung *Cecropia* zu, die als Pioniere nach Rodungen bekannt sind und in dem hier vorgefundenen Sekundärwald stark vertreten waren. Der Unterwuchs war durch megaphylle Blätter und trichterförmige Kronen gekennzeichnet, was mit dem gehäuften Auftreten von Baumfarnen korrelierte. Der Plot, der trotz seiner Lage in Mindo nicht in Cluster

III eingeordnet wurde, zeigte größere Wuchshöhen und höhere Stammdurchmesser (bis 60 cm) und war damit dem primären Schluchtwald (Cluster VI c) ähnlicher als dem Sekundärwald.

C.3.5 Primärwald in Cajanuma (Cluster IV)
Ebenfalls außerhalb des eigentlichen Untersuchungsgebietes, aber in größerer Meereshöhe (2700-3100 m ü.NN) und in direkter räumlicher Nähe (15 km) wurden in Cajanuma im Podocarpus Nationalpark 12 Testplots angelegt. Diese Plots bildeten ebenfalls ein eigenes Cluster, dessen oberste Baumschicht durch nur 10-15 m hohe, bis 40 cm starke Bäume mit unregelmäßiger oder schirmförmiger Krone geprägt war. Gefiederte, semisklerophylle Blätter mit einer Blattlänge kleiner als 2 cm waren überrepräsentiert. Diese Merkmale wurden insbesondere von Vertretern der Gattung *Weinmannia* (*Cunoniaceae*) gezeigt. Ihr Vorkommen sowie die dichten Moos- und Farnpolster auf Stämmen und Ästen und die häufig verkrüppelten Kronen charakterisierten dieses Waldtyp als „Elfenwald". Im Unterwuchs war Bambus allgegenwärtig und überwucherte Jungbäume und Baumsturzlücken.

C.3.6 Natürliche Waldränder (Cluster V)
In diesem Cluster wurden sechs Plots zusammengefaßt, die nicht benachbart lagen, aber alle natürliche Waldränder an Flüssen oder Baumsturzlücken bildeten. Die Kronenschicht erreichte nur Höhen bis 15 m, die Stämme waren mit 20-30 cm dbh relativ dünn, aber dennoch war die Deckung dieser Schicht mit bis zu 80% sehr hoch. Gefingerte Blätter waren häufig. Epiphyten waren rar und fehlten im Unterwuchs ganz. Bambus als verbindendes Element war überdurchschnittlich häufig. Wie auch im Sekundärwald in Mindo waren viele Vertreter der Gattung *Cecropia* am Aufbau der Kronenschicht beteiligt. Die hohe Präsenz dieser Pionierbäume und die dichte Vernetzung mit Bambus im Unterwuchs lassen auf ein Stadium der Sukzession schließen, die in diesem Falle durch natürliche Störungen ausgelöst wurde, bzw. im Falle der Plots am Flußufer durch wiederkehrende Hochwässer als Dauerstadium etabliert sein könnte.

C.3.7 Sekundärer Schluchtwald (Cluster VI a)
Cluster VI a vereint 14 Plots, die alle in geringer Meereshöhe (1820-1870 m ü.NN) im untersten Teil des Untersuchungsgebietes lagen. Sie befanden sich alle entlang kleinerer Zuflüsse des Rio San Francisco nördlich der Straße (also im bewirtschafteten Umland) oder entlang des Weges, der im Untersuchungsgebiet den Zugang zu einem Wasserkraftwerk erlaubt. Die Lage aller Plots deutete auf eine hohe Wahrscheinlichkeit anthropogener Störung. Die

mit 20-30 cm dbh unterdurchschnittlich dünnen Stämme der bis zu 25 nur 10-15 m hohen Kronenbäume waren auffallend epiphyten- und moosarm. Der Unterwuchs deckte 60%. Das Fehlen größerer Bäume trotz wachstumsbegünstigender Höhenlage (d.h. geringe Meereshöhe, höhere Jahresmitteltemperaturen, weniger Starkwindereignisse im Vergleich zu Kammlagen) und die Lage der Plots ließen auf einen Sekundärwald schließen.

C.3.8 Schluchtwald mit Anzeichen menschlicher Einflußnahme (Cluster VI b)
In dieser Gruppe wurden 22 jeweils dreischichtige Plots vereint, die entweder nahe dem Weg zum Wasserwerk oder an dem am stärksten wasserführenden Seitenbach des Rio San Francisco in einer Höhe von 1820-1970 m ü.NN lagen. Die Kronenschicht bestand aus nur 1-5 Individuen, die bis zu 25 m hoch und durchschnittlich 50-60 cm dick waren. Epiphyten und Lianen waren vorhanden. In der mittleren Baumschicht in 10-15 m Höhe dominierten unregelmäßige oder schirmförmige Kronen, im Unterwuchs kamen die trichterförmigen Kronen von Baumfarnen hinzu. Im Gegensatz zu dem als sekundär betrachteten Schluchtwald des Clusters VI a wurde hier die Kronenschicht nur von einigen wenigen, aber deutlich höheren und kräftigeren Bäumen gebildet, wenngleich Emergenten fehlten (im Vergleich zu Cluster VI c). In einigen Plots wurden jedoch abgesägte Baumstümpfe und Reste gefällter Bäume (besonderes riesige Vertreter der *Podocarpaceae*) gefunden. Der Seitenbach, entlang dem diese Plots lagen, zeigte Reste eines Fußpfades und war dadurch der am leichtesten zugängliche Bach überhaupt. Es wurde also zwar auf einen primären Schluchtwald geschlossen (in Abgrenzung zu Cluster VI a), in dem aber durch Einzelstammentnahme menschliche Nutzung bereits stattgefunden hatte.

C.3.9 Primärer Schluchtwald tieferer Lagen (Cluster VI c)
In diesem Cluster wurden 19 Plots zusammengefaßt, die in ihrer Höhenlage (1840- 2030 m ü.NN) und ihrer Lage entlang von kleinen Seitenbächen den Plots des vorangegangenen Clusters ähnelten. Auch der Aufbau der Vegetation war ähnlich, allerdings fanden sich hier die größten und stärksten Bäume des gesamten Untersuchungsgebietes mit über 35 m Wuchshöhe und einem dbh von bis zu 130 cm. Dadurch erreichten die Merkmale Baumhöhe, Brusthöhendurchmesser, Höhe des tiefsten Astes und Höhe der Hauptverästelung überdurchschnittlich hohe Werte.

Von den 11 Plots, die in der ersten Clusterung nicht zugeordnet werden konnten und bei denen die mittlere Baumschicht als Kronenschicht eingesetzt wurde (vergleiche Methoden), fanden sich neun in diesem Cluster wieder. Dies war insofern zu erwarten, als die zunächst nicht zuordenbaren

Plots in unmittelbarer räumlicher Nachbarschaft zu den Plots dieses Cluster lagen und der Grund für die Probleme bei ihrer Zuordnung ja gerade in der Kartierung der Emergenten als eigener Baumschicht lag. Aufgrund der Tatsache, daß die wirtschaftlich wertvollen Baumriesen noch gefunden werden konnten, wurde dieser Waldtyp als primärer Schluchtwald bezeichnet, der keine oder zumindest weniger offensichtliche Zeichen menschlichen Einflusses zeigte.

C.3.10 Primärer Schluchtwald höherer Lagen (Cluster VI d)
In dieser Gruppe wurden 7 Plots vereint, die alle in einem Seitenbach deutlich höher als die Plots des vorangegangenen Clusters lagen (2180-2280 m ü.NN). Die dreischichtigen Bestände waren 20-25 m hoch und die Kronenschicht wurde aus 5-25 Individuen mit durchschnittlich 40 cm dbh gebildet. Epiphyten waren häufig und stehende tote Bäume überrepräsentiert. Ebenfalls überdurchschnittlich häufig waren Stelzwurzeln. In der mittleren Baumschicht war der hohe Anteil an Palmen und Baumfarnen (und damit die Häufigkeit megaphyller, gefiederter Blätter und trichterförmiger Kronen) auffällig. Im Unterwuchs waren Vertreter der *Piperaceae* mit assimilierender Rinde häufig. Zeichen von Nutzung konnten nicht gefunden werden, weshalb der Wald als primär eingestuft wurde. Im Unterschied zum primären Schluchtwald der tieferen Lagen fehlten Emergenten, Gesamthöhe und Dicke der Stämme waren geringer und die Kronenschicht war aus mehr Individuen zusammengesetzt.

C.3.11 Mikrophyller Gratwald (Cluster VII a)
Cluster VII a vereinte 21 zweischichtige Plots in Höhen von 2170-2650 m ü.NN. Damit umfaßte dieser Waldtyp die größte Höhendifferenz. Die Vegetation war gekennzeichnet durch eine 10-15 m hohe Kronenschicht aus 5-25 Individuen mit 20-30 cm dbh, deren schirmförmige oder unregelmäßige Kronen nur 30-40% deckten. Die Blätter waren nano-mikrophyll bis mikrophyll und von semisklerophyller Konsistenz. Die Kronenschicht wurde von *Purdiaea nutans* (*Cyrillaceae*) dominiert und nahezu alle Baumindividuen waren dicht mit Epiphyten besetzt. Die Präsenz von Vertretern der Gattung *Clusia* (*Clusiaceae*) war für die Häufung semisukkulenter Blätter verantwortlich. Im Unterwuchs traten *Cyclanthaceae* verstärkt auf, was zur überdurchschnittlichen Häufigkeit der Blattform „anders“ führte. Aufgrund der spärlichen Kronenschicht empfing auch der Unterwuchs genügend Licht, um dichten Epiphytenbewuchs zu erlauben. Die Plots dieses sehr gut abgrenzbaren Clusters lagen alle entlang von Graten, was den Namen Gratwald begründete.

C.3.12 Mesophyller Gratwald (Cluster VII b)
In diese Gruppe fielen nur drei Plots, die alle dreischichtig waren. Die oberste Baumschicht war 15-20 m hoch, deckte 50-60% mit 5-25 Individuen pro Plot und zeigte hauptsächlich mesophylle Blattgrößen. Die meisten Kronenbäume waren stark mit Epiphyten bewachsen und mit Lianen oder Bambus verbunden. Diese Merkmale und das Vorhandensein fächerförmiger Kronen aus schrägen Stämmen grenzten dieses Cluster von den anderen Typen des Gratwaldes ab. In der mittleren Baumschicht waren Palmen häufig, im Unterwuchs überwucherte Bambus junge Bäume. Auf einer Höhe von 2050-2080 m ü.NN lagen die drei Plots zwischen der Höhenstufe des primären Schluchtwaldes und der des mikrophyllen Gratwaldes. Die geringe Plotzahl, die auffällige Häufung gestürzter Bäume und die starke Überwucherung durch Bambus legten die Vermutung nahe, daß es sich bei diesem Waldtyp nicht um eine eigene Höhenstufe handelte, sondern eher um ein spätes Sukzessionsstadium nach Kronenöffnung durch Umfallen einzelner Bäume.

C. 3.13 Makrophyller Gratwald (Cluster VII c)
Cluster VII c vereinte sechs zweischichtige Plots in einer Höhe zwischen 2000-2190 m ü.NN. Das bis 10 m (teilweise bis 15 m) hohe Kronendach war mit 70% Deckung und einem Kronenabstand kleiner als 1 m besonders dicht und durch makrophylle, oft zweifarbige Blätter semisklerophyller Konsistenz geprägt. Diese Merkmalsgruppierung wurde durch das häufige Vorkommen von Vertretern der *Melastomataceae* (Gattungen *Miconia* und *Graffenrieda*) gebildet. Im Unterwuchs trugen das Auftreten von zusammengesetzten Blättern und verholzenden Epiphyten (verursacht durch Vertreter der Gattung *Schefflera* der *Araliaceae*), sowie die Baumfarne zur Abgrenzung von anderen Waldtypen bei. Der makrophylle Gratwald nahm auf einem der Grate eine Höhenstufe von etwa 200 m ein und war dank der oft zweifarbigen Blätter auch im Gelände optisch sehr auffällig. Einige Plots dieses Clusters waren besonderes reich an bodenlebenden Bromelien.

C.3.14 Megaphyller Gratwald (Cluster VII d)
In dieser Gruppe wurden nur drei Plots zusammengestellt, die in einer Höhe von 2050-2140 m ü.NN zu finden waren. Die bis zu 20 m hohe Kronenschicht deckte 60-70% und war durch das Vorkommen megaphyller, gefiederter Blätter und trichterförmiger Kronen ohne Seitenäste geprägt. Diese Merkmalskombination war durch das Auftreten von Palmen (cf. *Dictyocarium*, *Arecaceae)* bedingt, die alle anderen Bäume überragten. Sonst war die Vegetation der des makrophyllen Gratwaldes sehr ähnlich. Obwohl der me-

gaphylle Gratwald lokal begrenzt war, war er durch die hoch aufragenden Palmen leicht abzugrenzen.

Um die Beschreibung der 14 Waldstruktureinheiten zusammenzufassen, kann festgestellt werden, daß primärer Wald nur südlich des Rio San Francisco angetroffen wurde, während auf der Nordseite im landwirtschaftlich genutzten Bereich nur Aufforstungen oder sekundäre Waldtypen entlang von Tiefenlinien gefunden wurden. Im unteren Bereich der Südseite zeigte der Wald noch Zeichen menschlicher Eingriffe. Die ungestörten Primärwaldbereiche konnten nach ihrer Lage in Schlucht- und Gratwälder unterteilt werden. Während in den Schluchten ein unterer Typus in einen oberen überging, koexistierten in den unteren Gratbereichen drei Waldtypen, bevor in den höheren Bereichen ein vierter Typus bis zur Waldgrenze dominierte.

Die zwei weiteren, außerhalb des engeren Untersuchungsgebietes zu Testzwecken aufgenommen Wälder wurde klar als eigene Typen ausgewiesen.

C.4 Reduzierter Merkmalskatalog

In einer Clusteranalyse sind nicht alle Variablen in gleichem Maße trennungswirksam. Insbesondere Variablen, die in fast allen Fällen in gleicher Ausprägung oder aber so gut wie nie auftreten, können entfallen, ohne das Ergebnis der Clusterung zu beeinflussen. Wenn zwei Variablen eng miteinander korrelieren, kann auf jeweils eine des Paares ebenfalls verzichtet werden. Eine Analyse der Frequenzen des Auftretens jeder Ausprägung jeder Variablen in allen Fällen führte zu einer ersten Reduzierung des Merkmalskatalogs (z.B. um die Merkmale „Blätter immergrün“ und „Brettwurzeln“, welche durchgehend bzw. nie auftraten).

Die Untersuchung der Korrelation jeder Variablen mit jeder anderen anhand des Spearman Korrelationskoeffizienten ergab signifikante Zusammenhänge zwischen einer ganzen Reihe von Merkmalspaaren. Diese Korrelationen konnten unterschiedlich erklärt werden, z.B. dadurch, daß beide Merkmale an das Vorkommen einer bestimmten taxonomischen Gruppe gekoppelt waren (megaphylle Blätter und Astlosigkeit als Merkmale von Palmen und Baumfarnen), oder z.B. durch das natürliche Wuchsverhalten von Bäumen unter Konkurrenz um Licht (natürliche Entastung führt zu einer Korrelation zwischen Gesamthöhe des Baumes und Höhe des tiefsten Astes).

Aufgrund der Korrelationsberechnungen konnte der Merkmalskatalog weiter reduziert werden und wurde von ursprünglich 151 Merkmalen in 39 Klassen auf 104 Merkmale in 32 Klassen gekürzt. Eine erneute Clusterung

unter Berücksichtigung nur der verbliebenen Variablen führte nur zu geringfügigen Umgruppierungen einzelner Plots, änderte das Gesamtergebnis der Einteilung in Waldstrukturtypen aber nicht.

Aus den verbliebenen Merkmalen wurde ein dichotomer Schlüssel zur Kartierung der 14 Typen entwickelt, der sehr einfach zu handhaben ist.

D Diskussion

D.1 Klassifikationssystem

Das Ziel der hier vorgestellt Untersuchung war die Entwicklung und Anwendung eines eigenen Systems zur Klassifizierung der Bergwaldvegetation auf der Basis struktureller Merkmale. Dieses Ziel wurde erreicht. Allerdings war es nötig, dazu die Rahmenparameter Plotgröße und Plotverteilung, sowie die Auswahl der aufzunehmenden Strukturparameter subjektiv vorzugeben. Die Plotgröße von 20 m x 20 m wurde deutlich kleiner gewählt, als die für Walduntersuchungen in gemäßigten Breiten vorgeschlagenen 100 m x 100 m (Braun-Blanquet 1964) oder 4000 m² für tropische Wälder (Richards et al. 1940). Aufgrund des sehr steilen und kleinräumig gegliederten Reliefs hätte eine Fläche von 100 m x 100 m keinen in sich homogenen Vegetationsausschnitt gebildet. Kessler & Bach (1999) wählten aus ähnlichen Gründen ebenfalls 20 m x 20 m für ihre floristischen Untersuchungen bolivianischer Bergwälder. Eine aus statistischer Sicht wünschenswerte rasterhafte oder zufällige Verteilung der Plots über das gesamte Untersuchungsgebiet war aufgrund der Unzugänglichkeit und Steilheit des Geländes unmöglich. Zugang gewährten nur selbst angelegte Fußpfade oder Seitenbäche, in denen gewatet werden konnte. Es wurde im Höhengradienten wenigstens alle 50 m ein Plot angelegt, in den meisten Fällen liegen die Plots dichter. Da die Plots zweier Grate zusammen- und den Plots mehrerer Tiefenlinien gegenüber gestellt wurden, war allerdings nicht zu erwarten, daß eine Einbeziehung weiterer Grate oder Bachläufe weitere Waldtypen ergeben hätte. Um nicht einen „Waldtyp an Hängen“ (im Sinne von Webb et al. 1999) zu verpassen, wurden zwei Grate unter Durchquerung der dazwischenliegenden Schlucht durch eine Linie von Plots miteinander verbunden. Hier grenzte der mikrophylle Gratwald an beiden Flanken direkt an den Schluchtwald, ohne daß ein weiterer Waldtyp dazwischen gelegen hätte.

Die Auswahl der aufzunehmenden Strukturparameter erfolgte aufbauend auf dem Test der Anwendbarkeit bestehender Systeme (Axmacher 1998) und wurde inbesondere um Merkmale zur Beschreibung der Epiphytenvertei-

lung und der Präsenz verbindender Elemente wie Lianen und Bambus ergänzt. Die Wichtigkeit dieser Lebensformen besonders in Bergwäldern betonen u.a. GRUBB et al. 1963, NADKARNI 1984, BOGH 1992, FINCKH & PAULSCH 1995, STERN 1995 und LAURENCE et al. 2001.

Sämtliche Strukturparameter wurden pro Baumschicht erhoben. Dabei wurde die Schichtung nicht in festgelegten Höhen über dem Boden eingeteilt, sondern in Relation zur Gesamthöhe des jeweiligen Bestandes. Nur so konnte gewährleistet werden, daß trotz der stark unterschiedlichen Gesamthöhen (5 m bis 35 m) jeweils Kronenschichten mit Kronenschichten und Unterwuchs mit Unterwuchs verglichen wurde. RICHARDS (1983) betont, daß eine Schichtenunterteilung so erfolgen sollte, daß die lichtdurchflutete Kronenschicht von der beschatteten Zone des Unterwuches abgegrenzt wird. Ein solche Grenze kann nur in Abhängigkeit von der jeweiligen Bestandeshöhe gefunden werden.

Die sich aus der Datenerhebung pro Schicht und damit ungleicher Zahl von Variablen in Plots mit verschiedener Schichtenzahl ergebenden Probleme bei der statistischen Auswertung konnten dadurch gelöst werden, daß die einschichtigen Plots separat geclustert wurden und bei der Clusterung aller mehrschichtigen Plots die mittlere Schicht der dreischichtigen Plots vernachlässigt wurde. Um Fehlinterpretationen der Ergebnisse zu vermeiden, wurden einerseits die einschichtigen Plots zusammen mit der Kronenschicht aller zweischichtigen Plots geclustert. Dabei fielen alle 9 einschichtigen Plots in ein Cluster und wurden nicht unter die anderen Plots gemischt. Zum anderen wurden alle dreischichtigen Plots miteinander unter Einbeziehung der mittleren Schicht geclustert. Dabei blieben die Gruppierungen aus der Gesamtclusterung erhalten, die (zumeist spärlich entwickelte) mittlere Baumschicht bewirkte also keine Neueinteilung der Plots.

Um zu testen, ob sich große Clustergruppen weiter unterteilen lassen, wurden die zwei mit jeweils 22 Plots plotreichsten Gruppen (VI b und VII a) ein weiteres Mal geclustert. Dabei ergab sich keine Unterteilung in Gruppen, sondern es wurden ausschließlich Paare gebildet oder die Plots kettenartig aneinander gehängt. Dies erlaubte den Schluß, daß das Niveau der gefundenen 14 Waldstrukturtypen die erste Schwelle darstellte, auf der die Plots zu Einheiten von ökologischer Bedeutung zusammengestellt werden konnten, da eine Untergliederung in Dutzende von Einheiten, die jeweils nur durch einen Plot vertreten wären, im Sinne einer Waldklassifizierung wenig Sinn ergäbe.

Obwohl über die Berechnung von T-Werten und Korrelationen zwischen Variablen Parameter ausgegrenzt werden konnten, die nicht zur Gruppenbildung beitrugen und um die der Merkmalskatalog gekürzt werden konnte,

war es nicht möglich, die Gruppenbildung durch einige wenige bestimmende Parameter zu erklären. Czimczik (1999), die mit einem nahezu identischen Merkmalskatalog die Gebüschvegetation oberhalb der Waldgrenze in unserem Untersuchungsgebiet beschrieb, versuchte, mittels einer Hauptkomponentenanalyse die bestimmenden Variablen zu finden, kam aber ebenfalls zu dem Ergebnis, daß nicht einige wenige Merkmale die Gruppenbildung erklären, sondern die graduellen Unterschiede einer Vielzahl von Parametern.

Obwohl Backhaus et al. 1996 und Everitt 1995 die Clustermethode nach Ward empfehlen, wurden zum Vergleich Clusterungen mit anderen Verfahren durchgeführt (z.B. city block metric). Die Einteilung der 14 Gruppen blieb dabei stabil, auch wenn einige wenige Plots die Clustergruppe wechselten. Die Gesamteinteilung war daher offenbar kein Artefakt der Aufnahme- oder Datenverarbeitungsmethode.

D.2 Verteilung der Waldstrukturtypen

Für die Höhenzonierung der Vegetation der Anden liegen verschieden Konzepte vor, u.a. die von Richards 1952, Beard 1955, Grubb et al. 1963, Ellenberg 1975, Gradstein & Frahm 1987 und Lauer & Erlenbach 1987. Allen Konzepten gemeinsam ist eine Grenze, die bei etwa 2300 m ü.NN zwei Höhenstufen trennt, „submontan" und „montan" (Ellenberg 1975, Lauer & Erlenbach 1987), „submontane rain forest" und „montane rain forest" (Richards 1952), „lower" und „upper montane rain forest" (Grubb et al. 1963) oder „montane rain forest" und „montane thicket" (Beard 1955) genannt. Mit dem in dieser Untersuchung entwickelten und angewandten System gelang es, eine feinere Untergliederung vorzunehmen, die zwischen Wäldern in Tiefenlinien und auf Graten differenziert. In Tiefenlinien liegt die o.g. genannte Grenze zwischen den Waldstrukturtypen Primärer Schluchtwald tieferer Lagen und dem höherer Lagen (Cluster VI c und d). Auf Graten koexistieren der mesophylle, makrophylle und megaphylle Gratwald (Cluster VII b, c, und d) unterhalb einer 2200 m-Linie, während der mikrophylle Gratwald den Bereich darüber bis zur Waldgrenze dominiert. Die strukturell basierte Klassifizierung widerspricht also nicht der allgemein anerkannten Höhengliederung der andinen Vegetation, sondern verfeinert diese im untersuchten Höhenbereich zwischen 1800 m ü.NN und 2600 m ü.NN.

Im Zuge der ökosystemaren Untersuchungen des gesamten DFG-Projektes wurden von verschiedenen Arbeitsgruppen Standortparameter be-

stimmt, die für die Interpretation der Verteilung der Waldstrukturtypen von maßgeblicher Bedeutung sind. Meteorologische Untersuchungen (RICHTER pers. Mitt.) ergaben, daß in Gratlagen die Winde Orkanstärke erreichen können und bei Schönwetterlagen die Einstrahlung besonders auf Graten zu Trockenstreß führen kann. ENDLICHER (1982), LAWTON (1982) und WEBB et al. (1999) führen xeromorphe Merkmale, verminderte Wuchshöhe und kleine Stammdurchmesser von Waldvegetation in großer Höhe auf Starkwindereignisse und dadurch entstehende Trockenheit zurück. Meine Untersuchung ergab maximale Stammdurchmesser und Baumhöhen für die Wälder geschützter Schluchtlagen, während insbesondere der mikrophylle Gratwald die geringsten Baumhöhen und die größte Präsenz semisklerophyller Blätter zeigte. EWEL & BIGELOW (1996) beschreiben Palmen als besonders windstabile Bäume. In der Tat sind die einzigen Emergenten auf den Graten meines Untersuchungsgebietes Palmen.

Studien an verschiedenen tropischen Bergwäldern (TANNER et al. 1990, TANNER & KAPOS 1992) zeigten, daß der Pflanzenwuchs N-limitiert war. In unserem Untersuchungsgebiet stellten SCHRUMPF et al. (2001) mit zunehmender Höhe abnehmende Profiltiefe, sinkende pH-Werte, abnehmende effektive Kationenaustauschkapazität, sich weitende C/N-Verhältnisse und zunehmenden Stauwassereinfluß fest. Daraus wurde auf mit der Höhe schlechter werdende N-Versorgung aufgrund zunehmend ungünstigerer Mineralisierungsbedingungen geschlossen. Obwohl dies kein Beweis für tatsächliche N-Limitierung des Pflanzenwuches bedeutet, könnte dennoch die abnehmende Wuchshöhe in zunehmender Meereshöhe mit ungenügender N-Versorgung zusammenhängen.

WHITMORE (1989), ALVAREZ-BUYLLA & MARTINEZ-RAMOS (1992) sowie LAURENCE et al. (2001) nennen Vertreter der Gattung *Cecropia* (*Cecropiaceae*) als Pionierbäume, die unter vollem Lichtgenuß besonders gut gedeihen. Insbesondere in den Strukturtypen Sekundärwald in Mindo (Cluster III) und Natürliche Waldränder (Cluster V) wurden gehäuft Merkmale festgestellt, die mit dem Vokommen von Cecropien verbunden waren (megaphylle, gefingerte Blätter, geringe Verästelung). Die natürliche bzw. menschlich verursachte Störung hatte hier für besonders lichte Bedingungen gesorgt.

Die hohe Abundanz von Epiphyten wird als Charakteristikum andiner Bergwälder angesehen (GRUBB et al. 1963, NADKARNI 1984, BOGH 1992). In meiner Untersuchung zeichneten sich inbesondere die als primär eingestuften Waldstruktureinheiten durch hohe Abundanzen an epiphytischen Bromelien und Orchideen aus, während in den offensichtlich gestörten Waldbereichen die Epiphytendichte gering war. Gerade in den gestörten Bereichen war aber der Grad der Vernetzung durch Lianen oder Bambus besonders

hoch, was nach LAURENCE et al. (2001) als Folge von Störung und Fragmentierung auch zu erwarten war.

Neben der Reliefsituation können also auch edaphische und meteorologische Befunde zur Interpretation der Verteilung der Waldeinheiten herangezogen werden.

D.3 Funktionale Zusammenhänge

Ziel der vorliegenden Arbeit war unter anderem die Bereitstellung eines einfach zu handhabenden Klassifikationssystems für die Vegetation des Untersuchungsgebietes als Grundlage für Untersuchungen anderer Arbeitsgruppen des DFG-Projektes zu funktionalen Zusammenhängen beispielsweise zwischen Vegetation und Tieren. DZIEDZIOCH (2001) dokumentierte Vorkommen und Phänologie von 72 kolibribesuchten Pflanzenarten auf einem Hektar im unteren Teil des Untersuchungsgebietes alle 14 Tage über ein Jahr. Für jedes Aufnahmequadrat von 10 m x 10 m wurde der Waldstrukturtyp mit Hilfe des dichotomen Schlüssels bestimmt, was zur Zuordnung der Quadrate zu fünf verschiedenen Waldstrukturtypen führte. Die Bestimmung von alpha- und beta-Diversität machte klar, daß die Verteilung kolibribesuchter Pflanzen (und damit die für Kolibris zur Verfügung stehende Nektarressource) mit den Waldstrukturtypen korrespondiert. Da ein Großteil der kolibribesuchten Pflanzen von epiphytischer Lebensweise waren, konnte diese Korrelation insbesondere deswegen gefunden werden, weil Merkmale zur Epiphytenverteilung in den Merkmalskatalog mit aufgenommen wurden. Dieser Befund war mit ausschlaggebend für die Entscheidung, diese Merkmale auch im verkürzten Merkmalsschlüssel zu belassen.

Derzeit laufende Untersuchungen der Nachfalterdiversität von SÜSSENBACH (in prep.) und BREHM (in prep.) werden zeigen, ob das Vorkommen bestimmter Mottengemeinschaften ebenfalls mit Waldstrukturtypen in Verbindung gebracht werden kann. Rezente Untersuchungen zur Diversität von Vogelgemeinschaften auf der Basis der Waldstrukturtypen haben bislang gezeigt, daß bestimmte Vogelarten nur in Schluchtwäldern, andere nur in Gratwäldern angetroffen werden (PAULSCH D. et al. 2001).

Der nächste Schritt in anschließenden Projekten müßte sich der Untersuchung widmen, welche strukturellen Merkmale für welche Funktionen im Ökosystem relevant sind. Das Konzept der „Plant functional types" (WESTOBY & LEISHMAN 1997) greift diesen Ansatz auf und EWEL & BIGELOW (1996) legen dar, daß die Untersuchung der Vegetationsstruktur Bestandteil jeder Ökosystemstudie sein sollte, wenn Aussagen über funktionale Zusam-

menhänge getroffen werden sollen. Das in dieser Arbeit vorgestellte Klassifikationssystem kann ein Werkzeug zur Untersuchung ökosystemarer Zusammenhänge sein, das (eventuell in leicht modifizierter Form unter Berücksichtigung lokaler Besonderheiten) auch außerhalb andiner Bergwälder angewendet werden kann und auch für Nicht-Botaniker leicht zu handhaben ist.

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1 Introduction

One of the most striking features of tropical rain forests is their enormous diversity of plant species and plant life-forms (Mueller-Dombois & Ellenberg 1974). These forests are considered to be the terrestrial ecosystems with the highest biodiversity on earth. In particular, montane rain forests in the neotropics have been identified as hotspots of biodiversitiy (Barthlott et al. 1996). Henderson et al. (1991: 22) stated that "for its size, the northern Andes is the most diverse region in the neotropics". If the conservation of hotspots of biodiversity could be a strategy to save diversity, Myers et al. (2000: 856) claim: "The Tropical Andes [...] should be considered as hyperhot candidate for conservation support in light of their exceptional totals of endemic plants: 20000." Nevertheless, tropical montane forests with an annual rate of loss of 1.1% are even more threatened than lowland forests which have an 0.8% loss (Doumenge et al. 1995). The Ecuadorian Andes have lost 90% of their original forest cover through human activity (Hamilton et al. 1995, Henderson et al. 1991). Anthropogenic pressure on montane forest ecosystems can lead to total destruction (clear cutting or burning) or can alter species composition, ending up with species extinction, and can change physiognomic and demographic structures (selective logging). Even without human influence, the Andean tropical forests are frequently disturbed by natural land-slides (Kessler & Bach 1999). The consequence of the various forms of disturbance is a mosaic of forest remnants of different size and open land, used as pasture or for agriculture. The loss of vegetation cover can lead to high rates of soil erosion, especially in extremely inclinated areas and hence ruin the potential for agricultural use or reforestation efforts.

If the remaining tropical montane forests of the Andes are to be protected in a long-term perspective their ecosystem functioning has to be better understood. Orians et al. (1996: 210) state: "Montane forests [...], because of the magnitude of anthropogenic alteration they are experiencing and their crucial contribution to tropical biological diversity, must be better understood if we are to document the range of variation of relationships between biological diversity and functioning of tropical ecosystems."

In 1997, the German Research Foundation (DFG) funded a comparative study in the montane region of southern Ecuador to investigate the edaphic, meteorologic, zoologic and botanic compartments of the forest ecosystem along an altitudinal gradient to gain a better understanding of ecosystem processes (Beck & Müller-Hohenstein 2001). If ecosystem processes such as energy flows, information flows, nutrient exchanges or changing biodiver-

sity are to be documented and understood, vegetation as a central part of the ecosystem has to be investigated (Ewel & Bigelow 1996) and classified. The study presented here is part of the above-mentioned comparative DFG-project and has the aim to provide a classification system for the vegetation types of the montane forest as a basis for parallel and further research in ecosystem functioning.

Approaches to classify vegetation are numerous and can be divided into two major groups: floristic approaches and physiognomic approaches (Beard 1973). The floristic approaches use plant species and species composition to describe vegetation or vegetation units (for a hierarchical system). The physiognomic approaches use plant architecture, life-form composition or structure to describe and classify physiognomic units.

Most of the floristic classification systems have been developed for temperate zones (Cajander 1909, Du Rietz 1930, Braun-Blanquet 1964) and are well established e.g. in middle Europe. They are not easily applied in the tropics owing to the enormous number of species present in tropical vegetation, especially where cryptogam species form an important part of the vegetation. Vareschi (1980) stated that about 80 different species of ferns exist in central Europe, whereas Venezuela alone hosts more than 1000. He concluded that there cannot be a "botanist of the tropics" who knows the complete flora of a tropical country but that specialisation in taxonomic groups or certain vegetation types is unavoidable. Hence, to describe the species composition of a tropical montane forest is highly complicated and time-consuming, when at all possible. Kessler & Bach (1999), who described montane forests of Bolivia, restricted their investigation to those particular taxonomic groups (palms, ferns, bromeliads, *Melastomataceae*, *Araceae*, *Acanthaceae*) they considered to be the most important. Madsen & Øllgaard (1994) investigated two 1-ha upper montane rain forest plots in southern Ecuador and found 75 and 90 species respectively; however, this study included only trees with a diameter at breast height (dbh) greater than 5 cm and neglected, for example, vascular epiphytes, not to mention mosses and lichens. The enormous species diversity of vascular plants in Ecuador is still only partly documented. The "Flora of Ecuador" (Harling & Sparre 1973-1986, Harling & Anderson 1986-1994) covers less than 25% of the more than 20000 species Harling (1986) estimated. Given the current floristic knowledge, such an approach might not be the most effective way to classify the vegetation of a diversity hotspot.

Nor are physiognomic approaches always suitable for the tropics, depending on where they have been developed. The classical life-form concept of Raunkiear (1934), for example, is of little value in the recognition of tropical

forest types because of the lack of a cold season (Beard 1973). It was very much improved by Mueller-Dombois & Ellenberg (1974) who created a system of vegetation units suitable everywhere. This system however has a globale scale and does not allow more distinct subdivisions on a local scale. The life-zone concept of Holdridge et al. (1971) also has a global scale.

Beard (1973) gave an excellent overview about the history of important concepts beginning with the ideas about life-forms of Warming (1909) and Schimper (1898) and discussed the major approaches up to the 1960. Paulsch & Czimczik (2001) reviewed newer approaches, particularly those that use a combination of floristic and structural features, to characterise tropical vegetation. They summarised that in many cases the investigation of structure is restricted to the classical parameters of forest inventories, that is height, diameter at breast height, and number of individuals per area (mostly only for woody species and individuals broader than a certain diameter), sometimes enriched by recording of epiphytes or leaf characters (Condit 1998, García 1998, Korning et al. 1990, Popma et al. 1988, Procter et al. 1988, Valencia 1995, Valencia & Jorgensen 1992, Valencia et al. 1998, Young 1998, Zomer et al. 2001). In these studies identification of species is the main tool to describe the forest vegetation.

Only a few approaches go into more detail with respect to the structure, recording growth-forms, architecture, or a longer catalogue of physiognomic features. These references are listed in the following:

Parsons (1975) used a set of 24 structural and functional characters such as life-form, growth-form, height, leaf size and shape, and bark texture to describe each woody species he found in Mediterranean scrub communities of California and Chile. He concluded that floristically distinct communities of comparable climatic regions display similarities in vegetation structure.

Hoheisel (1976) classified cloud forests in Venezuela with the help of structural and floristic data and presented six units he called "Strukturtyp" (structural forest type). Nevertheless the description of these types lists mainly dominant species and parameters of forest inventories.

Vareschi (1980) described tropical vegetation types on the basis of formations. He characterised each formation by climatic and edaphic data, species per area rates and morphological features, especially those of leaves. To obtain this information, the number of different species has to be estimated (species do not necessarily have to be identified) and for each species the leaf category has to be chosen from a catalogue of different types. Thus a leaf type spectrum can be constructed for each formation. The ecological meaning of this spectrum however is not investigated.

Kielland-Lund (1982) compared four forest types in Tanzania based on the percentage of occurrence of almost 40 structural features. This method led to an insight in structural differences of the forest types but was not used as a classification system, because the forest types were determined a priori by dominant species.

On the basis of the concept of Hallé & Oldeman (1970), Tomlinson (1983) suggested a method of classifying tropical forest trees using their architecture. Each species has to be placed in one of 23 basic architectural models that reflect different branching patterns. This idea seems somewhat artificial because it requires optimal growing conditions so that each tree can develop its typical architecture. These conditions will hardly be met under competitive conditions in a dense tropical forest, and Ewel & Bigelow (1996) observed that trees are so plastic that different tree architectures can converge on the same crown morphology.

Orshan (1986) proposed an extended catalogue of physiognomic features describing the above-ground shoot system, the photosynthetic organs, the below-ground organs, longevity and regeneration to be recorded for each species. A kind of "passport" could be established for each species to classify the structure of a plant community if the species composition is known. Unfortunately the root system especially of trees can only be investigated by destructive methods.

Halloy (1990) produced classification keys for five morphological subsystems of a plant (silhouette, leaf group, stem, root and inflorescence) in 60 well-defined categories and used the alpine flora of New Zealand as an example. Dissatisfyingly, it is not explained how a certain plant type (constructed from a combination of one category for each sub-system) should be named, and how the vegetation of an area should be described as a sum of types and be compared with the vegetation somewhere else.

The identification of species is still a central point of the studies of Parsons (1975), Hoheisel (1976), Vareschi (1980), Kielland-Lund (1982), Tomlinson (1983), Orshan (1986), and Halloy (1990). There are only some approaches that compare floristic classifications with the results of structural investigations and thus provide a tool to describe structure independently of species composition. These approaches are described in the following:

Webb et al. (1970) compared the results of a floristic and a structural investigation of an Australian rainforest where 513 tree species were determined and a set of 33 structural features such as canopy height, existence of emergents, bark consistency and leaf size were registered per plot. Webb et al. (1970: 222) stated: "The results presented [...] suggest that a classifica-

tion based on a limited number of physiognomic features noted by untrained observers can prove as useful as a floristic classification."

Werger & Sprangers (1982) carried out a comparative study of floristic and structural data from a tropical dry forest in India. On 63 plots they found 192 species and mapped the abundance of 128 structural features such as life-form, form of branching, and leaf and crown characteristics. They concluded that the results of a floristic and of a physiognomic classification are strikingly similar with the latter being far less time-consuming. The authors remarked that advanced calculation facilities are necessary to obtain these results, but today this problem seems to be solved by modern software packages.

Lux et al. (1994), (derived from the ideas of Barkman 1979), classified bush vegetation in two European regions and compared the results based on floristic data and structural data. The latter contain particular information on strata and growth-form spectra. The authors stated that the investigation of structures allowed more conclusions about processes of succession that do not necessarily go along with a change of species composition.

Le Brocque & Buckney (1997) investigated the relationships between floristic composition and stand structure in Australia with multivariate methods. Structure in this case meant foliage projective cover of 8 different strata. The comparison showed that floristic composition gradients were well recovered by the structure data, although two floristically dissimilar communities exhibited very similar multivariate structural characteristics.

All the authors who compared floristic classification with structural investigations (Webb et al. 1970, Werger & Sprangers 1982, Lux et al. 1994, Le Brocque & Buckney 1997) concluded from their data that the investigation of structure led to comparable results, but was much easier to achieve.

Given the evidence of the above-mentioned studies, an approach based on structural characteristics seemed to be the most effective way to provide a classification of the montane forest vegetation. This decision was not only made with respect to limited investigation time. Investigation of vegetation structure can document differences between vegetation units that might not be discovered by floristic approaches, as Gentry (1988: 2) stated: "Contrary to the accepted opinion, equivalent forests on the three continents [South America, South Asia, Africa] are similar in plant species richness and (with a very few notable exceptions) in floristic composition but are markedly different in structure." Sánchez & Islebe (1999) investigated vegetation changes in Mexico affected by hurricane Gilbert and documented that forest structure (density, height, foliage cover) had changed immensely while species composition was virtually unaffected. Moreover, investigations of plant-an-

imal-interactions, especially in birds, showed that bird-communities in tropical forests are restricted to distinct vegetation strata (PRELEUTHNER et al. 1998) or that parakeets need emergent trees with horizontal branches to deal with fruits they transport from other trees (ROTH 1982). COSSON et al. (1999) observed changing foraging behaviour of woodpeckers after habitat alteration leading to a higher percentage of dead trees. To investigate such functional relationships, a description of vegetation structure is a necessary and more profound basis than a floristic approach. TRICHON et al. (1998: 228) even concluded: "Forest structure is the heart of the whole ecosystem functioning and dynamics, as it is all together the result and the framework of many fundamental ecological processes."

Many of the above mentioned structural approaches are not suitable to investigate the vegetation of an area of a few square kilometres of tropical montane forest in detail: MUELLER-DOMBOIS & ELLENBERG (1974) as well as HOLDRIDGE et al. (1971) have a scale which is too global. LE BROCQUE & BUCKNEY (1997) and VARESCHI (1980) concentrated on only a few characters, while ORSHAN's (1986) description of the root system could only be gained by destructive methods. Other approaches, like those of PARSONS (1975), HALLOY (1990), or LUX et al. (1994) were neither meant for forest vegetation nor for the tropics. Furthermore, the definition of "structure" varies between the different approaches.

Hence the aim of the present study is to provide a method to distinguish forest units with the help of structural features. Structure has to be defined. I followed BARKMANN (1979), who defined structure as the "horizontal and vertical arrangement of vegetation". The method must select a set of features that should be documented (out of the potentially unlimited possibilities) and has to quantify the presence of these features. The quantitation should lead to a grouping of investigation units to vegetation units with low within-unit-variation but high between-unit-variation. If such vegetation units exist, their spatial distribution has to be documented and related with abiotical site conditions. Out of the set of documented features those have to be selected which have the highest potential to distinguish between units. If possible, this selection should lead to a key to vegetation units, especially for areas, where the floristic inventory is still incomplete. This key should be easy to handle even for non-botanists who need a basis for research in ecosystem functioning.

2 Material and Methods

2.1 Investigation area

Ecuador on the Pacific side of South America, can be divided into three main regions: the coastal region in the west (la costa), the upper part of the Amazon basin in the east (el oriente) and the mountain range of the Andes in the centre (la sierra). The sierra consists of two main ranges: the eastern Cordillera Real is separated from the western Cordillera Occidental by the inner Andean depression (Sauer 1971). The investigation area was part of the eastern slope of the Cordillera Real in a southern latitude of 4° 00' and a western longitude of 79° 05' in the provinces of Loja and Zamora-Chinchipe. The fieldstation Estación Científica San Francisco (ECSF) at 1850 m a.s.l. served as a basis for the study. The station property covered an altitudinal gradient from 1800 m a.s.l to 3100 m a.s.l. (Figure 1).

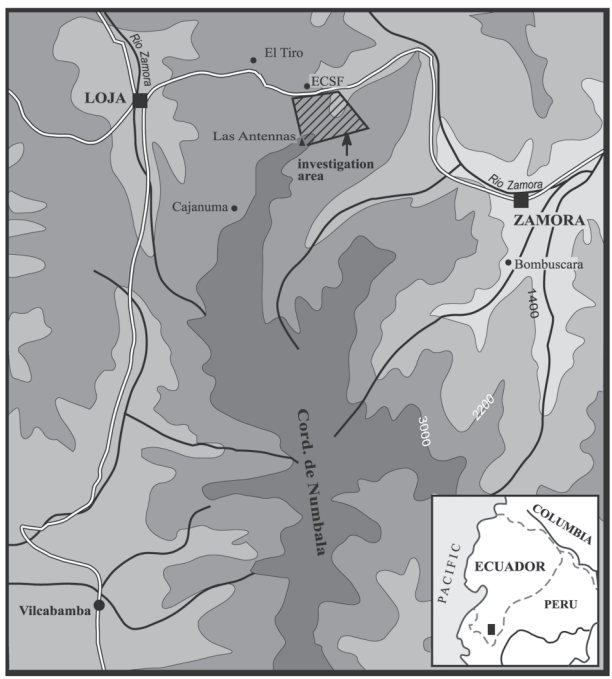


Figure 1: Location of the investigation area between Loja and Zamora (from Beck & Müller-Hohenstein 2001, modified).

From a geological point of view the investigation area is part of the so called Loja Terrane (LITHERLAND et al. 1994) which consists of Palaeozoic metamorphorised sediments and Triassic granites. The Chiguinda-unit, extending from the southern Cordillera Real into northern Peru, is built up of quartzites, metamorphic loamstones, graphitic slates and phyllites (LITHERLAND et al. 1994). Continuous rising of the Andes tilted the layers and led to a highly differentiated relief where slopes are inclined up to 60°. Landslides are common even in areas without human impact.

SCHRUMPF (1999) identified mainly sandstones and phyllites as parent material for soil development in the same investigation area and classified the soils in the lower parts as Dystrudepts according to the Soil Taxonomy (SOIL SURVEY STAFF 1998). At higher altitudes Humaquepts and Petraquepts were distinguished. Some profiles were categorised as Saprits and Epiaquepts in the uppermost parts. Soil reaction was strongly acidic and the N-nutritional status decreased with increasing altitude (SCHRUMPF 1999). A lower rate of N-mineralisation together with the influence of water logging might limit plant growth in the upper parts of the investigation area.

Although a seasonal variability in the annual rainfall and an extraordinary hygro-thermical complexity can be observed in southern Ecuador (RICHTER, pers. comm.), the eastern slope of the eastern Cordillera has 12 humid months. The maximum of rainfall in June and July is explained as an effect of south-east trade winds bringing moisture from the Amazon basin. The minimum in November is interpreted as an effect of a low-level-jet stream (BENDIX & LAUER 1992). 2220 mm were measured as the average annual rainfall of the years 1998-2000 (YASIN 2001).

According to the climate, the sierra of Ecuador should be covered with montane rain forest (see Introduction and Discussion and VALENCIA et al. 1999). As the history of land use in the Andes goes back to the end of the last ice age (ELLENBERG 1979, DOLLFUS 1982, RUTHSATZ 1983), major parts of the Andean region in Ecuador are already deforested (HAMILTON et al. 1995). Although in 1993 28% of the population were working in the rural sector, contribution to national income was only 12% (BORSDORF & STADEL 1997). This can be explained by the fact that 70% of the farms together own only 7% of the cultivated area (minifundios), whereas 27% of the area belongs to only 0.3% of the farms (latifundios). Thus most farms practice only subsistence economy (BORSDORF & STADEL 1997, KNAPP 1991). In particular, the highly inclined regions with unfavourable soils and a high risk of landslides are minifundios (BEBBINGTON 1993).

Nevertheless, for the largest part of the investigation area, land-use history does not go back longer than 60 years when the already existing footpath was

converted into an unpaved road connecting the provincial centres Loja and Zamora. In the 1950ies a hydroelectric plant was constructed in the San Francisco Valley. The construction of the necessary water channel directly influenced the lower parts of the investigation area because all the wood needed was taken directly from the forest. Thus, these parts of the investigation area could be seen as secondary forest with a maximum age of 50 years.

Colonisation of the valley began to boom when the road was paved at the end of the 1980ies. The facts that the forest was needed as protection for the water catchment of the strategically important hydroelectric plant, and that the street runs on the northern side of the valley, saved the primary forest on the southern side from human influence.

Thus, primary forest, secondary forest and recently colonised land-use areas form a mosaic allowing investigation of structures on different scales in one region.

2.2 Mapping structure on a landscape level

To overview the units of different land use and areas of undisturbed primary forest a map of land-use units was produced with the help of aerial photographs (Instituto Geográfico Militar 1998) and a topographical map (Instituto Geográfico Militar, Loja Norte 1981, Zamora 1994, Loja Sur 1996, 1:50 000).

The landscape mapping was carried out in a scale of 1:25000 following the road from the ECSF station to the town of Zamora on a gradient from 2000 m a.s.l. to 1000 m a.s.l.. For the term "landscape" the definition of FORMAN (1997) was followed: "a landscape is a mosaic where the mix of local ecosystems or land uses is repeated in similar form over a kilometer-wide area."

2.3 Mapping structure on a patch level (land-use areas)

Within the region of intense land use for 12 farms (fincas) along the altitudinal gradient structure was mapped on a patch level (SCHNEIDER 2000). For the fincas, size and shape of patches (1:3000) were noted based on the concepts of FORMAN (1997) and WIENS (1999) (Figure 2).

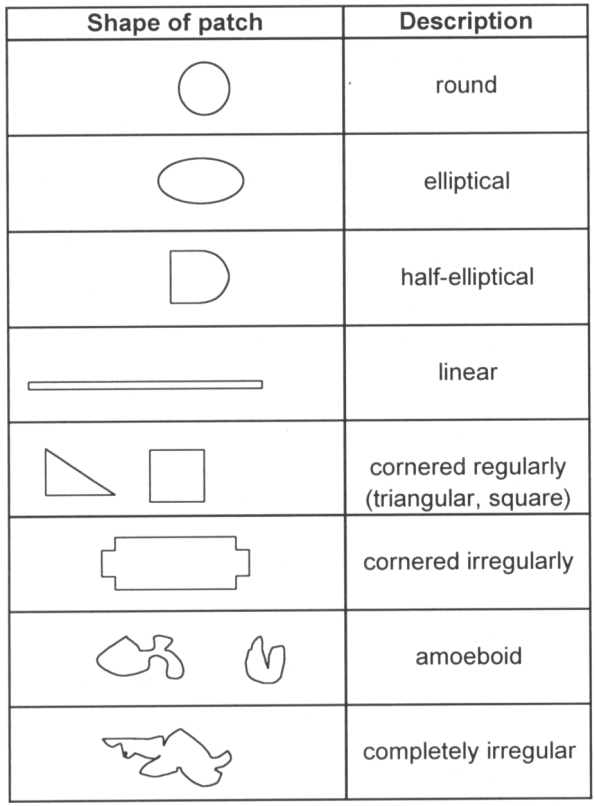


Figure 2: Shape of patches, based on FORMAN *(1997) (from* SCHNEIDER *2000, modified).*

Man-made boundaries like fences or roads were also considered, even if the neighbouring patches did not obviously differ in vegetation structure. For each patch, the number of neighbouring patches and the sharpness of boundaries were observed. Considering that the whole investigation area should be covered with montane forest (VALENCIA et al. 1999), the intensity of clearing, the density of remaining trees, their height and diameter, the number of vegetation layers, the vegetation cover and the percentage of dead wood were estimated for each patch. Structures resulting from the main type of land use (breeding cattle) such as cattle tracks and planted grass tussocks were also registered. As the quality of grazing areas is drastically reduced by an invading fern (*Pteridium aquilinum* (L.) KUHN), the fern cover was estimated too. Figure 3 shows a typical arrangement of dead wood, cattle tracks, a fence, fern and bushes in a pasture patch. In order to group patches into classes of similar characteristics a cluster analysis was carried out with the SPSS software package (SCHNEIDER 2000).

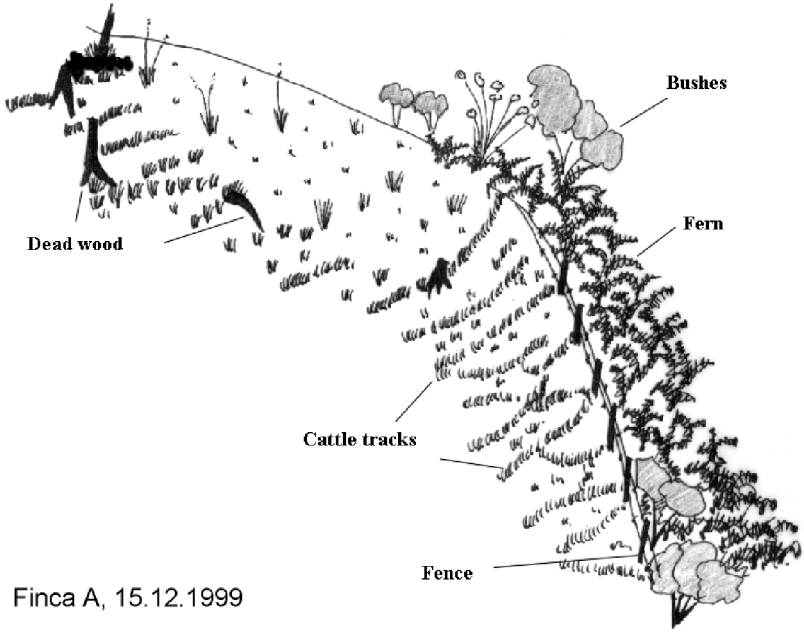


Figure 3: Typical arrangement of structural elements in a pasture patch (from SCHNEIDER *2000, modified).*

At each of the fincas, the owners were interviewed to collect information about how long the land had already been used, how many people worked and lived there, what kind of treatment was invested in each group of plots, if a rotation system existed or if fertilizers or other chemicals were applied. This information could not be used for statistical interpretation since some of the land owners were not willing to answer all questions or simply did not know how to answer. Thus the collected information will only be used to support interpretation.

2.4 Mapping structure on a plot level (forest areas)

To describe vegetation structure in the areas that were classified as forest, first the applicability of a choice of already existing classification systems had to be tested (see Introduction). The chosen systems investigate structure on different scales: WERGER & SPRANGERS (1982), ORSHAN (1986), and PARSONS (1975) studied the structure of every individual plant on a given plot, whereas

RICHARDS et al. (1940) and WEBB et al. (1970) described the structure of the plot as a whole. MUELLER-DOMBOIS & ELLENBERG (1974) and BEARD (1955) investigated the structure of plant formations. These seven systems were tested and compared on 15 plots (AXMACHER 1998). These plots were partly placed in the forest (plot 1-8) and partly in areas with secondary growth after landslides or clear cutting (plot 9-15). A plot size of 20 m x 20 m was chosen as a compromise between the minimum area concept (BRAUN-BLANQUET 1964) which proposed 100 m x 100 m for forests in temperate zones, RICHARDS et al. (1940) who proposed an acre (4047 m²) for tropical forests and the fact that the montane forest is very heterogeneous. KENKEL & PODANI (1991) compared estimation efficiency for different plot sizes and recommended the largest plot size that can be handled within a reasonable time period. For the system based on the structure of plant individuals we chose 400 m².

Data were collected for each individual plant with a dbh of at least 2 cm following the catalogue of characters given by each author (as far as possible under field conditions). To compare the systems of each scale, the percentage of character classes in common, the number of applicable characters and the frequency of occurrence were determined.

Based on the results of this preliminary investigation a new classification system was developed. The new system was designed for plot scale. On each plot the new system was applied *to each stratum* of woody plants. The canopy was treated as first tree stratum. A second tree stratum was distinguished if tree crowns in a layer between one-third and two-thirds of the canopy height covered more than 10% of the plot. A third tree stratum was distinguished if tree crowns in a layer lower than one-third of the canopy height covered more than 10% of the plot.

For each stratum, two groups of character classes were investigated: the first group of eight classes (Table 1) contained metric parameters describing the stratum as a whole such as number of trees or ground cover. Data were collected as an *average value* for the stratum and thus were exclusive (for example if the average distance between crowns was between 3 m and 6 m, then it could not be between 1 m and 3 m in the same stratum).

Table 1: Scaling of metric parameters

Character class	Character				
Number of trees	<5	<25	<50	<100	>100
Ground cover	<10%	<20%	<30%	<40%	and so on
Diameter at breast height	<10cm	<20cm	<30cm	<40cm	and so on
Height of stratum	<5m	<10m	<15m	<20m	and so on
Height of lowest branch	<5m	<10m	<15	<20m	and so on
Height of main ramification	<5m	<10m	<15m	<20m	and so on
Distance between stems	<1m	<3m	<6m	<9m	and so on
Distance between crowns	<1m	<3m	<6m	<9m	and so on

The second group of 31 character classes (Table 2) contained 143 parameters in an ordinate scale. This scale followed that of WEBB et al. (1970) and was defined as:

0 = absent (no tree individual of the stratum shows, for example, the character "crown cylindrical")
1 = rare (less than one-third of the individuals show the character "crown cylindrical")
2 = abundant (less than two-thirds of the individuals show the character "crown cylindrical")
3 = dominant (more than two-thirds of the individuals show the character "crown cylindrical").

Thus the characters did not exclude each other but could not add up to more than 100%. The existence of one-third of crowns being cylindrical did not exclude other crowns from being umbrella-shaped, but there could not be two-thirds of cylindrical crowns and another two-thirds umbrella-shaped. Nevertheless, characters had not necessarily to add up to 100% for each class. If, for example, "epiphytic ferns" did not exist either on stems or on branches the sum for the class was still zero.

Table 2 also lists the tested systems on which character classes were based. Blanks signalise characters that have been added. This includes in particular parameters describing distribution and abundance of epiphytes. Epiphytes are an important part of the montane rainforest vegetation and are likely to differentiate between forest units, thus they should not be neglected. (GRUBB et al. 1963, NADKARNI 1984).

Table 2: Definition of ordinate scaled parameters. For further explanation see text.

Character class	Character	Based on system of	Explanation
Woodiness	axylous	Orshan (1986)	
	hemixylous	Orshan (1986)	
	holoxylous	Orshan (1986)	
Stem characters	polycormous		
	vertical		
	diagonal		
	dead		
Bark characters	green thin smooth	Werger & Sprangers (1982)	thin: <2mm
	green thin rough	Werger & Sprangers (1982)	
	green thick smooth	Werger & Sprangers (1982)	thick: <1cm
	green thick rough	Werger & Sprangers (1982)	
	non-green thin smooth	Werger & Sprangers (1982)	
	non-green thin rough	Werger & Sprangers (1982)	
	non-green thick smooth	Werger & Sprangers (1982)	
	non-green thick rough	Werger & Sprangers (1982)	
	non-green very thick rough		very thick: >1cm
	flaky	Werger & Sprangers (1982)	
Roots	tabulate roots		
	stilt roots		
	aerial roots		
Crown volume	restricted to top	Werger & Sprangers (1982)	
	restricted to upper third	Werger & Sprangers (1982)	
	restricted to upper half	Werger & Sprangers (1982)	
	reaching deeper than half	Werger & Sprangers (1982)	
Crown development	full		
	restricted by neighbours		
	stunted		
Crown shape	round	Werger & Sprangers (1982)	
	umbrella-shaped	Werger & Sprangers (1982)	
	cylindrical	Werger & Sprangers (1982)	
	conical	Werger & Sprangers (1982)	
	funnel-shaped/umbelliferous fanshaped	Werger & Sprangers (1982)	
	irregular	Werger & Sprangers (1982)	
Crown overlap	Type 1		no overlap, distance to next crown >1m
	Type2		no overlap, distance to next crown <1m or touching
	Type 3		crowns overlaping and penetrating each other
Branches	mostly horizontal		
	mostly diagonal		
	mostly vertical		
	dead		
	missing		
Branching pattern	Type 1	Parsons (1975), modulated	only leafs of terminal 20cm

Table 2: (continued) Definition of ordinate scaled parameters. For further explanation see text.

Character class	Character	Based on system of	Explanation
Branching pattern	Type 2	Parsons (1975), modulated	branching twice
	Type 3	Parsons (1975), modulated	branching more than twice
Leaf shape	simple		
	narrow leaved		
	palmately lobed		
	compound		
	other		
	with drip-tip		
	absent		
Leaf consistency	hymenophyll	Werger & Sprangers (1982)	
	malacophyll	Werger & Sprangers (1982)	
	semi-sclerophyll	Werger & Sprangers (1982)	
	sclerophyll	Werger & Sprangers (1982)	
	semi-succulent	Werger & Sprangers (1982)	
	succulent	Werger & Sprangers (1982)	
Leaf colour	green	Orshan (1986)	
	red	Orshan (1986)	
	bicoloured	Orshan (1986)	
Tree phenology	evergreen	Werger & Sprangers (1982)	
	deciduous	Werger & Sprangers (1982)	
Leaf size	sub-leptophyll	Orshan (1986)	$<0{,}1\text{cm}^2$
	leptophyll	Orshan (1986)	up to $0{,}25\text{cm}^2$
	nanophyll	Orshan (1986)	up to $2{,}25\text{cm}^2$
	nano-microphyll	Orshan (1986)	up to $12{,}25\text{cm}^2$
	microphyll	Orshan (1986)	up to $20{,}25\text{cm}^2$
	micro-mesophyll	Orshan (1986)	up to $56{,}25\text{cm}^2$
	mesophyll	Orshan (1986)	up to $180{,}25\text{cm}^2$
	macrophyll	Orshan (1986)	up to $1640{,}25\text{cm}^2$
	megaphyll	Orshan (1986)	$>1640{,}25\text{cm}^2$
Leaf length	<1cm	Orshan (1986)	
	up to 2cm	Orshan (1986)	
	up to 5cm	Orshan (1986)	
	up to 10cm	Orshan (1986)	
	up to 20cm	Orshan (1986)	
	up to 50cm	Orshan (1986)	
	>50cm	Orshan (1986)	
Leaf width	<1cm	Orshan (1986)	
	up to 2cm	Orshan (1986)	
	up to 5cm	Orshan (1986)	
	up to 10cm	Orshan (1986)	
	up to 20cm	Orshan (1986)	
	up to 50cm	Orshan (1986)	
	>50cm	Orshan (1986)	
Leaf angle	mainly hanging down	Parsons (1975), modulated	
	mainly horizontal	Parsons (1975), modulated	
	mainly between horizontal and 45°	Parsons (1975), modulated	
	mainly steeper than 45°	Parsons (1975), modulated	
Spinescence	spines on stem	Werger & Sprangers (1982), modulated	

Table 2: (continued) Definition of ordinate scaled parameters. For further explanation see text.

Character class	Character	Based on system of	Explanation
Spinescence	spines on branches	Werger & Sprangers (1982),	modulated
	spines on leafs	Werger & Sprangers (1982),	modulated
Hairiness	hairs on stems	Werger & Sprangers (1982),	modulated
	hairs on branches	Werger & Sprangers (1982),	modulated
	hairs on leafs	Werger & Sprangers (1982),	modulated
Epiphytic lichens	crustose lichens		
	foliose lichens		
	shrubby lichens		
	beard-like lichens		
Epiphytic mosses	on stem		
	on branches		
Epiphytic ferns	on stem		
	on branches		
Woody epiphytes	on stem		
	on branches		
Epiphytic Araceae	on stem		
	on branches		
Epiphytic bromeliads	on stem		
	in branching		
	in vertical branches		
	on diagonal branches		
	on horizontal branches		
	on dead branches		
	on organic ground material		
Epiphytic orchids	on stem		
	in branching		
	on vertical branches		
	on diagonal branches		
	on horizontal branches		
	on dead branches		
Mixed accumulation of epiphytes	on stem		
	in branching		
	on vertical branches		
	on diagonal branches		
	on horizontal branches		
	on dead branches		
Sum of vascular epiphytes	none		no vascular epiphytes
	some		cover of vascular epiphytes <10% of stem surface
	many		cover of vascular epiphytes >10% of stem surface
Connecting elements	lianas on stem		
	lianas in tree crown		
	lianas connecting stems		

Table 2: (continued) Definition of ordinate scaled parameters. For further explanation see text.

Character class	Character	Based on system of	Explanation
Connecting elements	lianas connecting crowns		
	bamboo on stem		
	bamboo in tree crown		
	bamboo connecting stems		
	bamboo connecting crowns		
Conspiciuos life forms	climbers		
	stranglers		
	Arecaceae	Richards et al. (1940)	
	Araceae	Richards et al. (1940)	
	Cyatheaceae	Richards et al. (1940)	
	Cyclanthaceae	Richards et al. (1940)	

The character class "conspicuous life-forms" is not a structural character in the narrower sense but was added to test whether certain structural characters correlated with taxonomic units which obviously contribute a great deal to the forest vegetation (for example "leaf size megaphyll" could correlate with "*Arecaceae*").The whole set of 151 characters was applied to each distinguished tree stratum on 139 plots. Table 3 lists date of data collection, part of investigation area, plot size, slope, inclination, and number of strata for all plots. Numbering of plots is partly discontinuous due to technical reasons during data collection. Missing plot numbers do not mean missing data; nevertheless, the original numbering of plots was maintained because other participants of the research project already use the same plots and numbering for their investigations of for example bats, hummingbirds, or moths. Thus the plot number will be used for plot identification throughout the whole investigation and interpretation. The majority of plots had a size of 20 m x 20 m. Exceptions had to be made at river banks where access to the forest could only be gained by wading the river bed (plots 6, 142, 143) or if 400 m² were already obviously inhomogeneous (plots 6, 89, 107, 135, 136). 119 of the plots were located in the investigation area itself (i.e. investigation areas ECSF and North of Street in Table 3). Inclination up to 60°, high landslide activity and the lack of footpaths in the investigation area made a randomised distribution of plots impossible. Footpaths had to be installed following two different ridges and plots were placed at least every 50 m of increasing altitude. To reach the upper part of the biggest tributary to the Rio San Francisco (Quebrada El Milagro), a connecting access that crossed the quebrada between the two ridges was installed. Where secondary forest in the lower

parts of the investigation area seemed inhomogeneous, plots were placed closer to each other.

To test the further applicability of the new system and to control the grouping of plots to forest units (see below), 12 plots were located on the west side of the Podocarpus National Park (4° 04' southern latitude, 79° 10' western longitude, i.e. investigation area Cajanuma in Table 3, plots 70-79, 94, 95) and another eight plots in an secondary forest in northern Ecuador (0° 05' southern latitude, 79° 10' western longitude, i.e. investigation area Mindo in Table 3, plots 27-29, 96-100). Plots 10-15 were only used for the preliminary testing and are not part of the main investigation and cluster analysis of 139 plots.

Table 3: Basic information about the date of data collection, part of investigation area, plot size, altitude, slope, inclination, and number of strata for all 139 plots.

Plot Number	Date	Investigation Area	Plot Size [m x m]	Altitude [m a.s.l.]	Slope [°]	Inclination [°]	Number of strata
1	7/29/97	ECSF	20 x 20	1900	270	30	3
2	7/30/97	ECSF	20 x 20	1910	20	40	3
3	7/29/97	ECSF	20 x 20	1920	330	55	3
4	8/9/97	ECSF	20 x 20	1870	350	55	3
5	7/30/97	ECSF	20 x 20	1870	340	40	3
6	8/12/97	ECSF	5 x 80	1820	130	60	3
7	8/12/97	ECSF	20 x 20	1890	20	40	3
8	8/9/97	ECSF	20 x 20	1900	190	40	3
9	9/3/97	ECSF	20 x 20	1930	350	60	3
10		ECSF	20 x 20	1890	300	40	
11		ECSF	20 x 20	1900	300	45	
12		ECSF	20 x 20	1890	0	40	
13		ECSF	20 x 20	1880	290	5	
14		ECSF	20 x 20	1890	300	30	
15		ECSF	20 x 20	1870	270	50	
25	11/22/98	ECSF	20 x 20	1830	290	50	3
26	11/23/98	ECSF	20 x 20	1870	290	50	2
27	5/10/99	Mindo	20 x 20	1620	40	20/60	2
28	5/10/99	Mindo	20 x 20	1600	20	45	2
29	5/10/99	Mindo	20 x 20	1570	290	5/30	2
30	5/25/99	North of Street	20 x 20	2020	130	50	2
31	5/25/99	North of Street	20 x 20	2070	180	15	1
32	5/26/99	North of Street	20 x 20	1830	220	20	1

Table 3: (continued) Basic information about the date of data collection, part of investigation area, plot size, altitude, slope, inclination, and number of strata for all 139 plots.

Plot Number	Date	Investigation Area	Plot Size [m x m]	Altitude [m a.s.l.]	Slope [°]	Inclination[°]	Number of strata
33	5/26/99	North of Street	20 x 20	1800	250	70	1
34	6/7/99	North of Street	20 x 20	1820	110	10/80	2
35	6/7/99	North of Street	20 x 20	1830	150	30	2
36	6/7/99	North of Street	20 x 20	2040	50	25	2
37	6/7/99	North of Street	20 x 20	2040	50	25	1
38	6/7/99	North of Street	20 x 20	2060	40	25	1
39	6/8/99	North of Street	20 x 20	1950	140	30/40	2
40	6/8/99	North of Street	20 x 20	1920	120	20	2
41	6/8/99	North of Street	20 x 20	1910	110	30/60	2
51	8/16/97	ECSF	20 x 20	1860	11	40	3
52	8/16/97	ECSF	20 x 20	1840	80	40	3
53	8/22/97	ECSF	20 x 20	1920	270	40	2
54	8/22/97	ECSF	20 x 20	1960	260	35	2
55	8/22/97	ECSF	20 x 20	1940	0	50	3
56	8/23/97	ECSF	20 x 20	1920	200	40	3
57	8/23/97	ECSF	20 x 20	1920	310	40	1
58	8/23/97	ECSF	20 x 20	1910	320	60	2
59	8/24/97	ECSF	20 x 20	1870	270	20	3
60	8/24/97	ECSF	20 x 20	1880	270	40	3
61	8/24/97	ECSF	20 x 20	1900	270	40	3
62	8/29/97	ECSF	20 x 20	1870	250	50	2
63	8/29/97	ECSF	20 x 20	1860	280	50	3
64	8/30/97	ECSF	20 x 20	1850	330	50	3
65	8/30/97	ECSF	20 x 20	1830	320	50	3
66	8/31/97	ECSF	20 x 20	1900	260	60	3
67	8/31/97	ECSF	20 x 20	1950	290	60	3
68	9/3/97	ECSF	20 x 20	1970	340	50	3
70	4/3/98	Cajanuma	20 x 20	2790	200	20	3
71	5/2/98	Cajanuma	20 x 20	2760	190	60	2
72	5/3/98	Cajanuma	20 x 20	2730	180	20	3
73	5/4/98	Cajanuma	20 x 20	2800	140	25	2
74	5/4/98	Cajanuma	20 x 20	2850	250	30	2
75	5/19/98	Cajanuma	20 x 20	2850	160	20	2
76	9/20/98	Cajanuma	20 x 20	2910	250	40	2
77	9/20/98	Cajanuma	20 x 20	2970	280	40	2

Table 3: (continued) Basic information about the date of data collection, part of investigation area, plot size, altitude, slope, inclination, and number of strata for all 139 plots.

Plot Number	Date	Investigation Area	Plot Size [m x m]	Altitude [m a.s.l.]	Slope [°]	Inclination [°]	Number of strata
78	9/20/98	Cajanuma	20 x 20	3020	270	20	2
79	9/20/98	Cajanuma	20 x 20	3100	230	40	2
80	4/25/98	ECSF	20 x 20	2020	320	40	2
81	4/25/98	ECSF	20 x 20	2050	290	5	3
82	4/25/98	ECSF	20 x 20	2100	340	30	2
83	4/30/98	ECSF	20 x 20	2170	300	30	2
84	4/30/98	ECSF	20 x 20	2220	350	10	2
85	4/30/98	ECSF	20 x 20	2250	340	5	2
86	5/11/98	ECSF	20 x 20	2310	10	35	2
87	5/11/98	ECSF	20 x 20	2380	250	20	2
88	5/11/98	ECSF	20 x 20	2450	320	20	2
89	5/29/98	ECSF	10 x 10	2600	90	5	2
90	5/29/98	ECSF	20 x 20	2500	90	10	2
91	6/14/98	ECSF	20 x 20	2190	270	20	2
92	6/14/98	ECSF	20 x 20	2110	270	35	2
93	6/14/98	ECSF	20 x 20	2000	350	40	2
94	9/21/98	Cajanuma	20 x 20	2750	220	20	3
95	9/21/98	Cajanuma	20 x 20	2780	130	40	2
96	5/8/99	Mindo	20 x 20	1610	280	5	2
97	5/8/99	Mindo	20 x 20	1610	260	5	2
98	5/8/99	Mindo	20 x 20	1600	310	10	3
99	5/9/99	Mindo	20 x 20	1600	110	35	2
100	5/9/99	Mindo	20 x 20	1610	230	20/60	2
101	3/24/98	ECSF	20 x 20	1990	330	30	3
102	3/25/98	ECSF	20 x 20	2000	340	40	3
103	3/25/98	ECSF	20 x 20	2000	250	45	3
104	3/25/98	ECSF	20 x 20	2080	0	35	3
105	3/30/98	ECSF	20 x 20	1920	350	35	2
106	3/30/98	ECSF	20 x 20	1960	70	45	3
107	4/7/98	ECSF	10 x 20	1990	0	0	3
108	4/7/98	ECSF	20 x 20	2040	340	30	3
109	4/7/98	ECSF	20 x 20	2120	280	30	3
110	4/9/98	ECSF	20 x 20	1840	270	35	3
111	4/9/98	ECSF	20 x 20	1870	320	40	3
112	4/11/98	ECSF	20 x 20	2150	340	10	2

Table 3: (continued) Basic information about the date of data collection, part of investigation area, plot size, altitude, slope, inclination, and number of strata for all 139 plots.

Plot Number	Date	Investigation Area	Plot Size [m x m]	Altitude [m a.s.l.]	Slope [°]	Inclination[°]	Number of strata
113	4/11/98	ECSF	20 x 20	2230	340	20	2
114	4/11/98	ECSF	20 x 20	2440	20	30	1
115	4/14/98	ECSF	20 x 20	2240	30	20	2
116	4/14/98	ECSF	20 x 20	2350	30	30	2
117	4/14/98	ECSF	20 x 20	2250	30	30	3
118	4/15/98	ECSF	20 x 20	1910	20	50	3
119	4/15/98	ECSF	20 x 20	1950	90	40	3
120	4/15/98	ECSF	20 x 20	1940	20	20	3
121	4/16/98	ECSF	20 x 20	1890	310	30	3
122	4/16/98	ECSF	20 x 20	1900	260	45	3
123	4/16/98	ECSF	20 x 20	1880	320	10	3
124	4/21/98	ECSF	20 x 20	2080	280	30	3
125	4/21/98	ECSF	20 x 20	2030	300	20	3
126	4/22/98	ECSF	20 x 20	2140	30	10	3
127	4/22/98	ECSF	20 x 20	2130	350	20	2
128	4/28/98	ECSF	20 x 20	2540	270	60	2
129	5/1/98	ECSF	20 x 20	1950	270	60	3
130	5/8/98	ECSF	20 x 20	2050	300	25	3
131	5/9/98	ECSF	20 x 20	2030	0	30	3
132	5/10/98	ECSF	20 x 20	2200	0	20	2
133	5/10/98	ECSF	20 x 20	2180	10	25	3
134	5/25/98	ECSF	20 x 20	2130	30	30	2
135	5/30/98	ECSF	10 x 10	2650	210	30	3
136	5/31/98	ECSF	10 x 10	2660	190	30	1
137	6/12/98	ECSF	20 x 20	2080	310	30	3
138	6/12/98	ECSF	20 x 20	2180	320	30	2
139	9/12/98	ECSF	20 x 20	2400	310	30	2
140	9/16/98	ECSF	20 x 20	2310	270	35	2
141	9/16/98	ECSF	20 x 20	2320	340	30	2
142	9/28/98	ECSF	10 x 30	1850	140	40	2
143	9/28/98	ECSF	10 x 30	1850	180	40	2
144	10/1/98	ECSF	20 x 20	2280	70	20	2
145	10/1/98	ECSF	20 x 20	2220	180	45	2
146	10/3/98	ECSF	20 x 20	2210	30	20	3
147	10/3/98	ECSF	20 x 20	2240	0	20	2

Table 3: (continued) Basic information about the date of data collection, part of investigation area, plot size, altitude, slope, inclination, and number of strata for all 139 plots.

Plot Number	Date	Investigation Area	Plot Size [m x m]	Altitude [m a.s.l.]	Slope [°]	Inclination[°]	Number of strata
148	10/3/98	ECSF	20 x 20	2200	80	15	3
149	10/4/98	ECSF	20 x 20	2180	70	30	2
150	10/4/98	ECSF	20 x 20	2190	5	10	3
151	10/11/98	ECSF	20 x 20	2250	0	20	3
152	10/11/98	ECSF	20 x 20	2280	30	20	3
153	10/30/98	North of Street	20 x 20	1960	180	20	2
154	10/30/98	North of Street	20 x 20	2000	170	30	2
155	10/30/98	North of Street	20 x 20	1960	170	25	2
156	11/1/98	North of Street	20 x 20	1930	120	30	2
157	11/1/98	North of Street	20 x 20	1950	110	35	2
158	11/1/98	North of Street	20 x 20	1980	160	25	1
159	11/3/98	North of Street	20 x 20	1950	90	15/60	2
160	11/3/98	North of Street	20 x 20	1980	120	20/80	2
161	11/9/98	ECSF	20 x 20	2130	350	20/50	2
162	11/9/98	ECSF	20 x 20	2120	350	15/30	2
163	11/10/98	ECSF	20 x 20	2370	250	20	2
164	11/10/98	ECSF	20 x 20	2340	290	15	2

If in Table 3 two informations about inclination are given for a single plot (for example plot 27), the plot is crossed by a little river. The first figure characterises inclination of the river bed, the second figure the inclination of the river bank rectangular to the river bed.
Figure 4 shows the location of all plots except those in Cajanuma (plots 70-79, 94, 95) and Mindo (27-29, 96-100).

2.5 Statistical interpretation

For statistical interpretation, cluster analysis with the SPSS-software package was used.

Cluster analysis reacts sensitively to objects being very different from the rest (here each plot is an object) (Everitt 1995, Backhaus et al. 1996). To avoid disturbance of the cluster process, such objects (outliers) had first to be eliminated. The "single linkage" method (synonym: nearest neighbour method) is suitable for recognising outliers (Backhaus et al. 1996). Thus, in

each step an analysis to recognise and eliminate outliers was performed before the main cluster analysis. For the main analysis, the Ward algorithm was used. SPSS recommends the squared Euclidean distance as distance measure.

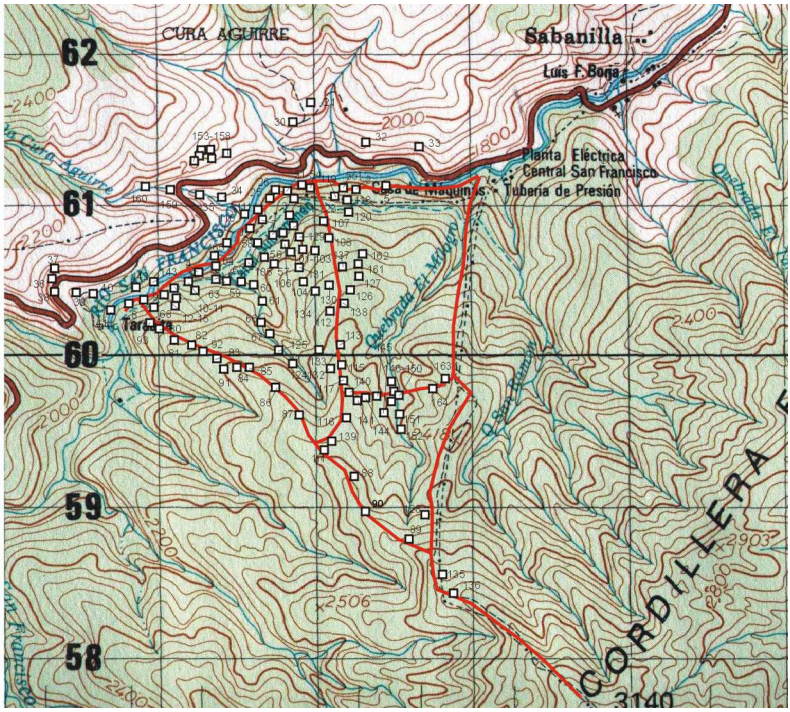


Figure 4: Location of plots in the investigation area.

Cluster analysis results in a grouping of the clustered objects but does not explain which variables were responsible for the grouping. As an aid for interpretation of a dendrogram, (BACKHAUS et al. 1996) recommend calculation of a T-value:

$$T = \frac{\bar{X}(J,G) - \bar{X}(J)}{S(J)}$$

with: $\bar{X}(J, G)$ = mean value of variable J (i.e. structural feature) for all objects in group G (i.e. all plots in a certain group)

$\bar{X}(J)$ = mean value of variable J for all objects (i.e. all plots)

S (J) = mean deviation of variable J for all objects

If the T-value is positive, the variable is over-represented in the considered group of plots compared to all plots. If the T-value is negative, the variable is under-represented. T-values were calculated for all variables for all groups of plots that resulted from the cluster analysis.

In a cluster analysis not all variables are similarly suitable for supporting the grouping of the objects to be clustered (BACKHAUS et al. 1996). If a variable does occur with a low frequency (or not at all) or with a very high frequency and with the same value in nearly every object, it can be excluded from the analysis without changing the result. The frequency of every value of every variable was determined to exclude those variables which did not support grouping.

Variables can also be redundant, i.e. they occur nearly always together or exclude each other. In this case, one variable out of each pair of highly correlated variables should be eliminated to avoid over-interpretation of one feature that is described by more than one variable. Correlation between all possible pairs of variables was determined using the Spearman Correlation Coefficient (BACKHAUS et al. 1996). Significantly correlating variables could partly be excluded. Cluster analysis then was repeated with the reduced and simplified set of variables to check if the grouping still led to the same result.

The result of the clustering then had to be interpreted and plots joined to structural forest units. The arrangement of these units had to be presented in a map. Figure 5 illustrates the steps of investigation.

Data collection for all presented results was performed between June 1997 and January 2000.

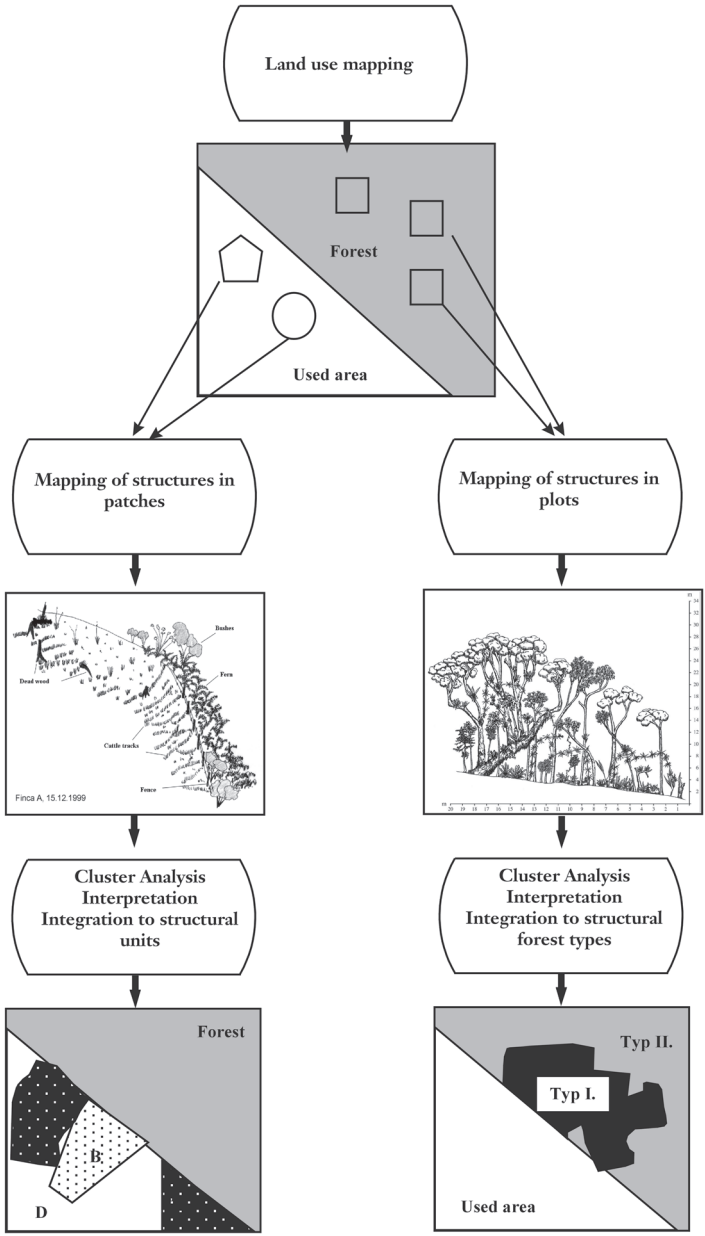


Figure 5: Steps of investigation

3 Results and Interpretation

The structure of primary forest, secondary forest and land-use areas as potential forest stands was mapped in different scales. The first part of this chapter describes the mapping on a landscape level, the second part shows the results on a patch level and the third part on the level of defined plots.

3.1 Landscape level

To overview the investigation area, the mosaic of different land-use units and undisturbed forest areas was mapped on the basis of aerial photographs and topographical maps. On a landscape level, differentiation was made between the following structures: forest (primary or secondary), reforestation (mostly with *Pinus patula*), bushes, pasture, recent and older clear cuts (including burnt areas), areas dominated by fern, landslides and farmland as shown in Figure 6. The road, rivers and houses were marked as well as the pylons of a high voltage line, the construction of which in 1997 forced an open strip through all traversed units which was still obvious in January 2000 (see below). The letters A-L (and the hatches) indicate the 12 fincas which were more closely investigated on a patch level.

It is obvious that colonisation followed the road and that the fincas are restricted to the slopes of the Rio San Francisco/Rio Zamora valley. Forest still covers the higher altitudes, particularly south of the Rio San Francisco. Recently cleared areas are mostly located at the upper border of a finca, indicating that clearing was enforced even in less favourable sites further away from the farm house itself. It could also be concluded that the main land use is pasture for breeding cattle whereas cultivating crops is only practised in small areas and is restricted to the southern (i.e. lower, warmer and drier) part of the investigation area. In the northern part comparatively large areas are covered with fern which caused severe problems to local farmers (see below).

Landslides as a consequence of road construction occurred along the whole extension of the road and often mud-streams blocked the road completely for days, especially in the rainy season in June and July. The local practise to shuffle the material to the downhill side of the road and dig the road further into the uphill side is worsening the problem. Stoyan (2000) who investigated landslide dynamics in the area concluded that the slopes will need decades to stabilise.

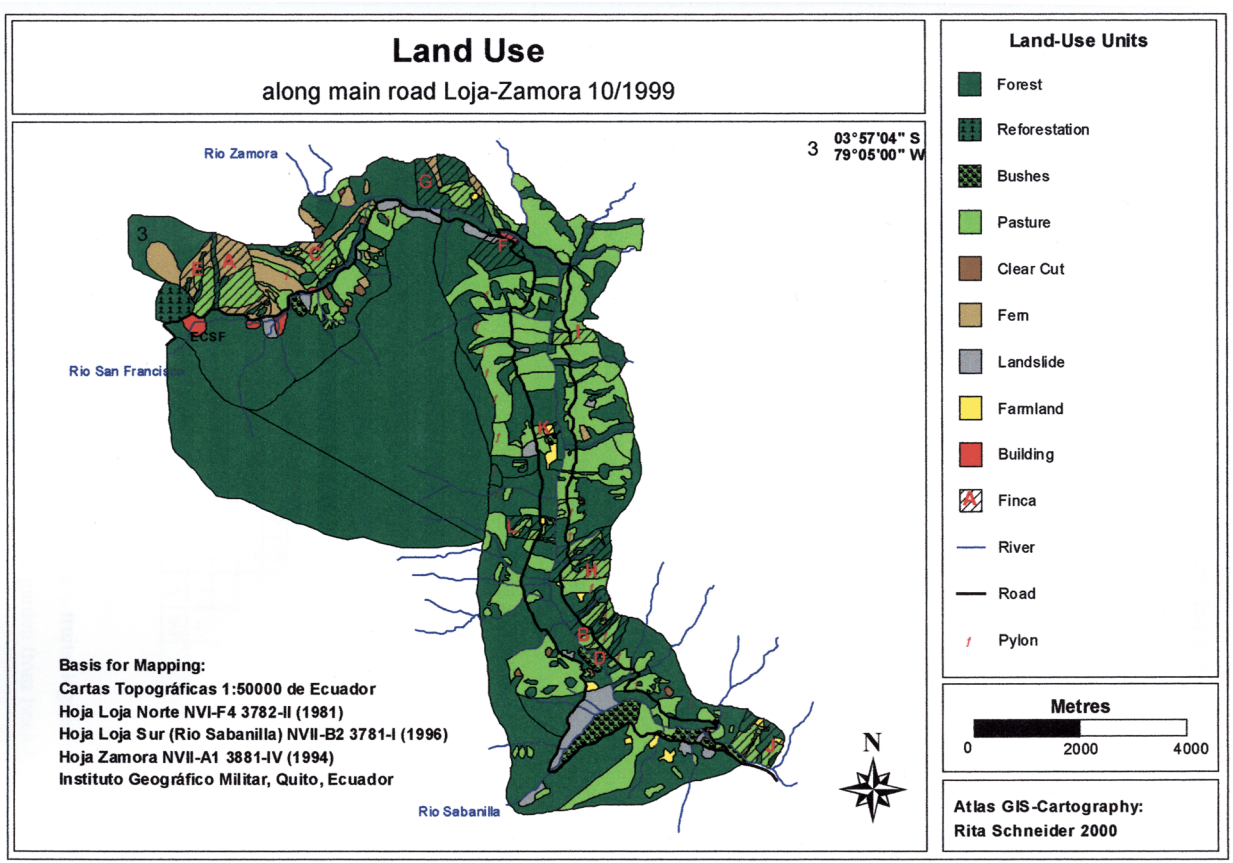


Figure 6: Land-use units in the investigation area (from Paulsch et al. 2001)

3.2 Patch level

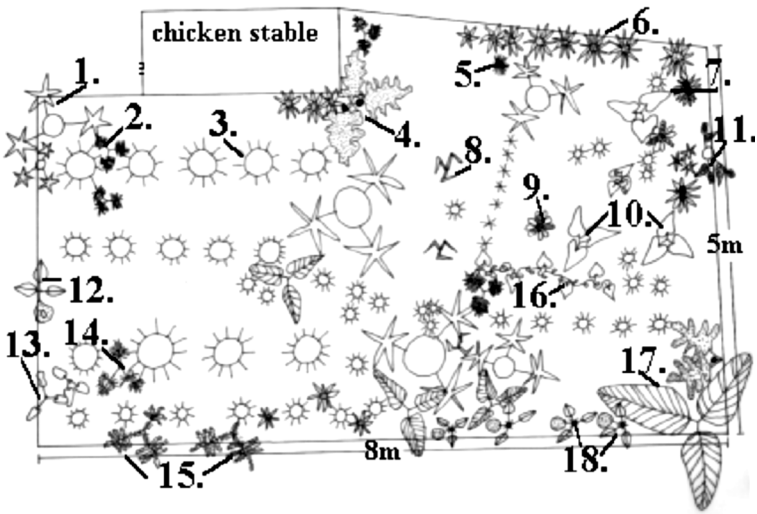
The 12 fincas marked in Figure 6 could be subdivided into 245 patches. These patches were assigned to the following land-use units: forests, reforestations, pastures (with and without trees), groups of trees, bushes, clear cuts, fern dominated patches, farmland, landslides, house gardens, houses, and streets. As outer boundaries the limits of the private property were used for every finca. In many cases these boundaries followed small rivers, ridges, or the street.

Table 4 indicates the distribution of patches and the altitude of the lowest/highest patch for all 12 fincas. The high number of pasture patches (61 patches with and without trees) supported the conclusion, already drawn from the high percentage in the overview mapping, that the main form of land use was pasture. Most pasture patches (45) contained trees which served as shade for cattle. Interviews revealed that these trees were not exclusively survivors of clear cutting but were partly planted by the farmers. Larger groups of trees (i.e. more than 5 individuals) were comparatively rare (5 patches).

Table 4: Altitude and distribution of 245 patches of 12 fincas

	Altitude [m a.s.l.]	Street	House	House garden	Farmland	Landslide	Clear cut	Fern area	Bush	Pasture without trees	Pasture with trees	Group of trees	Forest	Reforestation	Sum
Finca A	1840-2350			2	1		1	3	3	5	4	1	4		24
Finca B	1120-1700			1			2	3	2		2		10	1	21
Finca C	1640-1970			1	1		1	5	2	1	7		4		22
Finca D	1100-2000		1	1			3	1	4		5		8		23
Finca E	1850-2600			2	1	4		4	1	3	3	1	5		24
Finca F	1590-1960	1	2	1		5	1		2	1	3		4		20
Finca G	1600-2150			1	3	2	2	2	4	1	3	1	3		22
Finca H	1350-1810			1	1				8		9		5		24
Finca I	1520-1830		1	1	1	1	1		1	2	3	1	3		15
Finca J	1050-1400			1	4		1		4	1	2		6		19
Finca K	1490-1600		1	1		1	1		3	1			3		11
Finca L	1360-1760		1	1	2	3			3	1	4	1	4		20
Sum		1	6	14	14	16	13	18	37	16	45	5	59	1	245

Every finca had at least one house garden patch, where fruits, legumes, and medical plants were intensively cultivated. Figure 7 shows a house garden from finca J.



1. Papaya (*Carica papaya* L.)
2. Tomato (*Lycopersicon esculetum* Mill.)
3. Sugar cane (*Saccharum officianum* L.)
4. Naranjilla (*Solanum quitoense* Lam.)
5. Hierba luisa (*Cymbopogon citratus* (Dc.) Stapf)
6. Ornamental plants
7. Corn (*Zea mays* L.)
8. Cariamanga (*Poaceae*)
9. Pea (*Pisum sativum* L.)
10. Papachina (*Colocasia esculenta* (L.) Scholt)
11. Coffee (*Coffea arabica* L.)
12. Avocado (*Persea americana* Mill.)
13. Chilli (*Capsicum chinense* N. Jacq.)
14. Carrot (*Daucus carota* L.)
15. Hortiga (*Loasa picta* Hokk.)
16. Bean (*Phaseolus vulgaris* L.)
17. Achira (*Musaceae*)
18. Sweet lemon (*Citrus limetta* Risso)

Figure 7: House garden from Finca J (from Schneider *2000, modified).*

Only three fincas (G, J, L) cultivated more than one patch of farmland with a maximum of four patches in finca (J) on the lowest altitude investigated. Even here the harvested products were not sold on a market but used exclusively by the family itself.

In addition, every finca included at least three patches of forest, mostly remnants of primary forest. They served as a reserve supply for further cutting or burning to gain more pasture if the actual pasture patches degraded or were invaded by fern. This was a particular problem on the fincas in higher

altitudes (A-E, G). Interviews showed that a major part of activities invested in improvement of the economical situation was needed to stop the fern (*Pteridium aquilinum*) from invading pasture patches. Farmers cut it down with machetes and justified regular burning of patches with the struggle against the fern. Nevertheless, they knew that the deeper lying rhizomes were not influenced by fire and the fern will sprout quicker than the grasses. The fern patches had to be set aside and new clear cuts were driven further into the forest remnants (only three farms had no obvious recently burnt or cleared patches). HARTIG (2000) and PAULSCH et al. (2001) observed that in the same investigation area *Pteridium aquilinum* could dominate the floristic composition of pasture plots and distinguished a fern-dominated stage of succession. Reforestation was not accepted as a possibility of long-term economy (only one patch in finca B) and there were no financial resources that allowed investigation of tree saplings.

The patches had 716 boundaries between each other or adjacent areas (e.g. the main road). For each unit the percentage of neighbouring units was calculated related to the number of boundaries of the unit. Figure 8 shows the percentage of neighbouring units for forest patches and landslides as an example (units with less than 5% of common boundaries were summarised in the category "others"). 41% of the boundaries of forest patches were boundaries with pasture patches (7% without trees and 34% with trees). This supported the information that recently burnt or cleared patches were immediately transformed into pasture. The farmers planted grass tussocks to accelerate the transformation and did not use these patches as farmland for long periods.

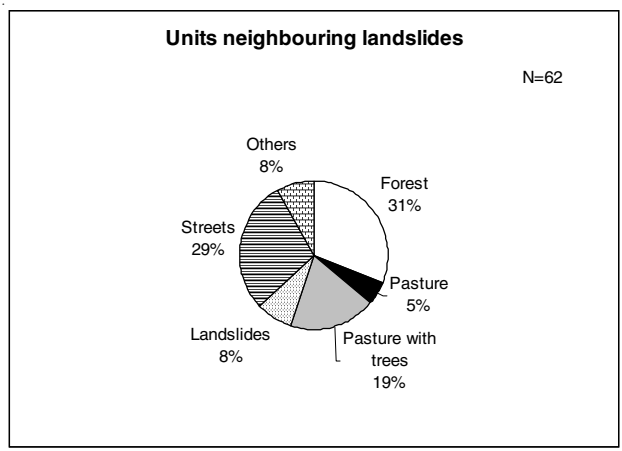


Figure 8a: Distribution of units neighbouring landslides (from SCHNEIDER 2000, modified).

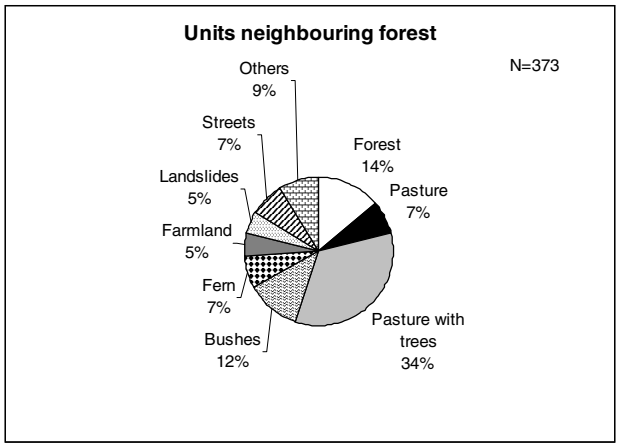


Figure 8b: Distribution of units neighbouring forest patches (from SCHNEIDER 2000, modified).

Sixteen landslide patches had 62 boundaries of which 18 (29%) were boundaries with the main road. This result supported the conclusion already drawn from the overview map that the construction of the road caused an increase in landslides.

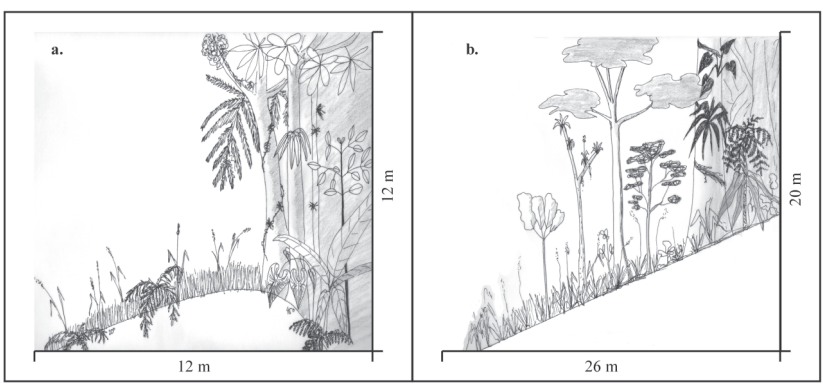


*Figure 9: **a.** Sharp boundary between pasture and forest. **b.** Gradual transition between pasture and forest (from SCHNEIDER 2000, modified).*

Only 2% of all boundaries were classified as sharp boundaries (i.e. showing a sudden change in dominating life-forms and number of vegetation layers). Figure 9 shows a sharp boundary between a forest patch and a pasture patch (a.) in comparison to a gradual transition between the same units (b.). The

fact that land use in the investigation area had only a history of some decades and cultivation of primary forest was still an ongoing process may explain the low percentage of sharp boundaries: patches and boundaries were not yet demarcated for a longer period and properties (that often mark sharp boundaries in long used areas) were not yet traded over generations. The low input of modern techniques and the use of unspecific measures like burning might also have hindered the establishment of fixed boundaries. Thus the whole mosaic of land-use units could not be seen as a stable equilibrium but was only a stage in a process of change.

For all 245 patches, a set of structural features (see Material and Methods) was registered. Cluster analysis led to a grouping into 14 structural units which could be arranged in six classes: forest-like units, bush-like units, pasture-like units, fern dominated units, garden-like units, and units without vegetation. Table 5 (p. 60) characterises the classes and groups. For each group, the number of patches, number of vegetation layers, the height of the highest layer, and percentage of vegetation cover is given. Dominant life-forms, intensity of clearing, shape of patches, and altitude of maximum occurrence are also listed.

As in Table 4 (p. 55), most of patches belonged to forests (forest-like units respectively) and pasture (pasture-like units respectively), however, the characterisation with the help of structural features allowed a more detailed subdivision than the land-use based characterisation alone (e.g. into three different forest-like units compared to one land-use unit forest).

A set of two maps was produced for each finca. The first set was based on the land-use units listed in Table 4. The second set was based on the structural units listed in Table 5. As an example, Figure 10 shows the land-use for finca A whereas Figure 11 shows the distribution of structural units for the same finca.

On comparing, it was obvious that the land-use units of Figure 10 could be subdivided into more detailed structural units in Figure 11: the two bush patches in the lower left had the same signature in the land-use classification but belonged to different bush-like structural units. One of them had the same structural characteristics as the patch in the lower right which was mapped as fern dominated in Figure 10. The pasture patches (light green in Figure 10) could be divided into two structural units (group VII and group VIII) of the pasture-like class. One of the patches (lower centre) even fell into the garden-like structural units and thus is more closely related to house gardens than to pasture.

Table 5: Description of 14 structural units in six classes.

Class	Group	Number of patches	Number of vegetation layers	Height of highest layer [m]	Vegetation cover [%]	Dominant life-forms	Intensity of clearing	Shape of patches	Altitude with maximum occurence [m a.s.l.]	Additional remarks
Forest-like structural units	I	63	3	>20	100	trees, bushes, herbs	none	completely irregluar	1400-1800	upper part of slopes, ridges
	II	6	2	10 to 20	90 to 100	trees, grasses	low	elliptical, linear	1400-1800	grass tussocks, cattle tracks
	III	8	1 or 2	10 to 20	10 to 70	trees	high	square	1400-2200	recently changed, high cover of dead wood
Bush-like structural units	IV	16	1	5 to 10	100	bushes	high	linear, square	1400-2200	middle part of slopes, strip under line of high voltage
	V	15	1 or 2	5 to 10	80 to 100	bushes, herbs, fern	high	completely irregular, linear, square	1400-2000	middle part of slopes, no dead wood
Pasture-like structural units	VI	21	2	10 to 20	70 to 80	grasses, few trees	high	rectangular, completely irregular,	1000-2000	tree layer sparse, high density of cattle tracks, grass tussocks, no dead wood
	VII	25	2	10 to 20	70 to 100	grasses, few trees	high	completely irregular	1000-2000	dead wood still standing
	VIII	13	1	<5	60 to 100	grasses, fern	high	completely irregular	1600-2200	high intensity of standing dead wood, grass tussocks, cattle tracks
Fern dominated structural units	IX	10	2	5 to 10	20 to 70	fern, few trees	high	square	1600-2400	high intensity of standing dead wood, signs of fire
	X	11	1	<5	100	fern, few grasses	high	square	1800-2200	set aside from pasture use, remnants of cattle tracks
Garden-like structural units	XI	12	1 to 3	<5 to 10	70 to 80	grasses, herbs, few trees	high	rectangular, irregular	1200-2000	partly with dead wood partly planted with corn
	XII	19	1 to 3	<5 to 10	20 to 50	herbs, grasses, few trees, bushes	high	square	1000-1800	no dead wood partly house gardens
	XIII	21	2	<5	50 to 70	grasses, herbaceous perennials	high	square	1000-1800	no dead wood, high percentage of herbaceous perennials
Units without vegetation	XIV	5	0	0	0	-	complete	linear, square, irregular cornered	1000-1800	no vegetation, yards, footpaths

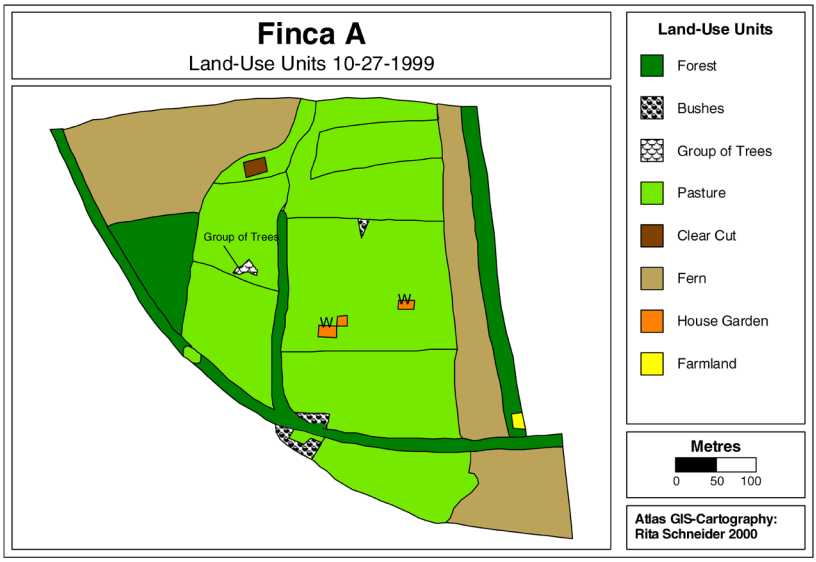


Figure 10: Land-use units in Finca A (from Paulsch et al. 2001)

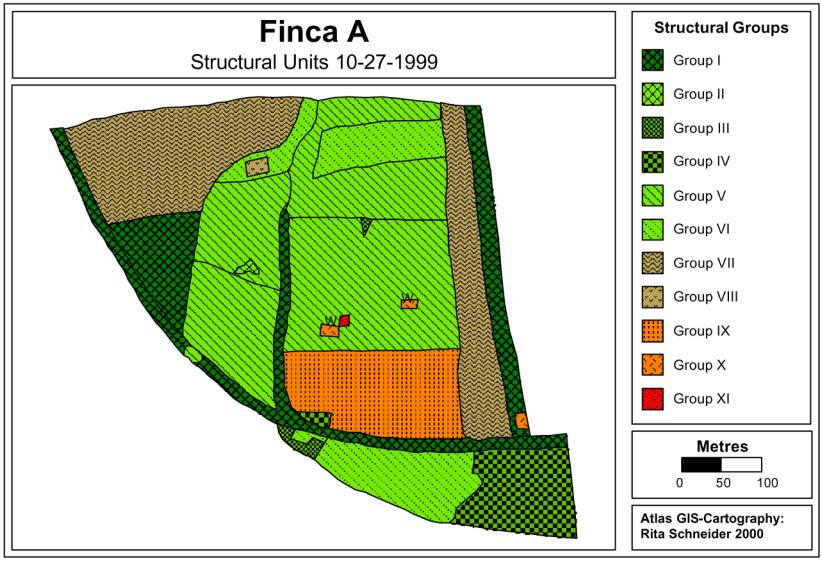


Figure 11: Structural units in Finca A (from Paulsch et al. 2001)

The investigation on both the landscape level and the patch level obviously showed that a landscape could be described as a mosaic of land-use units. It also revealed that a more detailed description of vegetation structure did not only lead to a more detailed subdivision of units, but also regrouped patches.

3.3 Plot level

3.3.1 Test of classification systems

As a first step in the investigation on a plot level, seven systems of classifying vegetation structure in forests were tested on 15 plots. The systems of Mueller-Dombois & Ellenberg (1974) and of Beard (1955), which consider plant formations as investigation units, both led to the result that all 15 plots belong to one unit. In the system of Mueller-Dombois & Ellenberg (1974), the plots belonged to "moist tropical montane forests, partly with bamboo (1.1.c.1./c.3.)", whereas in the system of Beard (1955), the plots had to be classified as "lower montane rain forest". Both systems did not allow further distinction between the plots for two reasons: they were designed for a global scale and thus have to be unspecific on a plot level and they were meant for primary vegetation only. None of them considers disturbance as a factor changing vegetation structure so that a differentiation of plots with different degrees of disturbance cannot be expected.

Applicability was not similar for those tested systems which consider individual plants (Parsons 1975, Werger & Sprangers 1982, Orshan 1986,) or plots (Richards et al. 1940, Webb et al. 1970) as investigation units. Table 6 shows that the system of Orshan (1986) led to the highest number of characters which could be found (91) in our investigation area. However, as Orshan (1986) proposed 234 characters, this result meant that only 39.9% of the characters could be detected by field methods. Following the system of Webb et al. (1970), 100% of the proposed characters could be found, but the absolute number of characters was only 28 and thus the lowest of all systems. The system of Richards et al. (1940) offered 42 characters of which 34 (80.9%) could be found. From the 105 characters proposed by the system of Werger & Sprangers (1982) 77 could be detected. Thus the latter system offered the most satisfying compromise between a high ratio of detectable characters (73.3%) and a high absolute number.

Table 6: Comparison of five classification systems tested for their applicability in the investigation area (for more details see AXMACHER 1998).

Tested classification system	**Werger & Sprangers** 1982	**Orshan** 1986	**Parsons** 1975	**Richards et al.** 1940	**Webb et al.** 1970
Investigation unit	individual plant	individual plant	individual plant	plot	plot
Number of characters proposed	105	234	94	42	28
Number of characters found	77	91	44	34	28
Percentage of characters found	73.3	39.9	47.8	80.9	100

Nevertheless, cluster analysis led to comparable grouping of the 15 plots for all five systems (Figure 12 a-e). In each case the forest plots (1-8) were grouped together and the plots on landslides or formerly cleared areas (9-15) were added at longer distance levels. The two plots 13 and 14 were always grouped together, plot 12 was added at the longest distance in three cases. The placing of forest plots within the group was not constant. Thus it can be concluded that the systems were capable of separating plots of different degrees of disturbance but that differentiation between forest plots is harder to achieve.

Cluster analysis was repeated using only presence/absence data and led to the same result. This might be explained by the fact that the significantly lower number of trees on heavily disturbed plots, for stochastic reasons, led to a lower number of characters present on these plots.

From these results it was concluded that the by far more time consuming systems which investigate each individual plant do not necessarily lead to more accurate results than the systems on a plot scale. If presence or absence of characters supports the grouping of plots, it is irrelevant how many individuals bear the character. Therefore the newly composed investigation system was designed to operate on a plot level.

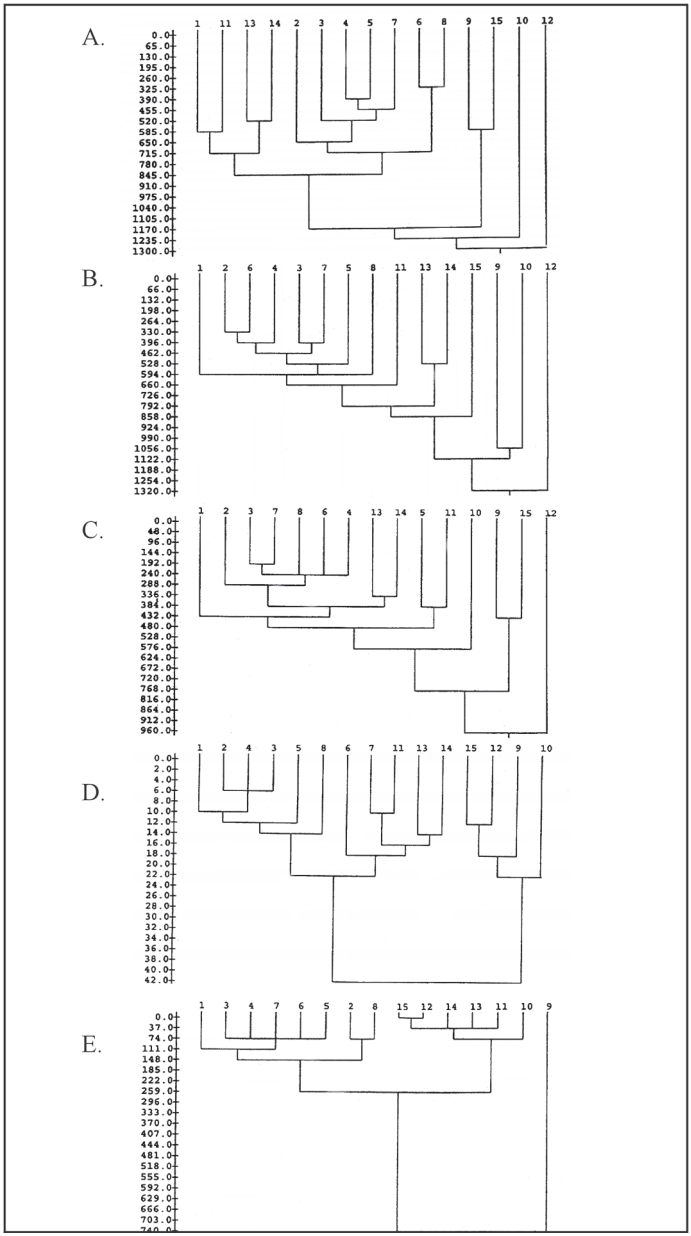


Figure 12: Comparison of dendrograms fo plots 1-15. System of data collection based on Werger & Sprangers 1982 (A.), Orshan 1986 (B.), Webb et al. 1970 (C.), Parsons 1975 (D.) and Richards et al. 1940 (E.). City-Block metric (from Axmacher 1998)

3.3.2 Cluster analysis

The new investigation system was applied to each vegetation stratum in each plot. Along the investigated altitudinal gradient, the canopy height differed greatly between forest stands. Therefore strata were not defined at fixed levels of tree height but were related to the canopy height of each stand (see Material and Methods and Discussion).

A cluster analysis for all 139 plots using all 453 characters (151 characters per stratum with a maximum of three strata) led only to a grouping into plots with one stratum (9 plots), with two strata (72 plots), or with three strata respectively (58 plots), because in a plot with only one stratum the characters of the other strata had to be treated as variables where the value was always zero. This neglected differences between plots with the same number of strata. To obtain a more detailed differentiation, the three groups of plots had to be analysed separately.

All the plots with only one stratum were not part of the natural montane forest but represented different stages of succession after landslides, slashing or burning. Therefore the classification of undisturbed forest units was not disturbed by splitting these plot off.

The plots with two or three strata all represented forest in different altitudes. Separation into two groups and independent interpretation was unsatisfying when attempting to compare all parts of the forest as a whole. The most promising way of analysing the two groups of plots together was to compare them on the basis of only two strata. Of course, these two strata had to be in a comparable position so that canopy was compared with canopy and undergrowth with undergrowth. This meant ignoring the middle stratum of the plots with three strata. In some cases, where the highest stratum of a plot with three strata was only built up by one emergent tree, it was preferred to ignore this stratum (see below).

3.4 Grouping of plots

3.4.1 Plots with one stratum

As listed in Table 3 (p. 45-49) and shown in Figure 4 (p.49), the nine plots with only one stratum (plot numbers 31-33, 37, 38, 57, 114, 136, 158) were all part of the investigation areas ECSF and North of Street and located in a small altitudinal belt between 1800 m a.s.l. and 2070 m a.s.l. (except 114 and 136 in altitudes > 2440 m a.s.l.). A first cluster analysis using the single link-

age method revealed plot 114 to be an outlier which had to be excluded from the main analysis using the Ward algorithm. This result was not surprising since plot 114 was part of the primary forest between plots 87, 88, and 139 (all with two strata) in contrast to the other plots of this group located on landslides or in cleared areas. What distinguished plot 114 from neighbouring plots was mainly the fact that vegetation was so dense that a clear separation of strata was impossible. This plot had finally to be grouped into one of the structural types using other criteria than cluster analysis (see below).

Clustering of the remaining eight plots led to separation of plots 31 and 136 and to a grouping into two blocks of three plots each: the first block with plots 32, 33 and 38, the second block with plots 37, 57, and 158 (Figure 13). Plot 31 was the remnant of a primary forest stand, where the undergrowth had been cleared by slashing and burning. The remaining stratum was the former canopy and thus differed strongly from the second growth on the other plots with one stratum. Plot 136, at an altitude of 2660 m .a.s.l., had the highest altitude of all investigated plots and marked the transition zone between upper montane forest and shrub páramo. Thus it can be explained why the plots 31and 136 did not fit into any group of forest plots.

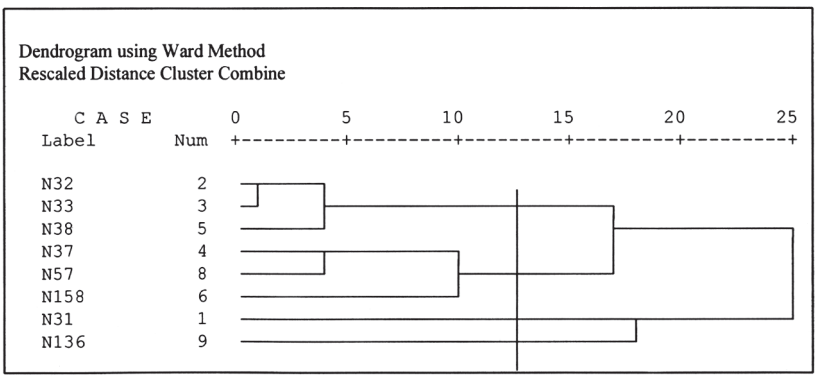


Figure 13: Cluster dendrogram for eight plots with one stratum. The vertical line marks the number of clusters.

Block one linked three plots (32, 33, 38) located directly along the road on the uphill embankment. They could be classified as second growth after disturbance caused by road construction. The second block consisted of three plots (37, 57, 158) on still obvious landslides (57, 158) or were located under a high voltage line (37) and therefore recently cleared. They could be classified as secondary growth after landslides or clearing. (For closer de-

scription see below). To summarise the results for the nine plots with only one stratum, it can be stated that cluster analysis separated plot 114 as an outlier, plots 31 and 136 as special cases which can be easily explained, and grouped six plots into two blocks of second growth vegetation after different disturbances.

3.4.2 Plots with more than one stratum

After separate interpretation of the nine plots with only one stratum 130 plots with more strata were left for further analysis, 72 of them with two strata and 58 with three strata.

Cluster analysis using the single linkage algorithm revealed plots 95 and 135 to be outliers in the group with two strata and plot 119 in the group with three strata. They were excluded from the next stage of analysis.

For the 127 remaining plots, a cluster analysis using the Ward algorithm was performed. For all plots with three strata, the middle stratum was ignored. This analysis led to the result that a number of plots were not arranged in groups but added at the bottom of the dendrogram. These were plots 108-110, 118, 125, and 131. In a search for an explanation, the data set was checked for four criteria:

- plots where only one emergent built the highest stratum (criterion 1). This separated plots 2, 108, 109, 118, 119, 129.
- plots where the highest stratum was built up by more than one emergent but less than five individuals (criterion 2), where the coverage of the highest stratum was not higher than 30% (criterion 3) and where the distance between stems of the trees of the highest stratum was at least 3 m (criterion 4). This separated plots 7, 107, 110, 117, 125.

These two groups included all the plots that did not integrate in the former cluster analysis (except plot 131) and even the outlier 119. This fact led to the conclusion that the sparse density of the highest stratum and the unavoidable lack of structural features if only one single tree builds the whole stratum could explain why these plots could not be arranged into groups in the cluster analysis. In these plots, the dense canopy was the middle stratum. Taking this into account, the cluster analysis was repeated using the data of the middle stratum for plots 2, 7, 107, 108, 109, 110, 117, 118, 119, 125, 129 and ignoring the formerly used data of the highest stratum. This led to the result shown in Figure 14. All plots were arranged into twelve groups, only plots 70 and 122 were added at the bottom.

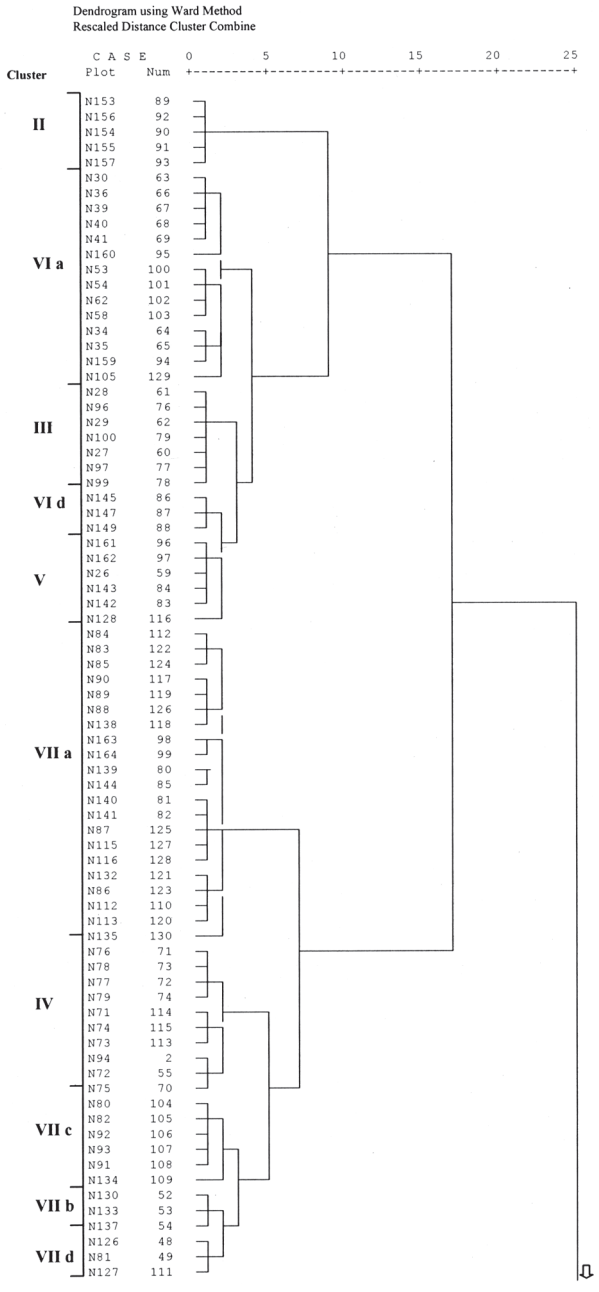


Figure 14: Cluster dendrogram for 129 plots with more than one stratum. Continued on next page.

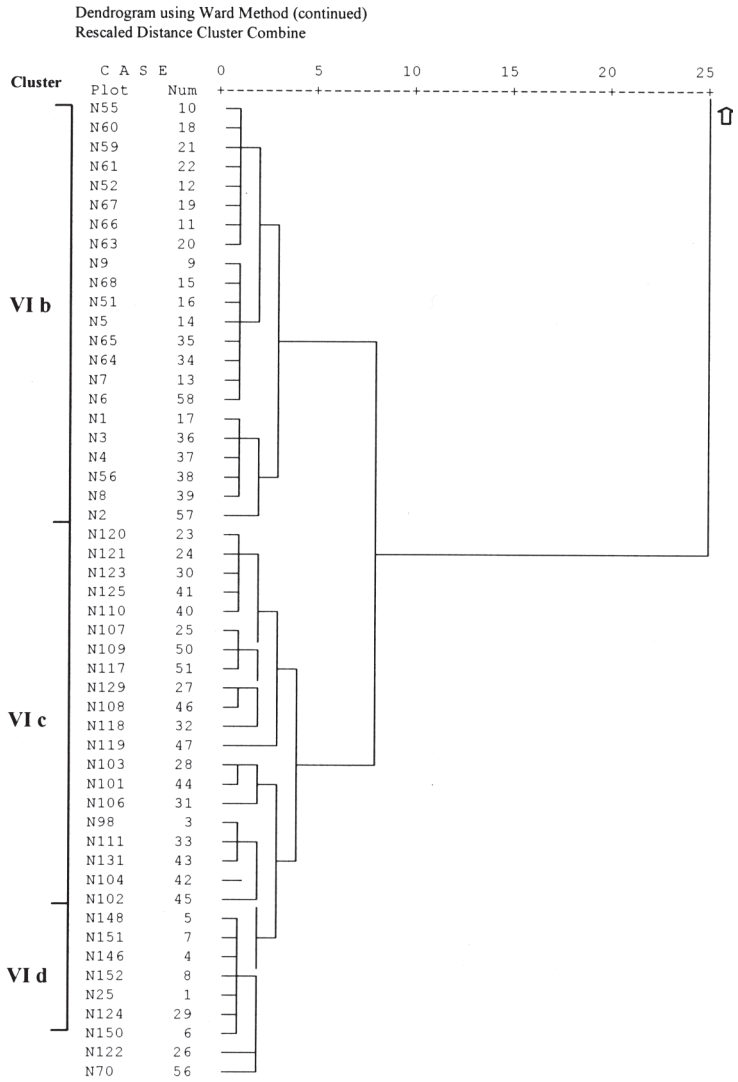


Figure 14 (continued): Cluster dendrogram for 129 plots with more than one stratum.

Together with the plots with only one stratum, all 139 plots could thus be divided into 14 groups as listed in Table 7 (p. 70). 129 plots were grouped by cluster analysis, ten had to be added by hand. This will be explained in the detailed description of each group (see below).

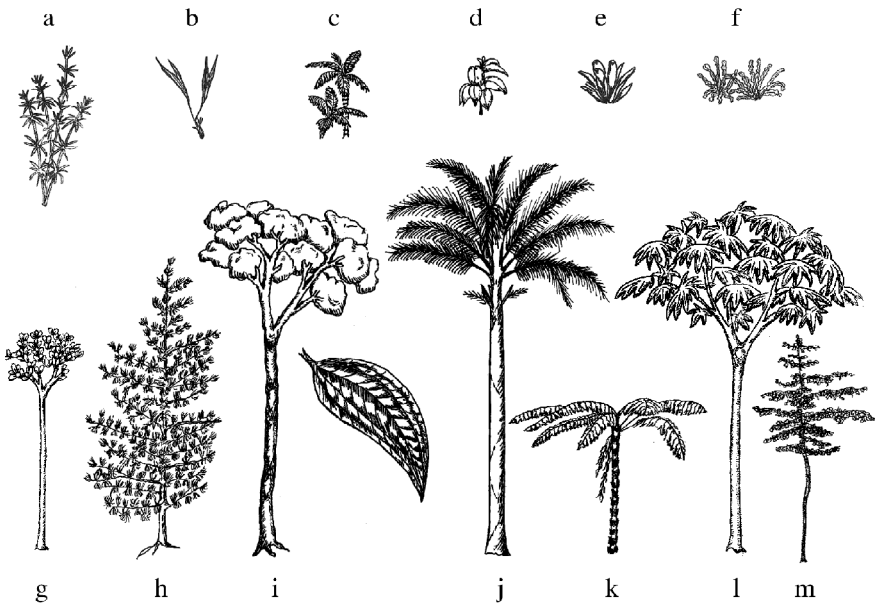
Table 7: Distribution of 139 plots in 14 structural forest types. For description see text.

Cluster	Plots from cluster analysis	Additional plots	Number of plots	Structural forest type
I a	32, 33, 38		3	Secondary growth after road construction
I b	37, 57, 158		3	Secondary growth after landslide
II	153, 154, 155, 156, 157		5	Plantation of *Pinus patula*
III	27, 28, 29, 96, 97, 99, 100	98	8	Secondary forest in Mindo
IV	71, 72, 73, 74, 75, 76, 77, 78, 79, 94	70, 95	12	Primary forest in Cajanuma
V	26, 128, 142, 143, 161, 162		6	Forest on edges of natural gaps
VI a	30, 34, 35, 36, 39, 40, 41, 53, 54, 58, 62, 105, 159, 160		14	Secondary ravine forest
VI b	1, 2, 3, 4, 5, 6, 7, 8, 9, 51, 52, 55, 56, 59, 60, 61, 63, 64, 65, 66, 67, 68		22	Ravine forest under human influence
VI c	101, 102, 103, 104, 106, 107, 108, 109, 110, 111, 117, 118, 119, 120, 121, 123, 125, 129, 131	122	20	Primary ravine forest at lower altitude
VI d	25, 124, 146, 148, 150, 151, 152	145, 147 149	10	Primary ravine forest at higher altitude
VII a	83, 84, 85, 86, 87, 88, 89, 90, 112, 113, 115, 116, 132, 135, 138, 139, 140, 141, 144, 163, 164	114	22	Microphyll ridge forest
VII b	130, 133, 137		3	Mesophyll ridge forest
VII c	80, 82, 91, 92, 93, 134		6	Macrophyll ridge forest
VII d	81, 126, 127		3	Megaphyll ridge forest
Exceptions		31, 136	2	Exceptional plots
Sum	129 plots	10 plots	139 plots	

For each group a T-value was calculated for each variable to detect which variables (i.e. structural characters) were over- or under-represented in each group (see Material and Methods). Per definition, a variable is over-represented if the T-value is positive and under-represented if the T-value is negative. This was true for nearly every variable. To provide an interpretation, a deviation from zero had to defined which made over- or under-representation significant. /0.7/ was chosen as a criterion. For all cluster groups, Table 8 lists those structural characters that showed a T-value > /0.7/. Over-representation is marked with + while under-representation is marked with -. (The complete set of mean values, standard deviations and T-values for all variables in all cluster groups is listed in the appendix).

In the following, all groups will be described in detail and be interpreted. Each group will be classified and named as a structural forest type. The description refers to the data listed in Table 7 and Table 8. All strata of each structural forest type will be described separately, always beginning with the

highest stratum, followed by the middle stratum and the undergrowth. The location of each plot can be seen in Figure 4 (p. 48). For most of the structural forest types, a profile was drawn in one of the included plots. All profiles refer to a 20 m long and 1 m wide strip. Elements that appear repeatedly in different profiles are shown in Figure 15. Due to canopy height, the scale for height had to be halved compared to the scale for length in all profiles. Only the profile of plot 8 has a different scale, because it was based on data from AXMACHER 1998.



a. Bambusoideae, b. Cyclanthaceae, c. Cyatheales, d. *Solanum quitoense* LAM., e. Bromeliaceae, f. Phyllitis, g. Clusiaceae, h. *Pinus patula* SCHIEDE & DEPPE, ex SCHLECHT, i. Melastomataceae, j. Arecaceae, k. Cyatheales, l. Cecropia, m. Podocarpaceae

Figure 15: Elements that appear repeatedly in the profiles (Illustration by Dziedzioch)

Table 8 (following pages): Structural characters with T-value >/0.7/ for canopy stratum (high) and undergrowth stratum (low) for all cluster groups. Over-representation is marked with + while under-representation is marked with -.

Cluster		II	II	III	III	IV	IV	V	V	VI a	VI a	VI b	VI b	VI c	VI c	VI d	VI d	VII a	VII a	VII b	VII b	VII c	VII c	VII d	VII d
Stratum		**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**
Number of trees																									
Ground cover		+	-	+			-	+										-	+			+			
Diameter at breast height								-	+	-		+		+				-				-			
Height of stratum		-		+	+							+		+				-				-			
Height of lowest branch		-					-					+		+		+	-	-				-			
Height of main ramification		-								-				+		+		-				-			
Distance between stems		-	+																			-			
Distance between crowns		-	+																			-			
Woodiness	axylous																		-						+
	hemixylous		+		+												+		-						
	holoxylous																				-				
Stem characters	polycormous		+						-												+		+		
	vertical		-																	-	-	-	-		
	diagonal	-				+	-													+	+	+	+	+	+
	dead															+	-		+		+				+
Bark characters	green thin smooth		-														+								+
	green thin rough																								
	green thick smooth																								
	green thick rough																								
	non-green thin smooth		+							+	+											-			
	non-green thin rough	-			-						-	-	-		+						+		+		
	non-green thick smooth																								
	non-green thick rough	-			+	+						+				+			+			+			
	non-green very thick rough	+																							
	flaky							+	+											+					
Roots	tabulate roots																								
	stilt roots															+								+	+
	aerial roots																								
Crown volume	restricted to top		-		+						-										+			+	+
	restricted to upper third	-	+						+																
	restricted to upper half		-						-														+		
	reaching deeper than half	+	-																		+				
Crown developement	full		-											-								-	-		
	restricted by neighbours		+											+								+	+		
	stunted					+															+		+		+

Cluster		II	II	III	III	IV	IV	V	V	VI a	VI a	VI b	VI b	VI c	VI c	VI d	VI d	VII a	VII a	VII b	VII b	VII c	VII c	VII d	VII d
Stratum		high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low
Crown shape	round																								
	umbrella-shaped	-		+	-														+						
	cylindrical		-																						+
	conical	+																							
	funnel-shaped/umbelliferous		-		+																+	+		+	+
	fanshaped																			+	+		+		+
	irregular		+	-			-		+			-													
Crown overlap	Type 1	-		-																					
	Type2	-	-													+									
	Type 3	+	-	+					-												+	+			
Branches	mostly horizontal	+													+										+
	mostly diagonal	-																							
	mostly vertical															+			+						
	dead		+	+		+				-	-	+	-						+	+	+	+	+		
	missing		-		+						-									+		+		+	
Branching pattern of terminal 20cm	Type 1	-		+	+	-				+		+	-			-				-					
	Type 2	+			-	+						-				+				+					
	Type 3	-	-			+			-				+				-	+	+		-				
Leaf shape	simple	-											-												-
	narrow leaved	+																	+						+
	palmately lobed		-	+	-			+															+		+
	compound		-		+	+					-													+	
	other																		+						+
	absent																								
	drip tips	-		+																					
Leaf consistency	hymenophyll																								
	malacophyll	+		+		-		+						+		+		-	-	-		-	-		
	semi-sclerophyll	-	-	-	-	+			-									+	+	+	+	+	+	+	
	sclerophyll																								
	semi-succulent																	+	+				+	+	
	succulent																								
Leaf colour	green																					-			
	red																								
	bicoloured																		+			+			+

Cluster		II	II	III	III	IV	IV	V	V	VI a	VI a	VI b	VI b	VI c	VI c	VI d	VI d	VII a	VII a	VII b	VII b	VII c	VII c	VII d	VII d
Stratum		**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**	**high**	**low**
Leaf phenology	evergreen																								
	decidious																								
Leaf size	sub-leptophyll																								+
	leptophyll																								+
	nanophyll	+	+																+						
	nano-microphyll																	+	+						
	microphyll																					+		+	
	micro-mesophyll	-	+	-	-	+														+					+
	mesophyll	-		+													+								
	macrophyll	-	-																	-		+			+
	megaphyll		-	+	+																			+	
Leaf length	<1cm																		+						
	up to 2cm					+													+						
	up to 5cm	-		-						-								+	+	-		+	+	+	
	up to 10cm	-	+	-	-															+	+				+
	up to 20cm	+															+								
	up to 50cm	-	-					+												-	+		+		+
	>50cm		-	+	+																			+	
Leaf width	<1cm	+																	+		+	+			
	up to 2cm																	+	+						
	up to 5cm	-	+	-		+						-	-							+	+			+	+
	up to 10cm	-										+						-			-	-			
	up to 20cm	-	-																	-		+			
	up to 50cm	-	-					+											+	-	+				
	>50cm		-	+	+														-					+	
Leaf angle	mainly hanging down	+							+				-								+		+	+	+
	mainly horizontal	-	+	+			-								+			-	-	-					
	mainly between horizontal and 45°	-	-		-	+																			
	mainly steeper than 45°																	+	+			+			
Spinescence	spines on stem												+												
	spines on branches																								
	spines on leafs				+																			+	+
Hairiness	hairs on stems												+												+
	hairs on branches																				+		+		

Cluster		II	II	III	III	IV	IV	V	V	VI a	VI a	VI b	VI b	VI c	VI c	VI d	VI d	VII a	VII a	VII b	VII b	VII c	VII c	VII d	VII d
Stratum		high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low
Hairiness	hairs on leafs				-			+													+		+		
Epiphytic lichens	crustose lichens				-							-	-						+		+		+		
	foliose lichens	-		-	-	+						-							+	+	+				
	shrubby lichens																								
	beard-like lichens					+						-				-		+	+	+	+	+	+	+	+
Epiphytic mosses	on stem	-	-		+					-	-		-								+				
	on branches	-	-							-															
Epiphytic ferns	on stem	-	-						-	-										+	+		+	+	+
	on branches	-				+				-										+		-		+	
Woody epiphytes	on stem	-				+				-		-							+	+			+	+	
	on branches					+													+	+					
Epiphytic Araceae	on stem			+	+											+				+					
	on branches																							+	
Epiphytic bromeliads	on stem	-	-													+							+	+	+
	bromeliads in branching	-		-		+													+	+					
	in vertical branches																								
	on diagonal branches	-										-							+	+					
	on horizontal branches				+														+			+			
	on dead branches	-		-																+					
	on ground																								
Epiphytic orchids	on stem	-	-		+			+		-	-								+		+		+	+	+
	in branching	-				+																			
	on vertical branches																								
	on diagonal branches	-										-							+						
	on horizontal branches																								
	on dead branches	-				+																			+
Mixed accumulation	on stem																		+	+				+	
of epiphytes	in branching					+														+					
	on vertical branches																								
	on diagonal branches									+														+	
	on horizontal branches																								
	on dead branches																								+
Sum of vascular	none	+								+															
epiphytes	some	-	-	+	+			+			-								+	-	+		+		+
	many	-				+				-										+			+		+

Cluster		II	II	III	III	IV	IV	V	V	VI a	VI a	VI b	VI b	VI c	VI c	VI d	VI d	VII a	VII a	VII b	VII b	VII c	VII c	VII d	VII d
Stratum		high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low	high	low
Connecting elements	lianas on stem	-	-															-		+	+		+		+
	lianas in tree crown	-	-											+						+	+		+		
	lianas connecting stems		-		-				-					+							+		+		+
	lianas connecting crowns		-	+					-					+							+		+		
	bamboo on stem		-		-	+	+		+											+		+	+	+	
	bamboo in tree crown		-		-		+		+											+	+	+	+		
	bamboo connecting stems		-		-	+	+		+											+	+	+	+		
	bamboo connecting crowns		-				+														+	+	+		
Conspicuous life-forms	climbers		-	+	+							-				+	+			+		+			
	stranglers													+											
	Arecaceae		-				-												+			+		+	+
	Araceae				+																				
	Cyatheaceae		-		+			+																	+
	Cyclanthaceae																		+				+		+

3.4.2.1 Secondary growth after road construction (Cluster I a)

The three plots of cluster I a (32, 33, 38) were located directly on the upper road bank of the main road at an altitude between 1800 m a.s.l. and 2060 m a.s.l.. Their vegetation consisted of only one stratum of woody plants with 25-50 individuals covering 70% which were no higher than 10 m. Trees had dbh less than 10 cm and the distance of the irregular or umbrella-shaped crowns was closer than 1 m. The malacophyll leaves were micro-mesophyll for most of the trees; only palms and treeferns had macrophyll leaves. Vascular epiphytes were lacking but the individual trees were connected by lianas and much bamboo.

From the location of the plots and the lack of any higher or thicker trees, it was concluded that the vegetation of these plots had to be considered as secondary and that it had been strongly influenced (if not completely disturbed) by the construction of the road. Hence this vegetation type was called secondary growth after road construction. Figure 16 shows a profile of plot 38.

Figure 16: Profile of Secondary growth after road construction (Cluster I a) of Plot 38 (Illustration by Dziedzioch)

3.4.2.2 Secondary growth after landslides or clearing (Cluster I b)

As in cluster I a, the three plots of cluster I b (37, 57, 158) had only one stratum of woody plants. Although tree height was less than 5 m, vegetation cover was higher (80%) due to the higher number of individuals (50-100). Distance of the cylindrical or irregular crowns was also less than 1 m and the dbh less than 10 cm. Leaf size and consistency were also comparable except for a higher percentage of mesophyll leaves. Vascular epiphytes were lacking and individual trees were only rarely connected by lianas and bamboo.

The plots were located on still obvious landslides (57, 158) or under a high voltage line (37) and therefore recently cleared. They could be classified as secondary growth after landslides or clearing at an altitude of 1920-2040 m a.s.l.. Figure 17 shows a profile of plot 37.

Figure 17: Profile of Secondary growth after landslides or clearing (Cluster I b) of Plot 37 (Illustration by Dziedzioch)

The differentiation between the two clusters was mainly based on the fact that in cluster I b the individual plants were smaller but more numerous and had cylindrical crowns. This might be the consequence of a more recent disturbance and therefore younger and less developed trees.

The six plots of cluster I (a and b) differed from all other plots by consisting of only one stratum and by being obviously disturbed (no higher or thicker trees, no epiphytes, partly much bamboo). Their vegetation could not be called secondary forest but only secondary growth because many of the woody plants were bushes and not trees. Hence the two clusters were not structural forest types in the narrower sense of the word and the difference compared to the other clusters was much greater than that between clusters I a and I b.

3.4.2.3 Plantation of Pinus patula *(Cluster II)*

The **canopy stratum** of the five plots of cluster II (153-157) consisted exclusively of individuals of *Pinus patula* planted at a density of 25-50 trees per plot at an altitude of 1930-2000 m a.s.l.. Canopy height was up to 15 m and dbh reached 20-30 cm. The distance of the conical crowns was less than 1 m which led to a coverage of 90%. The malacophyll leaves (needles) were narrow and pendant. The trees had no vascular epiphytes and were not connected by lianas or bamboo.

The sparse **undergrowth stratum** reached only 10-20% coverage with 3-6 m distance between the irregular crowns. The thin trees (dbh less than 10 cm) had no vascular epiphytes, bamboo was lacking and connecting lianas were rare. The malacophyll and simple leaves were micro-mesophyll and were held horizontally. Figure 18 shows a profile of plot 156.

The plots of cluster II had a high number of over- or under-represented characters which separated them from the other clusters: The high density of the plantation resulted in the highest coverage of the canopy stratum and an under-representation of the distance between crowns and stems in that stratum. The typical shape of the conifers led to an over-representation of conical crowns, of horizontal branches, and of a crown volume reaching deeper than half of the tree height. Consequently, the characters describing an "average" canopy tree of a tropical montane forest were under-represented (crown volume restricted to upper third, crown umbrella-shaped, branches mostly diagonal, compare e.g. cluster VI c). The needles of the *Pinus*-trees fell into the categories narrow and nanophyll which were over-represented, while larger leaf sizes and broader leaf widths were under-represented. The complete lack of vascular epiphytes led to under-representation in nearly all characters describing the distribution of orchids and bromeliads. Even mosses were missing.

The high density of the canopy stratum allowed only a sparse undergrowth so that ground cover was under-represented while distance between stems and between crowns was greater than in other forest types.

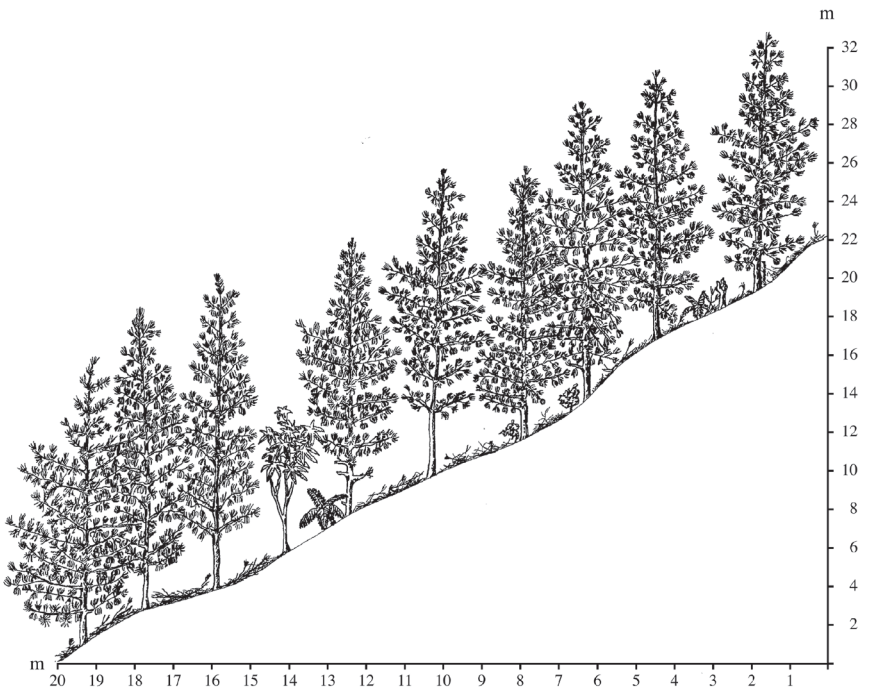


Figure 18: Profile of a Plantation of Pinus patula *(Cluster II) of Plot 156 (Illustration by Dziedzioch)*

Hence the plots of cluster II were separated from the other clusters by the uniformity and high density of a planted monoculture of an imported tree species. The difference is extremely large due to the fact that conifers are rare in the natural forests of that region (except *Podocarpaceae*).

3.4.2.4 Secondary forest in Mindo (Cluster III)

To test the applicability of the system, eight plots were placed in a 18-year-old secondary forest north of Quito close to the village of Mindo at an altitude of 1570-1620 m a.s.l. (see Material and Methods). Seven of these plots were grouped in Cluster III by cluster analysis (27-29, 96, 97, 99, 100). Plot 98 fell into cluster VI c.

The **canopy stratum** was up to 25 m high and 5-25 trees per plot led to a coverage of 70-80% with a crown distance of less than 1 m. Dbh was 40-50 cm. Most of the crowns were umbrella-shaped, the mesophyll or megaphyll leaves were simple or palmately lobed and of malacophyll consistency. They were held mostly horizontally or at an angle up to 45°. The trees had some

vascular epiphytes and were partly connected by lianas or bamboo and often hosted climbers.

In comparison to all other plots, canopy height and umbrella-shaped crowns were over-represented. Also megaphyll leaves and branching pattern type 1 (i.e. only leaves on the terminal 20 cm of a branch) were over-represented. These characters, together with the palmately lobed leaves, are typical for the genus *Cecropia* whose members are known as pioneer trees in secondary forests. Of the vascular epiphytes, *Araceae* were over-represented.

The **lower stratum** was 5-10 m high and 25-50 trees per plot covered 50-60%. The stems had a diameter of less than 10 cm and crown distance was 3-6 m. Most of the crowns had an irregular shape or were funnel-shaped. The simple or compound leaves were meso-, macro- or megaphyll and of malacophyll consistency and were held horizontally or at an angle of up to 45°. As in the canopy stratum, most trees hosted some vascular epiphytes and were partly connected by lianas or bamboo. Climbers were conspicuous. The height of the lower stratum and the number of trees with a crown volume restricted to the top were over-represented as well as trees without branches, branching pattern type 1 and megaphyll leaves. These characters are typical for treeferns which were more numerous than in other forest types. Figure 19 shows a profile close to plot 96. Hence the secondary forest of Mindo could be described by structural characteristics that correspond to a high percentage of *Cecropiaceae* in the canopy stratum and many members of the *Cyatheaceae* in the lower stratum. In Table 7 (p. 70), plot 98 is added to cluster III because it was located in Mindo and thus at an elevation 200 m lower than the lowest plots in the main investigation area. Plot 98 was the only plot with three strata within the eight plots of Mindo, canopy height was 30 m and some canopy trees had a dbh of 60 cm. This explains the exceptional status of plot 98 and the similarity to the plots of cluster VI c.

3.4.2.5 Primary forest in Cajanuma (Cluster IV)

In addition to the above-mentioned plots of Mindo, a series of 12 plots was located outside the main investigation area. These plots were placed in the Podocarpus National Park at an elevation of 2700-3100 m a.s.l. and thus at least 100 m higher than the highest plots in the main area. Ten plots (71-79, 94) were grouped in Cluster IV by cluster analysis, one plot (70) was added at the end of the dendrogram and one plot (95) was already identified as an outlier in the first step of analysis.

The **canopy stratum** was only 10-15 m high, 5-25 trees per plot covered 40-50% and crown distance was 1-3 m. Trees had a dbh of 40 cm and mostly irregular or umbrella-shaped crowns. The simple or compound leaves were

micro-mesophyll, had a semi-sclerophyll consistency and were held horizontally. All trees had many vascular epiphytes, some were connected by lianas and many were connected by bamboo.

Figure 19: Profile of Secondary forest in Mindo (Cluster III) close to Plot 96 (Illustration by Dziedzioch)

The number of diagonal stems, stunted crowns and dead branches was over-represented. Branching pattern type 3 (i.e. branching more than twice on the terminal 20 cm), compound and semi-sclerophyll leaves and leaf length less than 2 cm were also over-represented. These structural characteristics all correspond to trees of the genus *Weinmannia* (*Cunoniaceae*) which contributed conspicuously to the canopy stratum. Also epiphytic mosses and ferns had a higher coverage than the average of other forest types.

In the **lower stratum** of 1-5 m height, 50-100 individual trees per plot led to a coverage of only 40% and crown distance was 3-6 m. The trees with dbh less than 10 cm had cylindrical, umbrella-shaped or irregular crowns and showed the same leaf characteristics as the canopy stratum. Only vascular epiphytes were lacking in the lower stratum. Bamboo, as connecting element between stems and tree crowns, was over-represented.

The primary forest of the ridge of Cajanuma could be described as an elfin forest where trees were small, stunted or with diagonal stems, where cover-

age of epiphytic mosses and vascular epiphytes was high for the canopy stratum which consisted partly of members of the genus *Weimannia*. The lower stratum had a comparably low coverage of woody plants but bamboo was omnipresent, overgrowing young trees and filling gaps.

Plot 95 was identified as an outlier by the cluster analysis due to a combination of characters of the canopy stratum that was not repeated in any other plot. The dense canopy covered 80% and was dominated by nano-microphyll leafs of semi-succulent consistency. Most of the trees were covered with mosses and had dead branches. The undergrowth was dominated by treeferns. As it was refused to base an extra forest type on just one single plot, plot 95 was added to cluster IV due to its location and the characters it had in common with the other plots of this cluster (low trees with irregular shaped crowns, dense moss cover, bamboo in the undergrowth). Nevertheless the vegetation of plot 95 has to be seen as a special case, perhaps marking a transition to another (undetected) forest type or representing a stage of succession.

3.4.2.6 Forest on edges of natural gaps (Cluster V)

In cluster V, six plots (26, 128, 142, 143, 161, 162) were grouped together that have no common location. Two plots were located on the river bank of the Rio San Francisco (142, 143) at 1850 m a.s.l. while three plots (26, 161, 162) were close to natural gaps caused by fallen trees at 1870 m a.s.l. and 2130 m a.s.l. respectively. Plot 128 was located in the uppermost part of a small ravine at 2540 m a.s.l..

The **canopy stratum** consisted of 5-25 trees per plot and covered 70-80%. Trees were 10-15 m high and had a dbh of 20-30 cm. The umbrella-shaped or irregular crowns had a distance less than 1 m, leaves were simple or palmately lobed. Leaf sizes could be micro-meso, meso,- or macrophyll and leaf consistency was malacophyll. Leaves were held up to an angle of 45°. Only some trees hosted vascular epiphytes or were connected by lianas or bamboo.

The analysis of T-values did not reveal many characters differing from the average, only ground coverage was over-represented while diameter at breast-height was under-represented.

The **lower stratum** was built up by 25-50 individuals per plot and reached a height of 1-5 m with a coverage of 50%. The distance of the irregular or funnel-shaped crowns was less than 1 m, the dbh was less than 10 cm except for a few stems up to 20 cm thick. The mesophyll or macrophyll leaves were simple or compound, of malacophyll consistency and held horizontally or up to an angle of 45°. There were virtually no vascular epiphytes but some lianas

and much bamboo. Bamboo as a connecting element was over-represented in this stratum.

Hence the forest type of the plots combined in cluster V was named forest on edges of natural gaps and was characterised by comparatively thin trees building a dense canopy at a low height. The conspicuously high percentage of palmately lobed and macrophyll leaves was caused by the presence of *Cecropia*-trees as in cluster III. Fast growing trees and much bamboo in the undergrowth might be interpreted as a pioneer stadium after treefall favoured by a sudden and high amount of sunlight. In case of the plots directly located at the bank of the Rio San Francisco, the gap situation will be renewed by frequent high waters and thus the pioneer stadium may be stable over longer periods.

3.4.2.7 Secondary ravine forest (Cluster VI a)

Cluster VI a combined 14 plots (30, 34-36, 39, 40, 41, 53, 54, 58, 62, 105, 159, 160) which were all located in the lower part of the investigation area at elevations between 1820 m a.s.l. and 1870 m a.s.l.. As shown in Figure 4 (p.49), the plots could be divided according to their location along small tributaries of the Rio San Francisco. Plots 39, 40, and 41 were located in one quebrada; 34, 35, 159, and 160 in another. Both quebradas originated at the north side of the street. Plots 53, 54, 58, 62, and 105 were all located close to the channel leading to the hydroelectric plant. Plots 30 and 36 belonged to small forest patches on the northern side of the street.

The **canopy stratum** reached only 10-15 m in height and 5-25 trees per plot covered 50%. Trees had a dbh of 20-30 cm and the umbrella-shaped crowns had a distance of 1-3 m. The mostly simple leaves were meso- or macrophyll and of malacophyll consistency. The leaf angle was horizontal or up to 45°. Some trees had vascular epiphytes but connecting elements were lacking. Compared to the canopy layer of all other plots, the diameter was under-represented and the coverage of epiphytic mosses or ferns extraordinarily low.

In the **lower stratum** of 1-5 m height, 50-100 individuals per plot reached a ground cover of 60%. Stems had a diameter less than 10 cm and the irregular, umbrella-shaped or cylindrical crowns had a distance less than 1 m. Leaves were smaller than in the canopy layer (micro-mesophyll), vascular epiphytes were absent and connecting elements rare.

From the low canopy height (compared to plots at the same elevation in cluster VI b and VI c) and the lack of thick trees, it was concluded that the forest had to be considered as secondary. The location of the plots close to the street or the channel made human influence also highly probable. The

lack of epiphytic mosses and ferns that led to a separation of this cluster could be explained by the comparatively dry conditions: the low coverage of the canopy (only 50%), the low altitude with high temperatures, less rain and less mist hindered the growth of mosses on stems and branches.

Considering the location of many plots along quebradas, the forest type of cluster VI a was termed secondary ravine forest. Figure 20 shows a profile of plot 36 while Figure 21 shows the special situation in plot 53: Here the canopy stratum was extremely sparse and the fern *Pteridium aquilinum* had invaded most of the plot.

Figure 20: Profile of Secondary ravine forest (Cluster VI a) of Plot 36 (Illustration by Dziedzioch)

3.4.2.8 Ravine forest under human influence (Cluster VI b)

In cluster VI b, 22 plots were grouped together (1-9, 51, 52, 55, 56, 59, 60, 63-68). All of them had three strata. The plots were located close to the channel or along one single quebrada at an altitude between 1820 m a.s.l. and 1970 m a.s.l.. From all quebradas that could be waded and investigated, this one was the widest and the most water-shedding.

Figure 21: Profile of Secondary ravine forest (Cluster VI a) of Plot 53 (Illustration by Dziedzioch)

The **canopy stratum** covered 50% and consisted of only 1-5 trees per plot reaching a height of 20-25 m. The trees had an dbh of 50-60 cm, the umbrella-shaped crowns had a distance of 1-3 m. The simple and micro-mesophyll leaves were malaco- or semi-sclerophyll and were held in an angle up to 45° or horizontally. Some trees had vascular epiphytes or were connected by lianas whereas bamboo was missing. In comparison to all other plots, the canopy height, the height of the lowest branch, the diameter, and the branching pattern type 1 were over-represented.

The **middle stratum** comprised 5-25 trees per plot and covered 60% at a height of 10-15 m. The stems had a dbh of 20-30 cm and the irregular or umbrella-shaped crowns had a distance of 1-3 m. Leaf characteristics and connecting elements resembled those of the canopy stratum.

In the **lower stratum** 50-100 trees per plot covered 60% attaining a height of 1-5 m. Trees had a dbh less than 10 cm and crown distance was less than 1 m. The crowns were irregular or funnel-shaped, the leaves simple or compound. Dominating leaves sizes were micro-mesophyll and megaphyll and the leaves had a malacophyll or sometimes sclerophyll consistency. While

vascular epiphytes were nearly absent, some tree individuals were connected by lianas or bamboo. The megaphyll leaves belonged mostly to treeferns.

Compared to the secondary ravine forest of cluster VI a, the forest type of cluster VI b was clearly distinguished by higher and thicker trees in the canopy stratum that consisted of fewer individuals. Nevertheless, giant emergent trees with a dbh of more than 80 cm were lacking (compare cluster VI c). The quebrada considered here was the only one easily accessible by an ancient footpath and the remnants of felled trees (in particular giant *Podocarpaceae*) could be found. It was concluded that in contrast to cluster VI a, the forest was not a secondary one but that selective logging and the disturbance caused by transporting the felled trees led to a distinguishable forest type termed ravine forest under human influence. Figure 22 shows a profile of the extremely inclinated plot 8.

3.4.2.9 Primary ravine forest at lower altitude (Cluster VI c)

Cluster VI c combined 19 plots (101-104, 106-111, 117-121, 123, 125, 129, 131), all located along small tributaries in the lower part of the investigation area at an elevation of 1840- 2030 m a.s.l. (except 117 at 2250 m a.s.l.) and all consisting of three strata.

In the **canopy stratum**, 1-5 individual trees covered 40-50%. The irregular or umbrella-shaped crowns had a distance less than 1 m. The canopy reached an average height of 25-30 m with trees of 60 cm dbh but single emergent trees grew 35-40 m high and had a dbh of 130 cm. The simple and malacophyll leaves were of micro-mesophyll or mesophyll size and were held horizontally or up to an angle of 45°. Most of the trees had some vascular epiphytes and some were connected by lianas or bamboo. In the whole investigation area, no trees higher or thicker than the canopy trees of cluster VI c could be found. Hence the characters height of stratum, height of lowest branch, height of main ramification and dbh were over-represented.

The **middle stratum** at a height of 10-15 m consisted of 5-25 trees per plot and covered 60%. The stems had a dbh of 20-30 cm and the irregular or umbrella-shaped crowns had a distance less than 1 m. Leaf characteristics resembled the canopy stratum but macrophyll leaves and those leaves with a semi-sclerophyll consistency were more abundant.

In the **undergrowth stratum**, 50-100 individuals per plot grew to a height of 1-5 m and covered 50%. The average crown distance was less than 1 m and the stems did not reach more than 10 cm dbh. Compared to the upper strata, funnel-shaped crowns and macrophyll and compound leaves were more abundant. This result corresponded with a high percentage of *Cyatheaceae*.

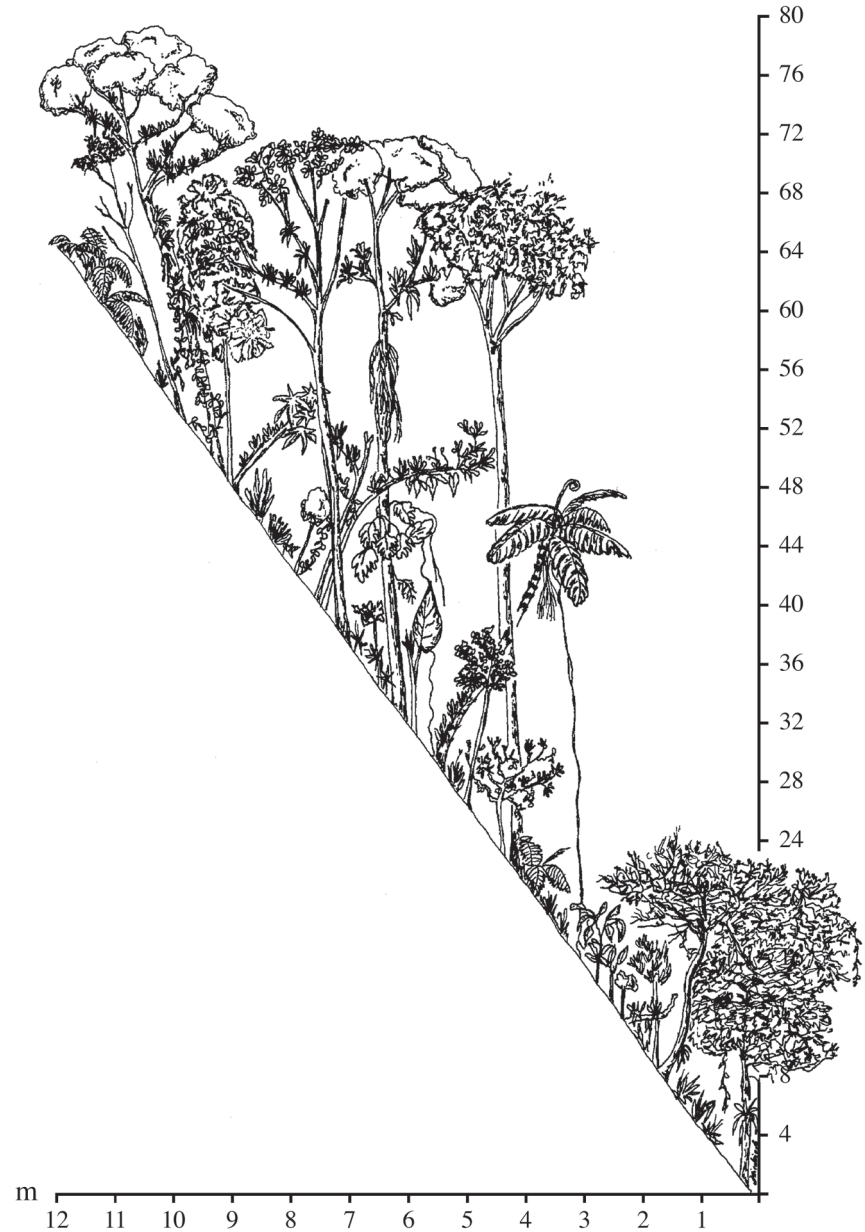


Figure 22: Profile of Ravine forest under human influence (Cluster VI b) of Plot 8. (Illustration by Dziedzioch based on Axmacher 1998)

As mentioned at the beginning of this chapter (p. 67), 11 plots could not be grouped in the original cluster analysis, but the data for the canopy stratum

had to be replaced by the middle stratum. Nine of these plots then fell into cluster VI c (107-110, 117, 118, 125, 129); only two were grouped into cluster VI b (2, 7). These 11 plots had been separated by the criteria that the canopy was only built by one emergent or less than five individuals which covered less than 30%. Now these plots fell into the cluster where height characteristics of the canopy stratum and comparatively thick stems were over-represented. Furthermore the nine plots grouped into cluster VI c were located in the direct neighbourhood of the rest of the plots of this cluster, whereas the two plots grouped into cluster VI b were located close to the channel like other plots in that cluster. Hence these results could be seen as a justification for the replacement of tree strata as mentioned above.

Plot 117 was an exception inasmuch as it was located at a higher altitude and on a ridge, but exactly at that point the ridge crossed a depression, marking the uppermost point of a quebrada. Plot 122 was not grouped by cluster analysis but added at the end of the dendrogram due to a rare combination of characters: although the canopy and middle stratum resembled those of the other plots of cluster VI c, the undergrowth was much denser (80% coverage) and was dominated by bamboo. Especially where an ancient footpath crossed the plot, bamboo was dense. Although the undergrowth stratum thus was untypical, plot 122 was placed into cluster VI c because of the resemblance of the upper strata. Its location amidst the other plots of this cluster also favoured this decision.

The forest type of cluster VI c contained the highest and thickest trees of the whole investigation area and had the highest percentage of emergent trees, partly the economically valuable *Prumnopitys montana* (Humb. & Bonpl. Ex Willd.) de Laub (*Podocarpaceae*). This supported the conclusion that this forest could still be called primary ravine forest or at least showed less human influence than the forest type of cluster VI b at the same altitude and with otherwise similar structural characteristics. Figure 23 shows a profile close to the plots 104 and 131.

3.4.2.10 Primary ravine forest at higher altitude (Cluster VI d)

Cluster VI d combined seven plots (25, 124, 146, 148, 150-152). Five of them (except 25, 124) were located in the upper part of the quebrada El Milagro and thus at the highest altitude where a quebrada could be reached (2180-2280 m a.s.l.). They all consisted of three strata.

The **canopy stratum** was 20-25 m high and 5-25 trees per plot covered 50-60%. The dbh was 40 cm, the irregular or umbrella-shaped crowns had a distance of 1-3 m. The simple and malacophyll leaves were held horizontally or at an angle of 45° and had mesophyll or micro-mesophyll sizes. Most in-

dividual trees hosted some vascular epiphytes, connecting elements were rare or absent, climbers conspicuous. The height of the lowest branch, the height of main ramification and branching pattern type 2 were over-represented. The percentage of standing dead trees was higher than average and stilt roots were abundant.

Figure 23: Profile of Primary ravine forest at lower altitude (Cluster VI c) close to Plot 104 (Illustration by Dziedzioch)

In the **middle stratum**, 5-25 trees per plot grew 10-15 m high and covered 40%. The stems had a diameter of 10-20 cm, crowns had a distance of 1-3 m. Crown and leaf characteristics resembled the canopy stratum but funnel-shaped crowns, compound and megaphyll leaves were more abundant. This corresponded with the higher percentage of palms and treeferns. Some trees were connected by lianas or bamboo.

In the **lowest stratum**, 50-100 trees of 1-5 m in height covered 50-60%. The trees did not reach diameters greater than 10 cm, crown distance was less than 1 m. Cylindrical crowns co-dominated with irregular or funnel-

shaped ones. Leaf characteristics were similar to the middle stratum, but vascular epiphytes were rare whereas *Cyatheaceae* and climbers were conspicuous. Hemixylous individuals with a green thin and smooth bark were overrepresented. They belonged partly to the *Piperaceae*.

Plot 124 was located at 2080 m a.s.l. in the uppermost part of the quebrada where the plots of cluster VI b were situated. It lay beyond the end of the ancient footpath and higher than the last obviously felled tree. Hence it might be located beyond the line of human influence in that quebrada.

Plot 25 was located at 1830 m a.s.l. on a slope between the channel and the Rio San Francisco. Although it was not situated in a quebrada, the structural characteristics resembled those of the other plots of cluster VI d.

Three plots (145, 147, 149) that were located in the quebrada El Milagro, consisted of only two strata. In the cluster dendrogram, they were grouped together and were placed close to the "Forest on edges of natural gaps" of cluster V. Their vegetation showed similarities to both, cluster VI d and cluster V. They were added to cluster VI d, although their location directly on the bank of the quebrada also was a kind of edge-of-gap situation.

Figure 24: Profile of Primary ravine forest at higher altitude (Cluster VI d) of Plot 150 (Illustration by Dziedzioch)

Compared to the primary ravine forest of cluster VI c at an altitude of 1840-2030 m a.s.l., the plots of cluster VI d were located at an altitude of 2200-2300 m a.s.l. The canopy was not that high, stems were thinner and the canopy composed of significantly more individuals. Emergent trees were not found.

Compared to the ravine forest under human influence of cluster VI b, there were also more but thinner individuals reaching the canopy, the branching pattern was different and standing dead trees more abundant. Signs of selective logging or footpaths were not found. Hence the forest type of cluster VI d was classified as primary ravine forest at higher altitude. Figure 24 shows a profile of plot 150, whereas Figure 25 shows a profile of plot 145, one of the plots added to cluster VI d.

Figure 25: Profile of Primary ravine forest at higher altitude (Cluster VI d) of Plot 145 (Illustration by Dziedzioch)

3.4.2.11 Microphyll ridge forest (Cluster VII a)

Cluster VII a combined 21 plots (83-90, 112, 113, 115, 116, 132, 135, 138-141, 144, 163, 164) all consisting of only two tree strata (except plot 135 where a palm emerged and was treated as a third stratum). They were all located on ridges.

The **canopy stratum** was 10-15 m high, covered only 30-40% and consisted of 5-25 trees per plot. Stem diameter was 20-30 cm and the umbrella-shaped or irregular crowns had a distance of 1-3 m. The nano-microphyll or microphyll leaves had a semi-sclerophyll consistency and were held at an angle of up to 45°. Nearly all trees hosted many vascular epiphytes but none were connected with lianas or bamboo. Compared to the canopy strata of all other forest types ground cover, dbh, height of stratum, height of lowest branch, and height of main ramification were under-represented. In contrast, branching pattern type 3 and semi-sclerophyll leaves were over-represented while malacophyll leaves were rare. This corresponded with the dominance of *Purdiaea nutans* Planch. (*Cyrillaceae*) in the canopy stratum. A high percentage of species of the *Clusiaceae* was responsible for the over-representation of semi-succulent leaves.

The **undergrowth stratum** of 1-5 m in height covered 70% and consisted of more than 100 individuals per plot. The stems were thinner than 10 cm while the irregular, umbrella-shaped or funnel-shaped crowns had a distance less than 1 m. Leaves were simple or compound of mesophyll or nano-microphyll size and had a semi-sclerophyll consistency. They were held up to an angle of 45°. Vascular epiphytes were abundant and some trees were connected by lianas. In the undergrowth, species of *Cyclanthaceae* were conspicuous. This corresponded with the over-representation of the leaf shape "other". Compared to other forest types, ground cover was over-represented as well as dead trees and trees with dead branches. Semi-sclerophyll and semi-succluent leaves were dominant as in the canopy stratum. A high percentage of species of the *Melastomataceae* led to an over-representation of bicoloured leaves. Epiphytic orchids and bromeliads as well as beard-like and crustose lichens were more abundant than in any other undergrowth stratum of other forest types.

The plots of cluster VII a were located at an altitude between 2170 m a.s.l. and 2650 m a.s.l.. Hence the microphyll ridge forest had the widest altitudinal range of all forest types in the investigation area. It was characterised by a low and sparse canopy layer and a dense undergrowth stratum where grasses, species of *Cyclanthaceae*, and ground-living bromeliads filled the space between the woody plants. Sunlight on the ridges was so intense and the canopy so sparse that all kinds of epiphytic plants could develop even in the lower stratum and were not restricted to the highest branches of emergent trees as in the primary ravine forest types.

Plot 114 had only one stratum but was identified as an outlier in the cluster analysis of the plots with one stratum. Due to its location in the direct neighbourhood of the plots of cluster VII a and after comparison of its structural

characteristics, it was placed in cluster VII a. Figure 26 shows a profile of plot 141.

Figure 26: Profile of Microphyll ridge forest (Cluster VII a) of Plot 141 (Illustration by Dziedzioch)

3.4.2.12 Mesophyll rigde forest (Cluster VII b)

Cluster VII b combined only three plots (130, 133, 137) located on a ridge. All plots had three strata.

The **canopy stratum** was 15-20 m high, covered 50-60% and consisted of 5-25 trees per plot. The distance between the umbrella-shaped or irregular crowns was 1-3 m; stem diameter was 50 cm. The simple leaves were micro-mesophyll or mesophyll and of semi-sclerophyll consistency. They were held at an angle of up to 45°. Most trees hosted many vascular epiphytes and nearly all were connected by lianas and bamboo. Compared to the canopy strata of other forest types, diagonal stems, fan-shaped crowns, dead branches, epiphytic ferns, and connecting lianas and bamboo were over-represented. Climbers were conspicuous.

In the **middle stratum**, 25-50 individuals of 5-10 m in height covered 60%. Crown distance was 1-3 m, dbh was 10-20 cm. Crown shape and leaf characteristics resembled the canopy stratum but with a higher percentage of

funnel-shaped crowns, compound and macrophyll leaves. This corresponded with a higher percentage of palms. Vascular epiphytes were less abundant while connecting elements and climbers still were conspicuous.

In the **lower stratum**, more than 100 individuals per plot covered 60% and grew to a height of 1-5 m. Stems were thinner than 10 cm and crown distance was less than 1 m. Crown shape and leaf sizes were similar to those of the higher strata but leaves were held horizontally. Lianas and bamboo were omnipresent and over-represented while vascular epiphytes were virtually lacking. Species of *Cyatheaceae* were frequent.

At an elevation of 2050-2180 m. a.s.l., the three plots were located in an altitudinal zone between the ravine forest and the microphyll ridge forest but were restricted to one single ridge. The high percentage of diagonal stems bearing a fan-shaped crown and the dominance of bamboo overgrowing even canopy trees favoured the conclusion that the mesophyll ridge forest could be a late stage of succession after landslide. Thick trees fell but survived and developed a fan-shaped crown while the opening of the canopy favoured bamboo and climbers. The resulting structural characteristics led to a separation of these three plots from the microphyll ridge forest of cluster VII a in the cluster analysis. Hence the mesophyll ridge forest might not be interpreted as a forest type of a certain altitudinal range but as a local variant of the widespread microphyll ridge forest. Figure 27 shows a profile close to plot 137.

3.4.2.13 Macrophyll ridge forest (Cluster VII c)

Cluster VII c combined six plots (80, 82, 91-93, 134) located at an altitude of 2000-2190 m a.s.l. on one single ridge (except plot 134). All plots had only two strata.

The **canopy stratum** was 5-10 m high (in some plots 10-15 m) and 5-25 trees per plot covered 70%. Stem diameter was 20 cm and the irregular or umbrella-shaped crowns had an average distance less than 1 m. Most of the simple and sclerophyll leaves had a macrophyll size whereas microphyll leaves were less abundant. Leaves were held at an angle of up to 45°. The trees hosted some vascular epiphytes, some were connected by lianas but bamboo and climbers were more frequent. Compared to the canopy strata of the other forest types, height of canopy, height of lowest branch and height of main ramification were under-represented and distance between crowns and stems less than average. Ground cover was higher and more crowns than in other forest types were restricted by their neighbours. Bamboo as connecting element was over-represented in the canopy stratum. The over-representation of macrophyll semi-sclerophyll and bicoloured leaves corre-

sponded with the high percentage of species of *Melastomataceae* (genus *Miconia* and *Graffenrieda*) in the canopy stratum.

Figure 27: Profile of Mesophyll ridge forest (Cluster VII b) close to Plot 137 (Illustration by Dziedzioch)

In the **lower stratum**, more than 100 individuals of 1-5 m in height covered 60%. Crown distance was less than 1 m and stems did not reach diameters greater than 10 cm. Irregular and funnel-shaped crowns co-dominated. Compared to the canopy stratum, palmately lobed and compound leaves were more frequent. This could be explained by the higher frequency of species of the genus *Schefflera* (*Araliaceae*) and treeferns. The conspicuous semi-succulent leaves corresponded to species of the *Clusiaceae*. In the undergrowth stratum, vascular epiphytes were rare but lianas and bamboo were over-represented. Epiphytic individuals of species of the genus *Schefflera* contributed to the higher than average number of woody epiphytes.

The forest type macrophyll ridge forest could only be found on one ridge in the investigation area and was located at an altitude where on the other ridge mesophyll ridge forest turned into microphyll ridge forest. Neverthe-

less, it stretched over an altitudinal range of 200 m before it was replaced by microphyll ridge forest. Due to the dominance of bicoloured species of the *Melastomataceae* in the canopy stratum, the macrophyll ridge forest was a very conspicuous although local forest type. Figure 28 shows a profile of plot 92 which was especially rich in ground-living bromeliads whereas Figure 29 shows a profile close to plot 80 with obviously higher trees.

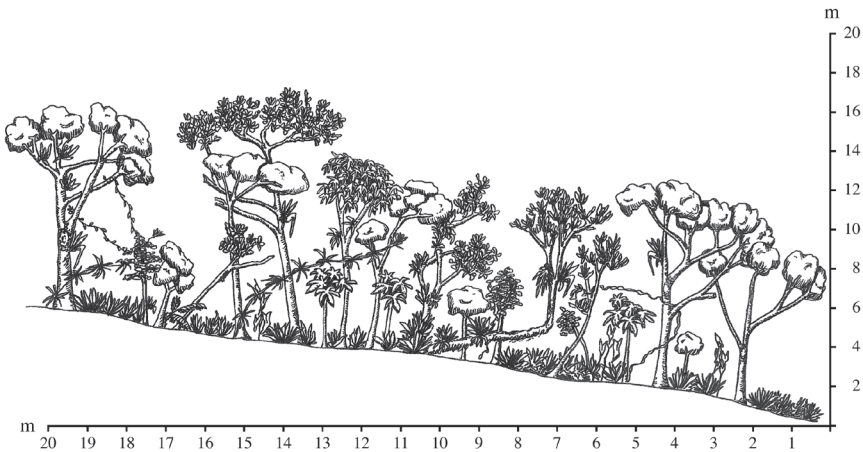


Figure 28: Profile of Macrophyll ridge forest (Cluster VII c) of Plot 92 (Illustration by Dziedzioch)

3.4.2.14 Megaphyll ridge forest (Cluster VII d)

Cluster VII d combined only three plots (81, 126, 127). While plot 127 had two strata, the other plots could be divided into three strata.

The **canopy stratum** consisted of more than 25 individuals per plot covering 60-70% and reaching a height of 15-20 m. Stems had a diameter of 40 cm and the umbrella- and funnel-shaped crowns had an average distance less than 1 m. The simple or compound leaves had a mesophyll or megaphyll size and a semi-sclerophyll consistency. Leaves were held at an angle of up to 45°. Most trees hosted some vascular epiphytes, some were connected by lianas or bamboo or had climbers. Palm trees (*Arecaceae*) were over-represented in the canopy stratum. This high percentage of palms corresponded with the over-representation of funnel-shaped crowns, a crown volume restricted to the top, the high number of trees without branches and the high percentage of megaphyll compound leaves.

In the **middle stratum**, 50-100 individuals per plot grew to a height of 5-10 m and covered 50-60%. Stems had a dbh less than 10 cm, the umbrella-

shaped or round crowns had a distance less than 1 m. Leaves were simple or palmately lobed, of mesophyll size and malacophyll or semi-sclerophyll consistency. Some connecting elements, climbers and vascular epiphytes could be found.

Figure 29: Profile of Macrophyll ridge forest (Cluster VII c) of Plot 80 (Illustration by Dziedzioch)

The **undergrowth stratum** consisted of more than 100 individuals of less than 1-5 m in height which covered 60-70%. Stems were thinner than 10 cm and crown distance was less than 1 m. Funnel-shaped, fan-shaped, and irregular crowns co-dominated. Leaves were simple, compound, or had the leaf shape "other". This corresponded with the high percentage of species of *Cyatheaceae* and *Cyclanthaceae*. Leaf size was macro- or mesophyll. Vascular epiphytes were absent but some trees were connected by lianas or bamboo. Hemixylous plants with a green thin smooth bark were over-represented.

The three plots were located at an altitude of 2050, 2130, and 2140 m a.s.l. on both ridges. Plot 81 lay amidst the plots of cluster VII c, while the plots 126/127 were situated in between the plots of clusters VII a and b. The common character separating cluster VII d was the high percentage of palms (cf.

genus *Dictyocarium*) emerging from the canopy stratum. This justified the name macrophyll ridge forest. Although very local, this forest type was very conspicuous. Figure 30 shows a profile of plot 81.

Figure 30: Profile of Megaphyll ridge forest (Cluster VII d) of Plot 81 (Illustration by Dziedzioch)

A brief summary of the description of all structural forest types is given in Table 9.

Table 9: Brief description of all strata for all cluster groups.

Canopy stratum							
Cluster	**I a**	**I b**	**II**	**III**	**IV**	**V**	**VI a**
Ground cover (%)	70	80	90	70-80	40-50	70-80	50
Number of trees	25-50	50-100	25-50	5-25	5-25	5-25	5-25
Height (m)	5-10	1-5	10-15	20-25	10-15	10-15	10-15
Diameter (cm)	<10	<10	20-30	40-50	40	20-30	20-30
Crown distance (m)	<1	<1	<1	<1	1-3	<1	1-3
Crown shape	irregular, umbrella	cylindrical, irregular	conical	umbrella	umbrella, irregular	umbrella, irregular	umbrella
Leaf shape	simple	simple	narrow	simple, palmately lobed	simple, compound	simple, palmately lobed	simple
Leaf size	micro-mesophyll macrophyll	mesophyll macrophyll	nanophyll	mesophyll megaphyll	micro-mesophyll	meso-, micro-mesophyll macrophyll	mesophyll macrophyll
Leaf consistency	malacophyll	malacophyll	malacophyll	malacophyll	semi-sclerophyll	malacophyll	malacophyll
Leaf angle	hanging, <45°	hanging, <45°	hanging	horizontal, <45°	horizontal	<45°	<45°, horizontal
Vascular epiphytes	none	none	none	some	many	some	some
Connecting elements	many lianas much bamboo	some lianas some bamboo	none	some lianas some bamboo	some lianas much bamboo	some lianas some bamboo	none
Conspicuous life forms				climbers			

Undergrowth stratum							
Cluster			**II**	**III**	**IV**	**V**	**VI a**
Ground cover (%)			10-20	50-60	40	50	60
Number of trees			25-50	25-50	50-100	25-50	50-100
Height (m)			1-5	5-10	1-5	1-5	1-5
Diameter (cm)			<10	<10	<10	<10	<10
Crown distance (m)			3-6	3-6	3-6	<1	<1
Crown shape			irregular	funnel, irregular	umbrella, cylindrical, irregular	irregular, funnel	irregular, umbrella, cylindrical
Leaf shape			simple	simple, compound	simple, compound	simple, compound	simple
Leaf size			micro-mesophyll	mesophyll, macrophyll megaphyll	mesophyll micro-mesophyll	mesophyll macrophyll	micro-mesophyll mesophyll
Leaf consistency			malacophyll	malacophyll	malaco,-semi-sclerophyll	malacophyll	malacophyll
Leaf angle			horizontal	horizontal, <45°	<45°	<45°, horizontal	<45°, horizontal
Vascular epiphytes			none	some	none	none	none
Connecting elements			some lianas	some lianas some bamboo	some lianas much bamboo	some lianas much bamboo	some lianas some bamboo
Conspicuous life forms				climbers, araceae, cyatheacea			

Table 9: (continued) Brief description of all strata for all cluster groups.

Canopy stratum							
Cluster	**VI b**	**VI c**	**VI d**	**VII a**	**VII b**	**VII c**	VII d
Ground cover (%)	50	40-50	50-60	30-40	50-60	70	60-70
Number of trees	1-5	1-5	5-25	5-25	1-5	5-25	25-50
Height (m)	20-25	25-30	20-25	10-15	15-20	5-10 (15)	15-20
Diameter (cm)	50-60	60 (130)	40	20-30	50	20	40
Crown distance (m)	1-3	<1	1-3	1-3	1-3	<1	<1
Crown shape	umbrella	irregular, umbrella	umbrella, irregular	umbrella, irregular	umbrella, irregular	umbrella, irregular	umbrella, funnel
Leaf shape	simple	simple	simple	simple	simple	simple	simple, compound
Leaf size	micro-mesophyll	mesophyll micro-mesophyll	mesophyll micro-mesophyll	nano-microphyll microphyll	micro-mesophyll mesophyll	macrophyll microphyll	megaphyll mesophyll
Leaf consistency	malaco-, semi-sclerophyll	malacophyll	malacophyll	semi-sclerophyll	semi-sclerophyll	semi-sclerophyll	semi-sclerophyll
Leaf angle	<45°, horizontal	<45°, horizontal	<45°	<45°	<45°	<45°	<45°
Vascular epiphytes	some	some	some	many	many	some	some
Connecting elements	some lianas	some lianas some bamboo	none	none	many lianas much bamboo	some lianas much bamboo	some lianas some bamboo
Conspicuous life forms			climbers		climbers	climbers	arecaceae, climbers
Middle stratum							
Cluster	**VI b**	**VI c**	**VI d**	**VII a**	**VII b**	**VII c**	**VII d**
Ground cover (%)	60	60	40		60		50-60
Number of trees	5-25	5-25	5-25		25-50		50-100
Height (m)	10-15	10-15	10-15		5-10		5-10
Diameter (cm)	20-30	20-30	10-20		10-20		<10
Crown distance (m)	1-3	<1	1-3		1-3		<1
Crown shape	irregular, umbrella	irregular, umbrella	irregular, funnel, umbrella		irregular, umbrella, funnel		umbrella, round
Leaf shape	simple, compound	simple	simple, compound		simple, compound		simple, palmately lobed
Leaf size	micro-mesophyll mesophyll	macrophyll mesophyll	mesophyll megaphyll		mesophyll macrophyll		mesophyll
Leaf consistency	malacophyll	malaco-, semi-sclerophyll	malacophyll		malaco-, semi-sclerophyll		malaco-, semi-sclerophyll
Leaf angle	<45°, horizontal	horizontal, <45°	horizontal		<45°		<45°
Vascular epiphytes	some	some	some		some		some
Connecting elements	some lianas some bamboo	some lianas some bamboo	some lianas some bamboo		some lianas some bamboo		some lianas some bamboo
Conspicuous life forms					climbers		climbers

Table 9: (continued) Brief description of all strata for all cluster groups.

Undergrowth stratum							
Cluster	**VI b**	**VI c**	**VI d**	**VII a**	**VII b**	**VII c**	**VII d**
Ground cover (%)	60	50	50-60	70	60	60	60-70
Number of trees	50-100	50-100	50-100	>100	>100	>100	>100
Height (m)	1-5	1-5	1-5	1-5	1-5	1-5	1-5
Diameter (cm)	<10	<10	<10	<10	<10	<10	<10
Crown distance (m)	<1	<1	<1	<1	<1	<1	<1
Crown shape	irregular, funnel	irregular, funnel	irregular, funnel, cylindrical	irregular, umbrella, funnel	irregular, funnel	irregular, funnel	funnel, fan, irregular
Leaf shape	simple, compound	simple, compound	simple, compound	simple, compound	simple, compound	simple, lobed, compound	simple, compound, other
Leaf size	micro-mesophyll megaphyll	macrophyll mesophyll	mesophyll megaphyll	mesophyll nano-microphyll	micro-mesophyll macrophyll	mesophyll macrophyll	macrophyll mesophyll
Leaf consistency	malaco-, semisclerophyll	malacophyll	malacophyll	semisclerophyll	semisclero-, malacophyll	misclerophyll, semisuccule	malacophyll
Leaf angle	<45°, horizontal	horizontal, <45°	<45°, horizontal	<45°	horizontal	<45°	<45°
Vascular epiphytes	none	none	none	some	none	none	none
Connecting elements	some lianas some bamboo	some lianas	some bamboo	some lianas	many lianas much bamboo	many lianas much bamboo	some lianas some bamboo
Conspicuous life forms		cyatheaceae	cyatheaceae, climbers	cyclanthaceae	cyatheaceae	cyatheaceae, climbers	cyatheaceae, cyclanthaceae

3.5 Distribution of structural forest types in the investigation area

In the investigation area close to the ECSF, only twelve of fourteen forest types could be found, due to the location of the plots of clusters III and IV in Mindo and Cajanuma. Figure 31 shows the distribution of these twelve forest types and marks in colours which plot was assigned to each forest type. As already shown on a landscape level (compare Figure 6, p. 54), the Rio San Francisco marked the boundary between the mainly deforested northern part of the investigation area and the southern part, still covered with forest.

In the northern part, secondary growth after road construction or landslides (clusters I a and b) flanked the road. A hillside north of the road was planted with *Pinus patula* (cluster II). A forest-like structure could only be found in ravines of the northern tributaries of the San Francisco river. In these ravines, partly crossed by the road, the secondary ravine forest (cluster VI a) was located.

In the southern part, a channel and a footpath paralleled the river at an altitude of 1900 m a.s.l.. Along this footpath (which served as main connection between Loja and Zamora before the construction of the road) ravine forest under human influence (cluster VI b) could be found. Three southern tributaries could be waded beginning at their intersection with the channel. In one of them, the human influence reached as far up as an altitude of nearly 2000 m a.s.l. (plot 67) while the other two quebradas hosted primary ravine forest at a lower altitude (cluster VI c) already in their lowest parts at 1840 m a.s.l (plot 110). One plot (125) in the tributary under human influence could be classified as primary forest and was located above the highest tree stump discovered. Hence it could be concluded that the forest type of cluster VI c was the original primary vegetation which would also probably cover the mentioned tributary if human activity had not changed the structure. Following the quebrada to an elevation higher than 2050 m a.s.l., the forest type changed and primary ravine forest at higher altitude (cluster VI d) could be found as in the quebrada El Milagro at the eastern edge of the investigation area. Unfortunately, due to technical reasons (waterfalls), it was not possible to access the lower part of the quebrada El Milagro to investigate whether the transition between the two primary ravine forest types could also be detected.

Beginning at the channel, two ridges were followed until they merged at 2440 m a.s.l. (plot 114) and further until the ridges met that marked the western and eastern boundaries of the investigation area at 2650 m a.s.l. (plot 135). On the western ridge, macrophyll ridge forest (cluster VII c) was found

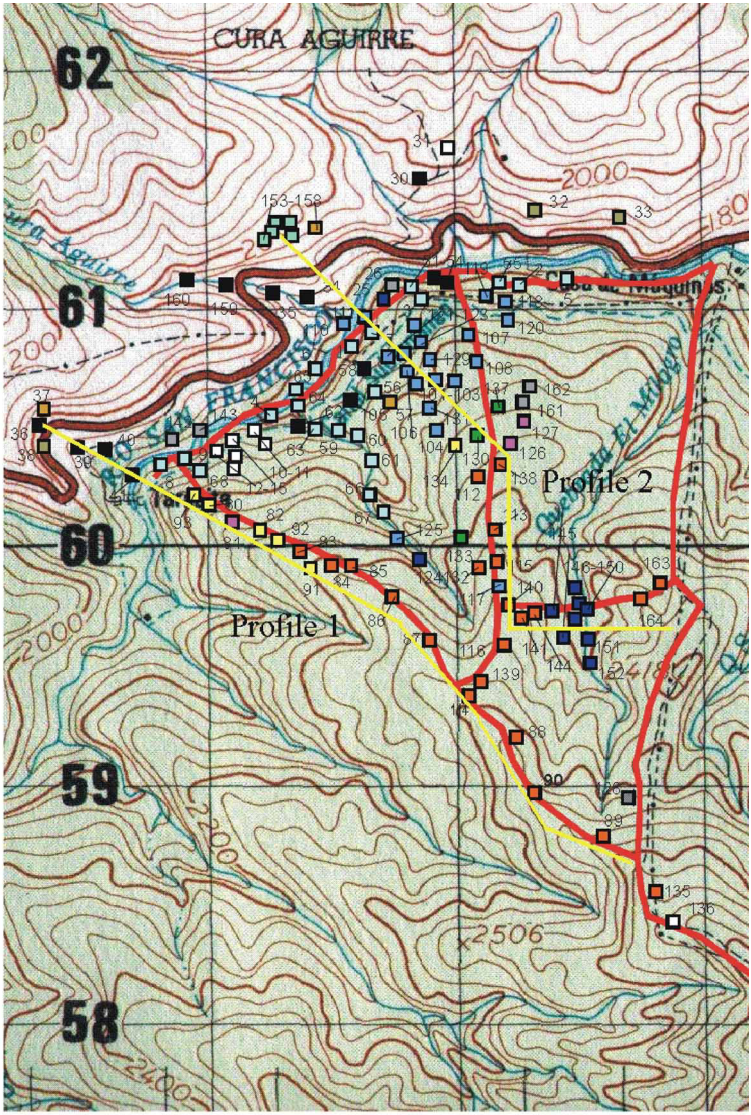


Figure 31: Distribution of structural forest types. Profiles 1 and 2 correspond to fig. 32 and 33.

beginning at 2000 m a.s.l (plot 93). With an interruption at 2050 m a.s.l. (plot 81), where megaphyll ridge forest (cluster VII d) dominated, the macrophyll forest type continued up to 2190 m a.s.l. (plot 91). Here the forest type changed and microphyll ridge forest (cluster VII a) dominated up to the timberline. Figure 32 shows a schematic profile from NW to SE beginning on the northern side of the road (plot 36) and following the western ridge. (The inclination of the trees is an artefact of composing the profile with the computer).

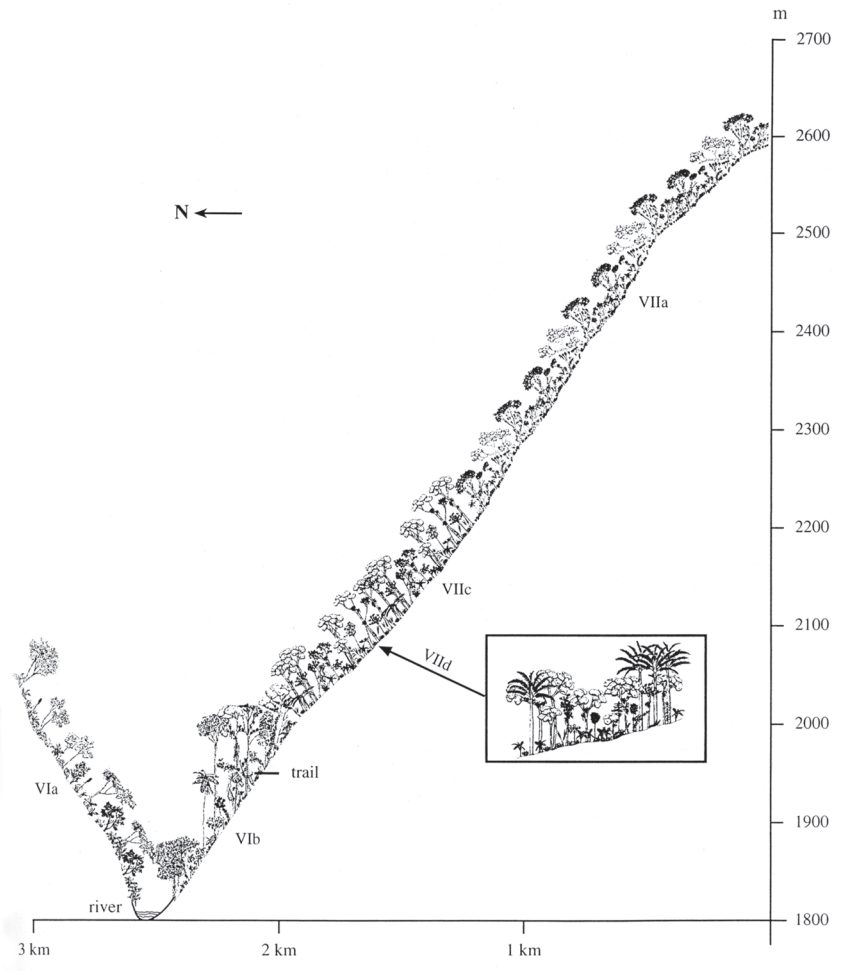


Figure 32: Profile of structural forest types on the western ridge.

The second ridge was not as sharp and steep as the western ridge and on its lower parts it was covered with primary ravine forest at lower altitudes (clus-

ter VI c) like the adjacent quebradas. Between 2050 m a.s.l. and 2140 m a.s.l., sections of mesophyll ridge forest (cluster VII b) and megaphyll ridge forest (cluster VII d) were crossed. Beginning at 2180 m a.s.l. (plot 138), microphyll ridge forest dominated as on the western ridge up to where the ridges met. The plots of cluster V (forest on edges of natural gaps) were scattered and did not form an altitudinal belt. Figure 33 shows a profile parallel to the one mentioned above but starting at the *Pinus patula* plantation north of the road, crossing the river and following a quebrada over the ridge, then leading into the quebrada El Milagro until it reaches the eastern boundary. Both profiles are indicated in Figure 31.

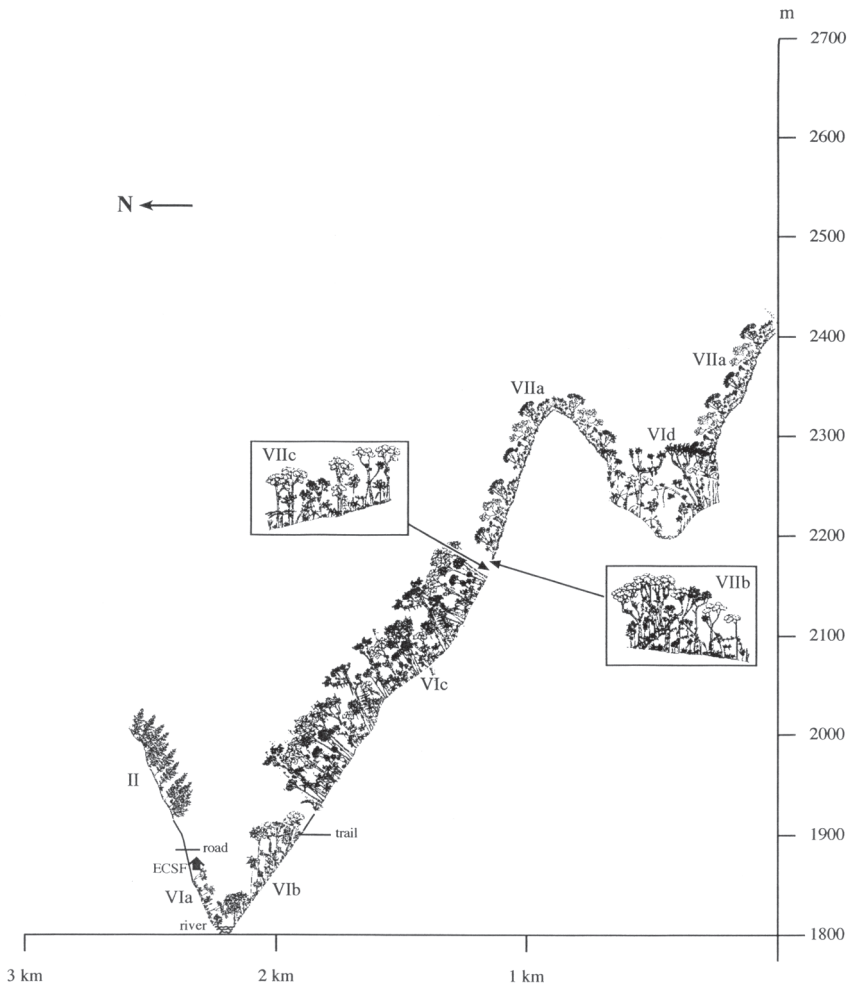


Figure 33: Profile of structural forest types crossing two quebradas and the eastern ridge.

Summarising the results describing structural forest types, it can be observed that primary forest only existed south of the Rio San Francisco while on the northern side, secondary growth or plantations were the only forest-like elements. The lower part of the southern side had to be classified as at least influenced by former human activity. In the undisturbed parts, a clear distinction could be made between forest types in ravines and on ridges. In the ravines, two types of primary forest could be distinguished at different altitudes. On the ridges, three types co-existed in the lower parts while a fourth type dominated most of the ridges. Hence the forest type depended on the relief situation and the altitude.

3.6 Frequency of structural characters and correlation between structural characters

As mentioned in chapter "Material and Methods" not all variables support a cluster analysis in the same way. It should be possible to exclude those variables from cluster analysis without changing the result that occur with a low frequency (or not at all) or with a high frequency and with the same value for every object (Backhaus et al. 1996). To avoid over-interpretation of one feature that is described by more than one variable (i. e. redundant variables) correlation between all possible pairs of variables was determined using the Spearman Correlation Coefficient (Backhaus et al. 1996).

The frequency of every value of every variable was determined. Table 10 lists all variables (i.e. structural characters) that were missing (i.e. value 0) in at least 90% of all plots in all strata or were omnipresent (i.e. value 3) in at least 90% of all plots in all strata.

This analysis revealed 26 structural characters that could be divided into five groups. Into the first group fell the characters "leaves green", "trees evergreen" and "branches mostly diagonal". Green leaves were omnipresent in two strata and had a frequency of more than 95% in the third stratum. Evergreen trees had a frequency of 100% in one stratum and a frequency of more than 99% in the other strata. Branches mostly diagonal occurred with a frequency of at least 90% in all three strata. The second group consists of four characters that did not occur at all in any plot in any stratum. The third group lists six characters that were missing completely in two strata and were also absent in more than 95% in the third stratum. The fourth group consists of nine characters that were missing in one stratum and were the frequency of value 0 was higher than 91% for the other strata. The fifth group lists four characters for which the frequency of

value 0 was higher than 90% in all strata but did not reach 100% in any stratum.

Table 10: Frequency of structural characters that were missing (i. e. value 0) in at least 90% of all plots in all strata or were omnipresent (i.e. value 3) in at least 90% of all plots in all strata

Character	Value	Frequency [%] in canopy stratum	Frequency [%] in middle stratum	Frequency [%] in lower stratum
Leafs green	3	95.7	100	100
Trees evergreen	3	99.3	100	99.2
Branches mostly diagonal	3	93.5	94.8	90
Aerial roots	0	100	100	100
Leafs hymenophyll	0	100	100	100
Bark green thick smooth	0	100	100	100
Bark green thick rough	0	100	100	100
Bark non-green thick smooth	0	99.3	100	100
Leafs succulent	0	99.3	100	100
Leafs red	0	100	100	98.5
Leafs sub-leptophyll	0	100	100	98.5
Tabulate roots	0	97.1	100	100
Leafs leptophyll	0	100	100	94.6
Trees decidious	0	99.3	100	100
Shrubby lichens	0	99.3	100	99.2
Leafs sclerophyll	0	99.3	100	96.9
Leafs absent	0	100	96.2	99.2
Spines on branches	0	100	96.6	98.5
Bark green thin rough	0	100	98.3	96.9
Epiphyt acc. vert. branches	0	96.4	94.8	100
Leaf length <1cm	0	97.8	100	91.5
Hairs on branches	0	100	96.6	90
Flaky bark	0	95.7	98.3	96.2
Epiphytic Araceae branches	0	91.4	98.3	99.2
Epiphyt acc. dead branches	0	94.2	91.4	97.7
Branches mostly vertical	0	92.1	93.1	90.8

Table 11 lists all pairs of variables where the Spearman Correlation Coefficient (r) was > /0.6/ in at least the canopy stratum or the lower stratum. This analysis revealed 77 variable pairs that could be divided into nine groups:

The first group consist of six pairs that showed a negative correlation. In each case both structural characters belonged to the same character class (e.g.

branching pattern). In four cases the character class had only three characters (e.g. branching pattern 1-3) what makes negative correlation highly probable. In the other two cases (leaf consistency and bark characters) the negative correlated structural characters were the most frequent of their classes.

The second group lists five pairs that were all formed by metric variables describing the architecture of the forest. A correlation between tree height and the height of the lowest branch and main ramification was probable as long as forest stands of mostly broad-leafed tree species composition were compared. The lack of correlation between height and dbh in the lower stratum was an artefact of the scaling because diameters less than 10 cm were not distinguished further and hence nearly all individuals of the lower stratum fell into the same diameter class. A scaling in steps of 1 cm would probably have led to the same correlation between height and dbh as in the canopy stratum.

The third group consists of 15 variable pairs that all described leaf sizes and leaf length or width respectively. Growing leaf sizes correlated with growing leaf length and width. This correlation corresponded with the result that all forest types detected (except the plantation of *Pinus patula*) had primarily simple leaves and hence leaf length and width were related like the two diameters of an ellipse. Thus e.g. nanophyll leaves were correlated with a length <2 cm and a width <1 cm.

In the forth group, eight pairs are listed that were formed exclusively by connecting elements. It became obvious that wherever lianas or bamboo existed they also had a tendency to connect tree individuals, especially in the case of bamboo in the lower stratum. Nevertheless, the presence of lianas did not necessarily correspond with the presence of bamboo.

The fifth group consists of 17 variable pairs which seemed to be related with several conspicuous life-forms. For the canopy stratum especially palm trees corresponded with missing branches and a crown volume restricted to the top which itself correlated with megaphyll and compound leaves and a funnel-shaped crown. In the lower stratum species of *Cyatheaceae* took that place, while species of *Cyclanthaceae* corresponded with the leaf shape "other".

The sixth group has only two pairs. Here the correlation was based on a common structural feature (vertical or dead branches) that was precondition for the structural character itself. Hence it could be concluded that if e.g. dead branches in the canopy stratum existed they hosted as well epiphytic bromeliads as orchids. In the seventh group, four pairs are listed where the conclusion was vice versa: if an outer condition (e.g. moisture) allowed the growing of mosses they grew as well on stems as on branches.

Table 11: Correlation of variables where the Spearman Correlation Coefficient (r) was > /0.6/ in at least the canopy stratum or the lower stratum

Group	Character a	Character b	r in canopy stratum	r in lower stratum
	Branching pattern 1	Branching pattern 2	-0.686	
	Some epiphytes	Many epiphytes	-0.635	
	Some epiphytes	No epiphytes		-0.735
1	Leafs malacophyll	Leafs semi-sclerophyll		-0.844
	Crown full	Crown restricted		-0.624
	Bark non-green thin smooth	Bark non-green thin rough		-0.613
	Height	DBH	0.835	
	Height	Height of lowest branch	0.809	
2	Height	Height of main ramification	0.898	0.605
	Height of lowest branch	Height of main ramification	0.822	
	Distance stems	Distance crowns	0.771	0.757
	Leafs leptophyll	Leaf length <1cm		0.786
	Leafs nanophyll	Leaf length <2cm	0.653	0.663
	Leafs nanophyll	Leaf width <1cm	0.8	0.642
	Leafs nano-mikrophyll	Leaf width < 2cm	0.726	0.645
	Leafs nano-mikrophyll	Leaf length <5cm	0.724	0.748
	Leafs mikro-mesophyll	Leaf length <10cm	0.775	
3	Leafs mesophyll	Leaf length <20cm	0.624	0.706
	Leafs makrophyll	Leaf length <50cm	0.669	0.697
	Leafs megaphyll	Leaf width >50cm	0.777	
	Leafs megaphyll	Leaf length >50cm	0.827	0.724
	Leaf length <1cm	Leaf width <1cm		0.698
	Leaf length <50cm	Leaf width <50cm	0.652	
	Leaf width >50cm	Leaf length >50cm	0.811	0.542
	Leafs narrow	Leaf width <1cm	0.883	0.658
	Leafs narrow	Leafs nanophyll	0.653	
	Lianas stem	Lianas crown	0.693	0.718
	Lianas connecting crowns	Lianas crown		0.75
	Bamboo stem	Bamboo crown	0.649	0.918
4	Bamboo stem	Bamboo connecting stems	0.661	0.862
	Bamboo crown	Bamboo connecting crowns	0.689	0.9
	Bamboo connecting stems	Bamboo connecting crowns	0.621	0.922
	Bamboo stem	Bamboo connecting crowns		0.837
	Bamboo crown	Bamboo connecting stems		0.89

Table 11: (continued) Correlation of variables where the Spearman Correlation Coefficient (r) was > /0.6/ in at least the canopy stratum or the lower stratum

Group	Character a	Character b	r in canopy stratum	r in lower stratum
	Crown funnel-shaped	Branches missing	0.881	0.723
	Crown funnel-shaped	Crown vol. res. to top	0.815	0.838
	Crown funnel-shaped	Leafs compound	0.601	0.853
	Crown funnel-shaped	Leaf length >50cm	0.6	0.698
	Crown funnel-shaped	Leafs megaphyll		0.602
	Crown vol. res. to top	Branches missing	0.813	
	Crown vol. res. to top	Leafs compound	0.654	0.857
5	Crown vol. res. to top	Leafs megaphyll	0.615	
	Crown vol. res. to top	Leaf length >50cm	0.636	0.691
	Branches missing	Leaf length >50cm		0.627
	Crown vol. res. to top	Palm trees	0.815	
	Branches missing	Palm trees	0.942	
	Crown vol. res. to top	Cyatheaceae		0.708
	Leafs compound	Cyatheaceae		0.737
	Leaf length >50cm	Cyatheaceae		0.657
	Cyclanthaceae	Leaf shape other		0.799
	Cyclanthaceae	Axylous		0.659
6	Bromeliads vertical branches	Orchids vertical branches	0.71	
	Bromeliads dead branches	Orchids dead branches	0.606	
	Fern on stem	Fern on branches	0.618	
7	Mosses on stem	Mosses on branches	0.624	0.576
	Woody epi. on stem	Woody epi. on branches	0.609	
	Orchids in branching	Orchids vertical branches	0.699	
	Beard-like lichens	Leafs semi-sclerophyll	0.707	0.545
	Beard-like lichens	Many epiphytes	0.601	
	Beard-like lichens	Axylous		0.608
	Beard-like lichens	Crustouse lichens		0.654
	Beard-like lichens	Cyclanthaceae		0.652
	Beard-like lichens	Leaf width <1cm		0.61
	Beard-like lichens	Leafs semi-succulent		0.628

Table 11: (continued) Correlation of variables where the Spearman Correlation Coefficient (r) was > /0.6/ in at least the canopy stratum or the lower stratum

Group	Character a	Character b	r in canopy stratum	r in lower stratum
8	Beard-like lichens	Leaf shape other		0.611
	Beard-like lichens	Leafs malacophyll	-0.707	
	Beard-like lichens	Brom. organic material		0.684
	Leafs semisucculent	Brom. organic material		
	Branching pattern 3	Leafs semi-sclerophyll	0.602	
	Bark non-green thick smo	Leafs sclerophyll	1	
	Leafs red	Trees deciduous		0.704
	Trees evergreen	Trees deciduous	-1	
	Bark green thin smooth	Hemixylous		0.72
	Bark non-green thin rough	Crustouse lichens		0.727
9	Bromeliads on stem	Some epiphytes		0.68
	Orchids on stem	Some epiphytes		0.718
	Mosses on branches	No epiphytes	-0.614	

The eighth group consists of 15 pairs where the reason for a correlation was not as obvious but could only be explained by the rareness of one of the characters involved. In nine cases one character was beard-like lichens. They were restricted to the forest type microphyll ridge forest where semi-sclerophyll or semi-succulent leaves, vascular epiphytes and *Cyclanthaceae* were over-represented while malacophyll leaves were less abundant. Hence the restriction of beard-like lichens to one single forest type explained the positive correlation with other characters typical for the same type and the negative correlation with a character that was under-represented in that forest type. This made beard-like lichens an indicator for the microphyll ridge forest.

The extraordinarily high correlation (r=1) of a non-green, thick and smooth bark with sclerophyll leaves could be explained by the fact, that this type of bark was only found once (an emergent *Prumnopitys montana*, *Podocarpaceae* in plot 119) and no other leaves (needles) were classified as sclerophyll. In plot 2, the canopy stratum consisted of only one emergent tree (*Tabebuia* spec., *Bignoniaceae*) which was classified as deciduous. The extreme rareness of that character and the lack of any other tree in the canopy of that plot explained the high negative correlation with evergreen trees.

In the ninth group, five pairs are listed. They could not be explained by a common scheme of interdependence. The first pair (bark green, thin,

smooth/ plants hemixylous) correlated only in the lower stratum, because both variables did only exist in that stratum. All other possible combinations of bark characters with green bark did not exist at all or were extremely rare (compare Table 10), so that the correlation could better be expressed as a correspondence between green bark and hemixylous plants. The pairs "some epiphytes/ bromeliads on stem" and "some epiphytes/orchids on stem" in the lower stratum could be explained by the fact that the lowest stratum consisted of young trees with thin or none branches and epiphytes were comparatively rare. Hence it could be concluded that the few existing epiphytes (no matter if bromeliads or orchids) were restricted to the stems of the undergrowth trees.

The aim of the calculation of frequencies and correlations between variables was to exclude characters which did not support cluster analysis and thus reduce the classification system. Based on the results mentioned above, the following chapter will explain, which variables and character classes were excluded.

3.7 Reduced classification system

The classification system used in this study consisted of 151 structural characters in 39 classes (see Material and Methods, Table 1, p. 40 and Table 2, p. 41–44).

Table 12: Scaling of reduced list of metric parameters.

Character class	Character				
Number of trees	<5	<25	<50	<100	>100
Ground cover	<10%	<20%	<30%	<40%	and so on
Diameter at breast height	<10cm	<20cm	<30cm	<40cm	and so on
Height of stratum	<5m	<10m	<15m	<20m	and so on
Height of lowest branch	<5m	<10m	<15	<20m	and so on
Distance between stems	<1m	<3m	<6m	<9m	and so on

Table 12 and Table 13 list the set of 104 structural characters in 32 classes of the reduced classification system. In the following, the differences will be explained based on the results of frequency and correlation analysis.

Table 13: Definition of reduced catalogue of ordinate scaled parameters

Character class	Character	Based on system of	Explanation
Woodiness	axylous	Orshan (1986)	
	hemixylous	Orshan (1986)	
	holoxylous	Orshan (1986)	
Stem characters	polycormous		
	vertical		
	diagonal		
	dead		
Bark characters	thin smooth	Werger & Sprangers (1982)	thin: <2mm
	thin rough	Werger & Sprangers (1982)	
	thick smooth	Werger & Sprangers (1982)	thick: <1cm
	thick rough	Werger & Sprangers (1982)	
Roots	stilt roots		
Crown volume	restricted to top	Werger & Sprangers (1982)	
	restricted to upper third	Werger & Sprangers (1982)	
	restricted to upper half	Werger & Sprangers (1982)	
	reaching deeper than half	Werger & Sprangers (1982)	
Crown development	full		
	restricted by neighbours		
	stunted		
Crown shape	round	Werger & Sprangers (1982)	
	umbrella-shaped	Werger & Sprangers (1982)	
	cylindrical	Werger & Sprangers (1982)	
	conical	Werger & Sprangers (1982)	
	funnel-shaped/umbelliferous	Werger & Sprangers (1982)	
	fanshaped		
	irregular	Werger & Sprangers (1982)	
Crown overlap	Type 1		no overlap, distance to next crown >1m
	Type2		no overlap, distance to next crown <1m or touching
	Type 3		crowns overlaping and penetrating each other

Table 13: (continued) Definition of reduced catalogue of ordinate scaled parameters

Character class	Character	Based on system of	Explanation
Branches	mostly horizontal		
	mostly diagonal		
	mostly vertical		
	dead		
	missing		
Branching pattern of terminal 20cm	Type 1	Parsons (1975), modulated	only leafs
	Type 2	Parsons (1975), modulated	branching twice
	Type 3	Parsons (1975), modulated	branching more than twice
Leaf shape	simple		
	narrow leaved		
	palmately lobed		
	compound		
	other		
	with drip-tip		
	absent		
Leaf consistency	malacophyll	Werger & Sprangers (1982)	
	semi-sclerophyll	Werger & Sprangers (1982)	
	sclerophyll	Werger & Sprangers (1982)	
	semi-succulent	Werger & Sprangers (1982)	
Leaf colour	bicoloured	Orshan (1986)	
Leaf size	sub-leptophyll	Orshan (1986)	$<0{,}1cm^2$
	leptophyll	Orshan (1986)	up to $0{,}25cm^2$
	nanophyll	Orshan (1986)	up to $2{,}25cm^2$
	nano-microphyll	Orshan (1986)	up to $12{,}25cm^2$
	microphyll	Orshan (1986)	up to $20{,}25cm^2$
	micro-mesophyll	Orshan (1986)	up to $56{,}25cm^2$
	mesophyll	Orshan (1986)	up to $180{,}25cm^2$
	macrophyll	Orshan (1986)	up to $1640{,}25cm^2$
	megaphyll	Orshan (1986)	$>1640{,}25cm^2$
Leaf angle	mainly hanging down	Parsons (1975), modulated	
	mainly horizontal	Parsons (1975), modulated	
	mainly between horizontal and 45°	Parsons (1975), modulated	
	mainly steeper than 45°	Parsons (1975), modulated	
Epiphytic lichens	crustose lichens		
	foliose lichens		
	shrubby lichens		
	beard-like lichens		

Table 13: (continued) Definition of reduced catalogue of ordinate scaled parameters

Character class	Character	Based on system of	Explanation
Epiphytic mosses	on stem or branches		
Epiphytic ferns	on stem or branches		
Woody epiphytes	on stem or branches		
Epiphytic Araceae	on stem or branches		
Epiphytic bromeliads	on stem		
	in branching		
	in vertical branches		
	on diagonal branches		
	on horizontal branches		
	on dead branches		
	on organic ground material		
Epiphytic orchids	on stem		
	in branching		
	on vertical branches		
	on diagonal branches		
	on horizontal branches		
	on dead branches		
Mixed accumulation of epiphytes	on stem or branches		
Sum of vascular epiphytes	none		no vascular epiphytes
	some		cover of vascular epiphytes <10% of stem surface
	many		cover of vascular epiphytes >10% of stem surface
Connecting elements	lianas in tree crown		
	lianas connecting crowns		
	bamboo in tree crown		
	bamboo connecting crowns		
Conspicuous life-forms	climbers		
	stranglers		
	Arecaceae	Richards et al. (1940)	
	Araceae	Richards et al. (1940)	
	Cyatheaceae	Richards et al. (1940)	
	Cyclanthaceae	Richards et al. (1940)	

Compared to Table 1, in Table 12 two character classes were deleted: height of main ramification and distance between crowns. The height of main ramification correlated with the canopy height and the height of the lowest branch. Furthermore the height of main ramification could be concluded from the information about canopy height and crown volume. The distance between crowns correlated with the distance between stems. From this pair

the first variable was deleted because the type of crown overlap included already information about crown distances.

In Table 13, compared to Table 2 the character classes woodiness and stem characters stayed unchanged. The class bark characters was reduced, because three of four characters describing green bark did not exist at all or were extremely rare. The fourth one (bark green thin smooth) correlated with woodiness hemixylous. Hence the differentiation between green and non-green bark was unnecessary and bark characters were reduced to the combinations of thin, thick, smooth and rough. Flaky bark was also rare and hence cancelled.

In the character class roots, only stilt roots were fairly common in some forest types, so that only this character was taken into the reduced list. All classes describing the crown (volume, development, shape and overlap) and branches (orientation and branching pattern) stayed unchanged. The class leaf shape was also left without change.

The characters leaves hymenophyll and succulent from class leaf consistency did not exist at all or were extremely rare and hence excluded. Within the class leaf colour, the variables green and red could be deleted because green leaves were omnipresent whereas red ones did not exist. So in this class, only the character bicoloured leaves remained that was characteristic for the macrophyll ridge forest. The class tree phenology was completely cancelled because virtually all trees were evergreen.

As already explained above, most leaves were shaped elliptic leading to the result that every leaf size correlated with a leaf length and width. Hence it was concluded that the characters describing leaf size already contained the information about length and width so that these classes could be neglected completely. The class leaf angle remained unchanged.

The classes spinescense and hairiness were removed as a whole because the characters were rare and sometimes hard to detect under field conditions. Furthermore, they were not typical for any forest type.

The four characters describing different types of lichens were left without change. As correlation analysis revealed, the presence of epiphytic mosses, ferns, *Araceae*, woody epiphytes and mixed accumulations of epiphytes on stems correlated with the presence on branches. Hence it was concluded that it was unnecessary to differentiate between the growing on stems and on branches but just register the presence of the mentioned epiphytic groups. For epiphytic bromeliads and orchids, on the other hand, the classes were left unchanged due to the high abundance and the separating function in the distinction of forest types. The class describing the sum of vascular epiphytes was also left without change.

For the connecting elements lianas and bamboo, the analysis of correlations showed such a high correspondence between the variables that they could be reduced to half. The additional information about conspicuous lifeform should not be neglected as a help for the interpretation of cluster results.

Hence the catalogue of structural characters could be reduced to 69% of its original length. To test if this reduced classification system led to the same result as the original one the cluster analysis was repeated with the reduced set of variables. The resulting dendrogram is shown in Figure 34. Compared to the original dendrogram (see Figure 14, p. 68/69), the overall cluster structure stayed unchanged with only slight differences. The two main differences concerned small cluster groups: the three plots of cluster VII d (megaphyll ridge forest) were separated from each other and two of them joined cluster VII b (mesophyll ridge forest). These two clusters had already been direct neighbours in the original clustering and the plots concerned were located close to each other in the investigation area. As already explained in the description of forest types, the megaphyll ridge forest was characterised especially by palm trees in the canopy stratum with an overrepresentation of leaf length and width. In the reduced set of variables, these characters were ignored. This explained the disintegration of cluster VII d. The combined new cluster was placed closer to the ravine forest of lower altitudes. This underlines the status of the few plots of clusters VII b and VII d as a transition between the great groups of ravine forest and microphyll ridge forest already concluded from their location at an intermediate altitude.

The second main difference was the reduction of cluster VI d (primary ravine forest at higher altitude) from seven to five plots. The remaining five plots were all located directly in the quebrada El Milagro. The two plots that changed the cluster (25, 124) were located at lower altitudes and were now placed in cluster VI c (primary ravine forest at lower altitude). The three plots that had already originally built a separate cluster that was added to cluster VI d due to the location of the plots (145, 147, 149) now moved into cluster VI a (secondary ravine forest) and cluster IV (primary forest in Cajanuma). Hence the forest type of primary forest at higher altitude was even more restricted to the quebrada El Milagro itself.

Three plots that could not be grouped by the original analysis and were added to different clusters (70, 98, 122) changed places in the new analysis. Plot 95 was again added as outlier. All in all, 12 out of 129 plots changed the cluster group.

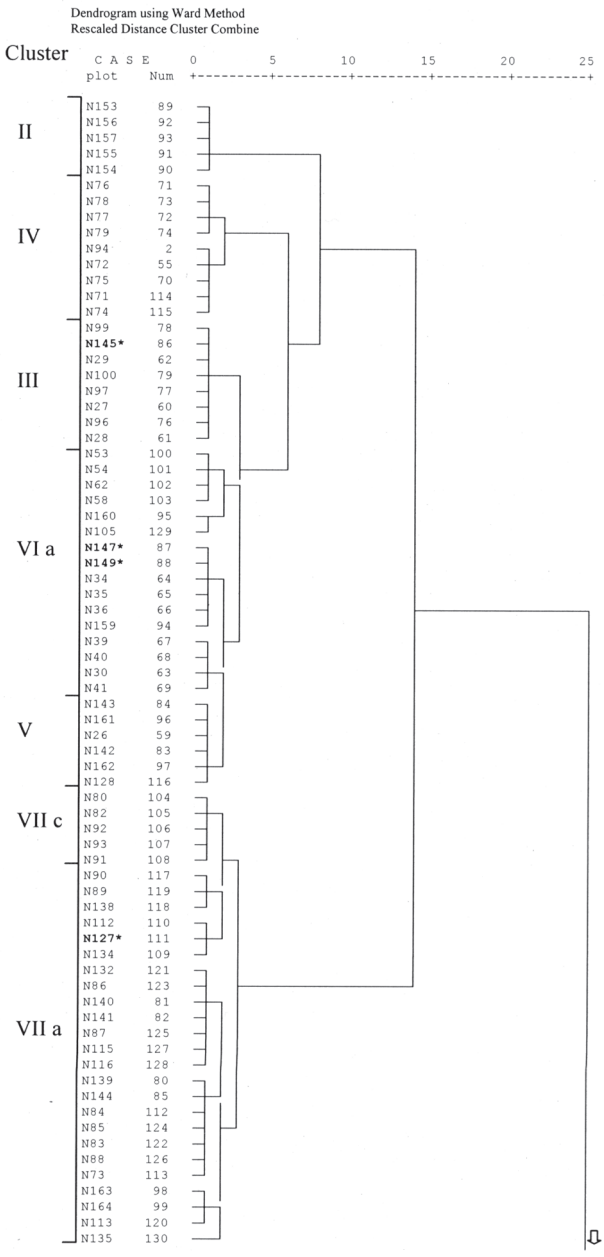


*Figure 34: Cluster dendrogram for 129 plots, based on the reduced catalogue of structural features. Plots marked with * changed position compared to the orignal dendrogram(compare figure 14 on page 68/69). Continued on the next page.*

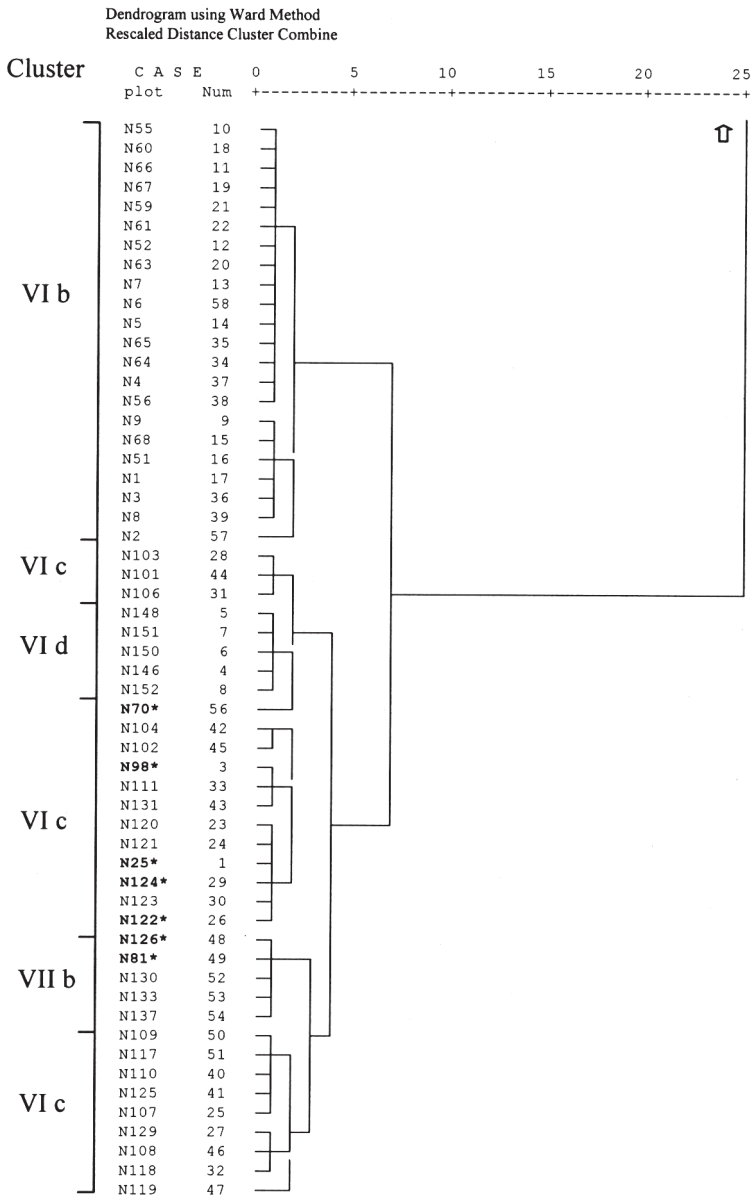


*Figure 34: (continued) Cluster dendrogram for 129 plots, based on the reduced catalogue of structural features. Plots marked with * changed position compared to the orignal dendrogram(compare figure 14 on page 68/69).*

This result made obvious that a reduction of the set of structural characters based on the frequency and correlation of variables as performed in the new analysis did not basically alter the cluster structure. It was concluded that the reduced catalogue of structural features as described in Table 12 and Table 13 is sufficient to allow the distinction of the structural forest types of the investigation area.

3.8 Proposal for a dichotomous key to the structural forest types of the investigation area

As mentioned in the introductional chapter, scientist of other research groups performed and will perform their investigations in the same area. To allow a quick assignment of their investigation plots to the structural forest types a dichotomous key was developed based on the main structural characteristics differentiating between the types.

1 dbh of canopy trees <10 cm
- 1* dbh of canopy trees >10 cm, see 3
- 2 number of woody individuals <50 per 20 m x 20 m, crown shape irregular or umbrella-shaped — Secondary growth after road construction
- 2* number of woody individuals >50 per 20 m x 20 m, crown shape irregular or cylindrical — Secondary growth after landslides
- 3 trees of canopy stratum mostly coniferous — Plantation of *Pinus patula*
- 3* trees of canopy stratum mostly broad-leafed
- 4 more than 30% of canopy trees with compound leaves
- 4* less than 30% of canopy trees with compound leaves, see 6
- 5 compound leaves of canopy trees micro-mesophyll, canopy trees with many vascular epiphytes — Primary forest in Cajanuma
- 5* compound leaves of canopy trees megaphyll, canopy trees with only some vascular epiphytes — Megaphyll ridge forest
- 6 canopy trees with microphyll leaves, stems and branches covered with beard-like lichens
- 6* canopy trees with meso-, macro- or megaphyll leaves, beard-like lichens missing or rare, see 8
- 7 more than 20% of canopy trees with diagonal stems and fan-shaped crowns, connecting bamboo reaching canopy — Mesophyll ridge forest
- 7* stems of canopy trees vertical, crowns irregular or umbrella-shaped, no connecting bamboo in canopy stratum — Microphyll ridge forest

8 canopy trees with macrophyll leaves, leaves simple, semi-sclerophyll and bicoloured Macrophyll ridge forest

8* canopy trees with mesophyll leaves, if leaves macro-or megaphyll then palmately lobed, green and malacophyll

9 more than 30% of canopy trees with megaphyll, palmately lobed and malacophyll leaves Secondary forest in Mindo

9* less than 30% of canopy trees with megaphyll , palmately lobed and malacophyll leaves

10 height of canopy stratum <15 m, dbh of canopy trees <30 cm

10* height of canopy stratum >15 m, dbh of canopy trees > 30 cm, see 12

11 coverage of canopy stratum <60%, no epiphytic mosses or ferns, trees of lower stratum only rarely connected by bamboo Secondary ravine forest

11* coverage of canopy stratum >60%, trees of lower stratum conspicuously connected by bamboo Forest on edges of natural gaps

12 canopy stratum build by less than five tree individuals per 20 m x 20 m, dbh of canopy trees >50 cm

12* canopy stratum build by more than five tree individuals per 20 m x 20 m, dbh of canopy trees <50 cm, trees partly with stilt roots Primary ravine forest at higher altitudes

13 emergent trees overgrowing canopy stratum, dbh of emergent trees >80 cm, no signs of felled trees Primary ravine forest at lower altitudes

13* no emergent trees overgrowing canopy stratum, stumps of felled trees conspicuous Ravine forest under human influence

4 Discussion

4.1 The structural classification system

The presented study provides a method to classify tropical montane forest vegetation with the help of structural features in an easy to handle and reproducible manner. Nevertheless, if a new method for vegetation classification is to be developed and tested under field conditions, a framework of parameters such as plot size, plot distribution, choice of structural features, and method of data collection and statistical interpretation has to be devised and is therefore subjective. These parameters should be assigned with respect to other studies to allow comparison of the results.

4.1.1 Plot size

A plot size of 20 m x 20 m was chosen, although 100 m x 100 m or even larger plots have been proposed for forest investigations (e.g. Braun-Blanquet 1964, Richards et al. 1940). Kenkel & Podani (1991) compared estimation efficiency for different plot sizes and recommended the largest plot size that can be handled within a reasonable time. Due to the heavily inclined relief and the disturbance caused by landslides and human activity, in my investigation area, the vegetation was inhomogeneous on such a small scale that a plot of 100 m x 100 m would not have represented a homogeneous part. Moreover, to allow a statistical interpretation, a reasonable number of plots had to be investigated in a comparably short time so that a plot size of 20 m x 20 m was chosen as a compromise. In their floristical investigations of montane forests in Bolivia, Kessler & Bach (1999) used 20 m x 20 m plots for the same reasons.

4.1.2 Plot distribution

To optimise objectivity, plots should be distributed randomly in the investigation area (Kreeb 1983). In our investigation area, this was impossible due to inclination up to 60° and lack of footpaths. The therefore unavoidable subjective choice of plot locations may have resulted in complete neglect of one or more forest types. Nevertheless, the plots from two ridges were grouped together by cluster analysis and contrasted with the plots from three

ravines. Here data collection for more ridges or ravines would probably not have revealed a new forest type. However, on the slopes connecting the ravine bottom with the ridge tops a "slope forest type" (sensu WEBB et al. 1999) could have been missed. To avoid this, a line of plots was installed crossing the Quebrada El Milagro, the biggest tributary to the Rio San Francisco. Here microphyll ridge forest directly neighboured primary ravine forest without an obvious intermedium stage.

4.1.3 Structural features

WEBB et al. (1970) stated that the number of features which could be described in a structural approach is theoretically unlimited and therefore a choice has to be made. The catalogue of features used in the study presented here is based on the results of an intense testing of the applicability of several approaches known from the literature (see Results and Interpretation and compare AXMACHER 1998 for more details). From the tested systems, those features were combined which were really present in the investigation area and detectable with field methods in tropical forest vegetation. The catalogue was prolonged by features concerning connecting elements like lianas and bamboo and features describing the distribution of epiphytes because of the importance of these life-forms, particularly for montane forests (GRUBB et al. 1963, NADKARNI 1984, BOGH 1992, FINCKH & PAULSCH 1995, STERN 1995, LAURENCE et al. 2001).

A scale had to be found for each feature. The ordinate scale comparable to that proposed by WEBB et al. (1970) (absent, rare, abundant, dominant) was chosen as a compromise between just documenting presence or absence and a very time-consuming classification in 10%-intervals or even finer subdivisions. This scale was used for 143 parameters, while eight parameters, describing a tree stratum as a whole, were metric scaled. This difference in scaling could have led to an over-interpretation of the metric data (BACKHAUS et al. 1996). Therefore, the metric data were rescaled (for example a ground cover of 40% was listed as 4). Additionally, the whole cluster analysis was repeated neglecting these eight parameters and resulted in the same grouping of plots. It was concluded that the grouping was not founded on an over-interpretation of the metric data.

4.1.4 Data collection

Data collection was performed for each tree stratum and strata were defined in relation to canopy height in each plot, not in fixed heights above ground. This was necessary due to greatly differing tree heights in the altitudinal gradient and was backed by the concept of RICHARDS (1983: 3), who stated "more important than the stratification of the trees is the boundary between the euphotic zone in which the crowns are more or less fully exposed to sunlight (the canopy), and the shaded oligophotic zone (the undergrowth) beneath."

This boundary clearly depends on canopy height and cannot be found in a fixed height above ground. Hence, this definition of strata provided that in the cluster analysis canopy was compared with canopy and undergrowth with undergrowth.

4.1.5 Statistical interpretation

On the other hand, the different number of strata in different plots caused problems in the statistical analysis due to the fact that a differing number of strata meant a differing number of variables for the clustering. Therefore, it was necessary to treat the nine plots with just one single stratum separately (see Results and Interpretation). Nevertheless, it was tested to cluster these plots together with all plots with two strata, using only the canopy stratum of the two-layered plots. This clustering placed all nine one-layered plots in one cluster and did not mix any of them with another group. This result justified the separate treatment of these plots.

For a comparison of plots with two strata and plots with three strata, the middle stratum of the latter had to be neglected (see Results and Interpretation). As a test, all plots with three strata were clustered separately using all three strata. This clustering resulted in the same grouping as the original one, so that the inclusion of the middle stratum did not alter the results. In some plots, the documentation of emergent trees as highest stratum led to difficulties in the clustering and the middle stratum had to be treated as canopy as it was the highest dense stratum. With that experience in mind, I would recommend to take emergent trees not as a separate stratum but as part of the canopy in future investigations. This parallels the conclusion of RICHARDS (1983: 9) who stated "If any meaning is to be given to the word "canopy", it should refer to the B storey, together with the crowns of the emergent A storey trees which rise above it."

The observation that the nine plots with one single stratum could be divided into two groups by cluster analysis encouraged the testing, if other cluster groups could also be subdivided. This test was performed for cluster VI b and cluster VII a which had 22 plots each. In both cases, cluster analysis did not lead to a grouping in blocks but only into pairs of plots or a chain of single plots. Although of course no plot is exactly like another, it does not make sense to construct a system of dozens of forest types, each represented by only one or two plots. It was concluded that the grouping into 14 structural forest types was the first integration level that combined plots to units that could be used for ecosystem studies.

For each cluster analysis, the Ward algorithm was used with the squared Euclidean distance as distance measure. Outliers were detected with the "single-linkage" method (synonym: nearest neighbour method). These steps were recommended by BACKHAUS et al. (1996) and EVERITT (1995) to keep the within-group variation low and the between-group variation high. Nevertheless, the choice of cluster algorithm and distance measure might influence the cluster result. To avoid artificial results determined by the choice of statistical methods, several cluster analyses were repeated with another cluster algorithm (complete linkage = furthest neighbour method) and the "city-block-metric". The results differed only slightly from those gained by the recommended method, which therefore was used throughout.

A cluster analysis results in a grouping of objects with respect to certain variables but does not explain which variables were responsible for the grouping. One way to detect these factors (variables) is the Principle Component Analysis (PCA). In her investigation of the shrub vegetation above timberline in our investigation area, CZIMCZIK (1999) tried a PCA for her catalogue of variables which was based on the one developed by me. She concluded from her results that the PCA could not detect a few variables responsible for the grouping of her plots, but that is was the combination of a great part of all variables investigated that led to the grouping. Even identification of responsible or neglectable character classes (like crown shape, leaf size, or connecting elements) was not possible. Based on that experience, I tried another way to detect which variables might be responsible for grouping, and used the T-value as recommended by BACKHAUS et al. (1996) as an aid in interpretation (see Material and Methods). Table 8 (p. 71-76) makes obvious that also from the T-values it was impossible to detect only a few "responsible" variables which alone would explain the clustering. On the contrary, each cluster is characterised by another set of over- or under-represented variables from different character classes. In fact, there is virtually no variable

that can not be used to explain a part of the grouping. Hence, the investigation of T-values confirms the conclusion already drawn by CZIMCZIK (1999) that it is the combination of nearly all structural features that caused the grouping and not a few outstanding variables alone. The fact that there are virtually no "unnecessary" variables may partly be explained by the composition of the catalogue. It was based on the pre-study of several classification systems (AXMACHER 1998) and tried to eliminate all variables beforehand that were too rare or too common to have a distinguishing value, or were not detectable with field methods. As the vegetation of the eastern Andes is described as a hotspot of species diversity, a high structural diversity was also expected, because each species has morphological characters that contribute to the structure of the vegetation of which the species is part. VARESCHI (1980) argued that in the tropics, plant-growth conditions are so good that many more different morphological possibilities can be realised than at higher latitudes where harsh conditions force plants to show only well adapted structures. This might also explain why even in a long catalogue of structural characters each variable can be found realised.

Nevertheless, reduction of the catalogue and easier handling were still a focus. With the help of frequency analysis and the investigation of correlation between variables it was attempted to detect, whether some variables could be neglected without altering the results of the cluster grouping. In particular, due to correlation of variables, the catalogue could be reduced by almost 30% and a final cluster analysis using only the variables of the reduced catalogue led to the same 14 structural forest types as before. Therefore, I conclude that my study provides an easy to handle, reproducible field method to classify montane rain forest vegetation based on structural features. From the beginning, I tried to keep handling of the classification system easy by clearly defining what plot size to use, how to distinguish strata and what is meant by each variable. During the field work, several students (partly non-botanists) helped to collect data and none of them had any difficulties in handling the system even without intense training. Thus, if an area like the Podocarpus National Park should be mapped (e.g. for a management plan), the structural classification offers an easy and quick way for local institutions with only a minimal training requirement. In contrast, a floristic classification would be very time-consuming and requires the knowledge of a team of experts for all the different plant taxa.

4.2 Distribution of forest types and site conditions

4.2.1 Altitudinal zonation

The study presented here was part of the DFG-project "Analysis of undisturbed and disturbed tropical mountain forest ecosystems in southern Ecuador" (Beck & Müller-Hohenstein 2001). Nevertheless, the expression "montane rain forest" needs explanation, as it is used in different contexts (e.g. Richards 1952, Beard 1955, Grubb et al. 1963, Ellenberg 1975, Lauer & Erlenbach 1987, Gradstein & Frahm 1987). Table 14 shows the altitudinal zonation of forest vegetation of the northern Andes as described by the above mentioned authors.

Lauer & Erlenbach (1987) paralleled the terms commonly used in South America (tierra caliente - tierra nevada) to the zonation normally used for the Alps (planar - nival, exception "andin" instead of "alpine"). With that zonation they followed the scheme Ellenberg (1975) introduced as "perhumid series" for the tropical Andes. Grubb et al. (1963) redefined the classification originally given by Richards (1952), replacing his "submontane rain forest and montane rain forest" by a distinction between lower and upper montane rain forest. In the classification of Beard (1955), montane rain forest was used as a synonym for cloud forest, followed by montane thicket and an elfin woodland or mossy forest. The zonation in German given by Lauer & Erlenbach (1987) is partly a translation of the expressions used by Beard (1955). Gradstein & Frahm (1987) based their concept on the distribution of bryophytes in the Peruvian Andes. Nevertheless, in all concepts the montane rain forest (even in its subdivisions) is placed in an altitudinal range between 800 m a.s.l. and 3500 m a.s.l. Hence, the investigation area of the DFG-project at a range between 1800 m a.s.l. and 3200 m a.s.l. clearly fell into the belt of montane rain forest. The aim of the study presented here was to provide a structure-based classification of this montane rain forest.

The clustering of 139 investigation plots resulted in 14 structural forest types (Table 7, p.70). The distribution of 12 types in the closer investigation area is shown in Figure 31 (p.104). It was already mentioned that north of the Rio San Francisco and in the lower parts south of that river, five types were caused (I a and b, II) or influenced (VI a and b) by human activity and only seven types (V, VI c and d, VII a, b, c and d) could be identified as primary vegetation. Additionally, the forest in Cajanuma was also seen as primary vegetation (IV), while the forest in Mindo (III) was secondary. Nevertheless, the relief situation could be named as a underlying factor of the grouping into ravine forest (all types in cluster VI) and ridge forest (all types in cluster VII).

Table 14: Comparison of altitudinal zonation of LAUER & ERLENBACH (1987), ELLENBERG (1975), RICHARDS (1952), GRUB et al. (1963), BEARD (1955), GRADSTEIN & FRAHM (1987), and integration of structural forest types

Altitude [m]	Lauer & Erlenbach (1987) Ellenberg (1975)			Richards (1952)	Grubb et al. (1963)	Beard (1955)	Gradstein & Frahm (1987)	Structural Classification System	
6000									
	tierra nevada	nival	Glacier			Tundra			
5000									
	tierra subnevada	subnival	Super-Páramo Páramo			Páramo			
	tierra helada	andin	Sub-Páramo			Elfin Woodland (Mossy Forest)			
4000									
	tierra fria	montan	Nebelwald Höhenwald	Montane Rain Forest	Upper Montane Rain Forest	Montane Thicket	Tropical Subalpine Forest	Shrub and Gras Páramo	
3000								Primary Forest Cajanuma	
								Primary Ravine Forest at higher Altitude	Microphyll Ridge Forest
							Tropical High Montane Forest		Macrophyll Ridge Forest
2000	tierra templada	submontan	Wolkenwald Bergwald	Submontane Rain Forest	Lower Montane Rain Forest	Montane Rain Forest (Cloud Forest)		Primary Ravine Forest at lower Altitude	Megaphyll Ridge Forest (Mesophyll Ridge Forest)
							Tropical Montane Forest		
1000							Tropical Submontane Forest		
	tierra caliente	collin	Regenwald	Tropical Rain Forest	Lowland Rain Forest	Lower Montane Rain Forest			
		planar					Tropical Lowland Forest		
0									

In Table 14 seven of the primary structural forest types were placed according to their altitudinal range and the relief position. In ravines, primary ravine forest at lower altitude (VI c) reached 2030 m a.s.l. before it changed into primary ravine forest at higher altitude (VI d) that ranged from 2080 m a.s.l. to 2280 m a.s.l.. On ridges, macrophyll ridge forest (VII c) dominated between 1900 m a.s.l. and 2190 m a.s.l. and then microphyll ridge forest covered the ridges up to 2600 m a.s.l.. On the western ridge the macrophyll ridge forest was interspersed by the palm-dominated megaphyll ridge forest (VII d), while on the eastern ridge this forest type directly neighboured the microphyll ridge forest. The three plots of mesophyll ridge forest (VII b) on the eastern ridge might be a late successional stage after disturbance and hence are not interpreted as an altitudinal vegetation zone (see below). In the closer investigation area the upper forest limit was reached at 2650 m a.s.l.. The

upper part of the mountain up to the summit at 3180 m a.s.l. was covered with a mosaic of shrub vegetation units with varying dominance of grasses, palms or bromeliads (CZIMCZIK 1999).

On the western flank of the main mountain range, 12 plots were placed in the Podocarpus National Park at Cajanuma (see Material and Methods) at an altitude of 2730-3100 m a.s.l.. They were classified as a primary forest type (IV) differing significantly from both, the ridge forest types and ravine forest types of the eastern flank. Here the transition into shrub vegetation was observed at about 3100 m a.s.l. (compare CZIMCZIK 1999).

GRUBB et al. (1963) and GRUBB (1977) proposed decreasing tree height (< 15 m) and microphyll leaves as structural features characterising the upper montane rain forest in contrast to the lower montane rain forest, where trees are higher and the leaves are mesophyll or even larger. These criteria would assign the microphyll ridge forest to the upper montane rain forest (sensu GRUBB et al. 1963 and GRUBB 1977). All other structural forest types would not be further distinguished and would be assigned to lower montane rain forest, thus placing the limit between the two forest formations at about 2200 m a.s.l.. Following the zonation of BEARD (1955), the microphyll ridge forest would belong to montane thicket (due to tree height), while the other forest types would be identified as montane rain forest (synonymous with cloud forest). HAMILTON et al. (1995) defined tropical montane cloud forest (TMCF) as the uppermost forest formation characterised by reduced tree height, increased diameter/height ratio, dense crowns and microphyll (semi-) sclerophyll leaves. Hence the microphyll ridge forest could be seen as a TMCF leading to the shrub páramo (CZIMCZIK 1999, PAULSCH & CZIMCZIK 2001). In his description of the floristic composition of our investigation area, BUSSMANN (2001) confirmed the zonation of GRUBB et al. (1963) setting a limit between "montane broadleaved forest" and "upper montane forest" at about 2100 m a.s.l..

In a summary, it can be observed that the altitudinal zonation of structural forest types is not contradicting the established zonation systems and reassures a change in forest formations at about 2200 m a.s.l.; moreover, it allows further distinction of forest types which would all be assigned to one single formation in the traditional classification systems. In the following, it will be tried to interpret the structural characteristics of these forest types with respect to some site conditions:

4.2.2 Wind

Webb et al. (1999) investigated forest structure in relation to topography in Samoa and distinguished forests on ridges, slopes and in valleys. They found tree height and maximum stem diameters decreasing from valley bottoms to ridges while tree density increased. This observation is paralleled by my results: maximum diameters and tree heights were found in the primary ravine forest (VI c) where the density of canopy trees was low. Webb et al. (1999) mentioned strong winds (hurricanes) as possible cause for limited tree height on ridges where storms are strongest. Drought problems or at least water-stress situations as limiting factors were also considered to be more likely on ridges than in valley bottoms. Lawton (1982) concluded that elfin structure of trees is an adaptation to wind-stress along exposed ridges and Endlicher (1982) explained the xeromorphic features of páramo plants also as an adaptation to strong winds. He argued that maximum winds combined with insolation maxima around midday force plants to develop xeromorphic characters which could not be explained by a lack of precipitation in a perhumid climate. Meteorological investigations in our research area detected wind speed to be at a maximum at highest elevations (Richter, pers. comm.). The microphyll and semi-sclerophyll leaves and decreasing tree height in the microphyll ridge forest (VII a) could therefore be an adaptation to water-stress caused by strong winds. Influence of strong winds could also be seen in the fact that within the forest types on ridges (VII a to d), the highest trees were the palms in the megaphyll ridge forest (VII d). While Moore (1973: 66) observed that "among montane formations, palms figure prominently in lower montane and montane rain forest or cloud forest", Ewel & Bigelow (1996) described palms as especially resistant to strong winds. Palm trees have a comparably flexible stem and only lose leaves when damaged, not branches like other trees. This might explain the fact that palm trees are part of most of the forest types in the investigation area but overtop the canopy only on ridges (and in páramo vegetation Paulsch & Czimczik 2001).

4.2.3 Soil

Studies from tropical sites suggest that plant growth in montane forests could be nitrogen-limited. Tanner et al. (1990) and Tanner & Kapos (1992) showed that fertilisation with N and P led to increased growth in montane forests in Jamaica and Venezuela. In our investigation area, Schrumpf et al.

(2001) investigated edaphic parameters in an altitudinal gradient along the western ridge (compare Figure 32, p.105). They described several tendencies with increasing altitude: decreasing profile depth, increasing acidity (with minimum pH in the root layer), increasing signs of periodic water stagnation, decreasing effective cation exchange capacity, and raising C/N-values. SCHRUMPF et al. (2001) concluded that the N-nutritional status decreased with increasing altitude due to unfavourable mineralisation conditions (low pH, water stagnation, low soil temperatures). Though this is no proof of N-limitation, decreasing N-nutrition status might affect plant growth at higher altitudes and partly explain lower tree heights following the altitudinal gradient. PROCTOR et al. (1999) tried to relate soil conditions with forest stature on a tropical mountain in the Philippines. They found no relationship between maximum tree height and the soil chemical factors analysed (P, K, Ca, Mg, Ni) but a directly proportional relationship between maximum tree height and soil water retention. However, they observed a dry season of several months which does not hold true for our investigation area where severe soil water deficits are not to be expected (WILCKE et al. 2001, YASIN 2001).

4.2.4 Light

Another factor influencing forest structure and hence the distribution of structural forest types might be the light conditions. In particular, cluster III (secondary forest in Mindo) and cluster V (forest on edges of natural gaps) showed an over-representation of structural features closely related to pioneer plants. These plants, in particular species of *Cecropiaceae*, are known to show rapid growth under full-light conditions (WHITMORE 1989, ALVAREZ-BUYLLA & MARTINEZ-RAMOS 1992). LAURENCE et al. (2001) investigated effects of forest fragmentation in Amazonia and found a 33-fold increase in the abundance of *Cecropia sciadophylla*, an ubiquitous pioneer tree, since fragments were initially isolated. The same authors showed that species diversity and abundance of lianas increased at forest edges, in isolated forest fragments and gaps. In our investigation area, cluster I a (secondary growth after road construction) showed a particularly high liana density while the above mentioned forest types had mostly bamboo as connecting element. Bamboo (genus *Chusquea*) is also known as a pioneer vegetation with the potential to hinder establishment of young trees due to competition for light (FINCKH & PAULSCH 1995, STERN 1995).

Tree ferns were registered as another conspicuous life-form. Their occurence in different structural forest types cannot be easily explained by site

conditions. As ARENS (2001) observed for the Colombian Andes, some species of tree ferns are restricted to sunny, open habitats, while others are only found in the understorey of a closed-canopy forest. Hence, in this case, identification of species would be necessary while documentation of the life-form itself is not detailed enough. Nevertheless, the secondary forest in Mindo (III) was especially rich in treeferns in the lower stratum. This might parallel the observation of ARENS (2001) that some species of tree ferns can persist for longer periods in the shade of a closed forest but need opening of the canopy to regenerate. These conditions were present in the 18-year-old secondary forest of Mindo.

High species diversity and abundance of vascular epiphytes are characteristic features of tropical montane forest (GRUBB et al. 1963, NADKARNI 1984, BOGH 1992). Investigation of epiphyte distribution showed that a high coverage of vascular epiphytes on stems and branches could be observed in the forest types classified as primary vegetation (especially clusters IV, VII a and b). Most epiphytes were restricted to the canopy stratum; only in the microphyll ridge forest (VII a), where the canopy was low and covered only 30-40%, bromeliads also covered dead wood on the forest floor. This can be explained by the increasing light intensity reaching the floor under a low and sparse canopy.

In summary, next to anthropogenic influence, the conditions of relief, soil, light and wind can help to explain the distribution pattern of the structural forest types.

4.3 Disturbance and succession

As mentioned above, abiotic site conditions could be related to the distribution of primary forest types. Nevertheless, five types of secondary vegetation can only be explained considering the impact of disturbance. SOLBRIG (1993) stated that nearly every ecosystem is permanently influenced by disturbance and therefore not in an equilibrium or stable. WEISHAMPEL et al. (2001) observed that mature tropical forests even without disturbance are in a state of disequilibrium, accumulating above-ground carbon and showing increasing mortality and recruitment rates. Hence, forests have to be seen as dynamic systems. In our investigation area the most important dynamic factor were frequent landslides, and STOYAN (2000) documented that landslide-areas could still be identified on aerial photographs some decades later. Succession on natural landslides in the investigation area was examined by OHL (2000) who identified species of *Gleicheniaceae*, *Melastomataceae*, *Orchidaceae* and

Ericaceae to be the vascular plants following an initial stadium of lichens and mosses. This combination of ferns, terrestrial orchids and bushes resembles the vegetation in clusters I a and b, classified as secondary growth (compare Figure 16, p. 77 and Figure 17, p. 79). STERN (1995) documented vegetation recovery in a lower montane forest in northern Ecuador after an earthquake caused landslides. He observed that recovery was slowest on the steepest parts where vegetation and soil had been removed. Recovery depended not as much on the seed bank as on resprouting of rhizomes and roots, and seeds transported from nearby forest remnants.

Canopy gaps caused by tree-fall can be seen as a small-scale disturbance. SCHNITZER & CARSON (2001) observed that gaps play a major role in preserving diversity of pioneer plants and lianas. HUBBELL & FOSTER (1986) ex STERN 1995 even assumed that a region with such a high frequency of disturbance as the tropical Andes held potential colonisers and chance immigrants which contributed to the extraordinarily high plant species diversity. The three plots which constituted the mesophyll ridge forest (cluster VII b) were all characterised by over-representation of diagonal stems, fan-shaped crowns, dead branches, lianas and bamboo in the canopy layer (see Table 8, p. 71-76). Fan-shaped crowns are the result of resprouting after damage. PACIOREK et al. (2000: 766) claimed resprouting to be "a key component of plant life history" after disturbance. This favoured the conclusion that the mesophyll ridge forest type could be a late successional stage after landslides or another disturbance, causing treefall without removal of the fallen stems.

Next to natural disturbances, human impact influences forest structure. The forest types VI b (ravine forest under human influence), VI a (secondary ravine forest), I a and I b (secondary growth) and II (plantation of *Pinus patula*) can be seen as a gradient of increasing anthropogenic influence beginning with selective logging, clearing and burning, and leading to the introduction of foreign species. HARTIG (2000) investigated successional stages after pasture in the northern part of our investigation area, e.g. adjacent to the plots of clusters I and II. She concluded that a stadium dominated by ferns is followed by bush vegetation, possibly leading to secondary forest. Input of seeds of forest trees was seen as a limiting factor. HOLL et al. (2000) formed the same conclusion for former pastures in Costa Rica and claimed that animal-dispersed seeds in particular did not reach the open pasture. Additionally, light competition of pasture grasses inhibited seedling establishment. The authors recommended planting of woody species to fasten forest regeneration. POSADA et al. (2000) proposed cattle grazing with a ten-times lower grazing intensity than during agronomic use for pastures in Colombia. Reduced grass biomass would favour the seedlings of woody species. Neverthe-

less, the authors also recommended the planting of native tree seedlings.

As the population of Ecuador is still rapidly growing and the need for wood, agricultural products and land for pasture is also increasing, it is not probable to assume that grazing intensity will decrease, burning of primary forest will stop and selective logging will never reach even remote areas. Nevertheless, there are reforestation efforts but if a sustainable forest usage should be established, native tree species should be used for reforestation. In Mindo (north of Quito, pers. observation), next to the test plots, reforestation with the native *Alnus acuminata* Hunth was tried on pasture. This fast growing tree species provides local farmers with fire wood and thus relieves pressure from the forest remnants. This might be a promising way, although a monoculture, even of native tree species, cannot have habitat qualities comparable to a primary forest.

4.4 Functional relationships

As mentioned in the introduction, the vegetation classification presented in this study was performed within the framework of a DFG-project which combined different research disciplines. The results of SCHRUMPF et al. (2001), WILCKE et al. (2001), YASIN (2001), STOYAN (2000), OHL (2000), and HARTIG (2000) were already cited for interpretation of site conditions and succession after disturbance. The classification of structural forest types was meant as a basis for investigation of functional relationships between vegetation and other components of the forest ecosystem.

DZIEDZIOCH (2001) studied species composition and phenology of hummingbird-visited plants in an one-hectare transect in the lower part of our investigation area. She identified 72 plant species and documented the numbers of species and individuals in each 10 m x 10 m subplot every 14 days for one year. With the help of the dichotomous key to the structural forest types each subplot was assigned to a structural type. Five types could be found: primary ravine forest at lower altitude (VI c), mesophyll ridge forest (VII b), megaphyll ridge forest (VII d), macrophyll ridge forest (VII c), and macrophyll ridge forest in a variety with dominance of ground-living bromeliads close to plot 92 (compare Figure 28, p. 105). Statistical interpretation (alpha-, and beta-diversity, discriminance analysis) revealed that the distribution of hummingbird-visited plant species and plant individuals reflected the structural forest types and thus the nectar resource was unevenly distributed in the one-hectare plot (DZIEDZIOCH 2001, DZIEDZIOCH & PAULSCH, submitted). The primary ravine forest offered the lowest nectar resource while the mac-

rophyll ridge forest (in the variety with many bromeliads) offered the highest. The most abundant life-form within the hummingbird-visited plant species and individuals were epiphytes (DZIEDZIOCH 2001). Neglecting epiphyte distribution in the catalogue of structural features might have led to failure to identify the close correlation between forest structure and hummingbird-visited plants. This conclusion supported the decision to keep the epiphyte distribution even in the shortened catalogue of features (see Table 13, p. 112-116).

As a consequence, the classification of structural forest types can now be used as an instrument to obtain a very rapid overview of habitat suitability for a certain functional group, i.e. hummingbirds or their food plants. Ongoing studies will show whether structural types and moth communities in the Ecuadorian montane forests can be related in a similar way (BREHM in prep. and SÜß ENBACH in prep.).

Based on the distribution of forest types presented in this study, PAULSCH, D. (in prep.) investigates bird communities. Preliminary results show that certain bird species are restricted to primary ravine forest or macrophyll ridge forest, respectively (PAULSCH, D. et al. 2001).

In conclusion, the present study reached its aim to provide a method to distinguish forest units with the help of structural features. A series of features was selected and quantifying documentation of these features led to vegetation units. The spatial distribution of these units could be documented and related to abiotic site conditions. A choice of features having the highest potential to distinguish between units was selected and a key for vegetation units developed. A test of that key and the significance of the distribution of vegetation types with respect to a certain zoologic functional group was performed by DZIEDIOCH (2001) in a parallel study in the same investigation area. Further research will show if moth and bird communities can also be related to certain structural forest types.

The next logical step of future investigation should be to examine *which* structural features are responsible for which functions. This idea is the basis for the concept of "plant functional types" (PFT) as summarised by SMITH et al. (1997). WALKER (1997: 93) stated: "In order to achieve a useful PFT-classification, there is a need for better definition and understanding of the critical ecosystem processes and environmental factors that determine the structure and function of an ecosystem." A study of ecosystem components, fluxes and functions like the DFG-project the study presented here was part of, could be a basis for what WESTOBY & LEISHMAN (1997: 105) seek: "a global key of plant functional types to predict vegetation dynamic under future global change." WALKER (1997) as well as LAWTON & BROW (1993) stated that

there is redundancy between plant species, meaning that if species become extinct, others can take their place without consequences for the ecosystem functioning; although "loss of a life-form is likely to precipitate changes in both, the composition and functioning of the ecosystem it was part of" (Ewel & Bigelow 1996: 116). Hence, the investigation of vegetation structure and function should be part of every ecosystem study that is used to model or predict changes under changing conditions. The new system to classify vegetation presented in this study (maybe with slight alterations with respect to local specialities) could be a tool applicable to a wide range of forest vegetation with the added advantage that its use is not restricted to experts.

5 Literature

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Maps:

Insituto Geográfico Militar, Quito Ecuador: Cartas Topofráficas 1: 50000 del Ecuador
Hoja Loja Norte NVI-F4 3782-II (1981)
Hoja Loja Sur (Rio Sabanilla) NVII-B2 3781-I (1996)
Hoja Zamora NVII-A1 38881-IV (1994)

Aerial photographs:

Insitito Geográfico Militar 1998, Quito, Ecuador
Proyecto Carta Nacional # 5361 R22RC30 from 20.05.1998

Appendices

Table A:

Mean value, standard deviation, and T-value for all variables in all cluster groups for the canopy stratum of 130 plots with more than one stratum.

Table B:

Mean value, standard deviation, and T-value for all variables in all cluster groups for the undergrowth stratum of 130 plots with more than one stratum.

Table A: Mean value, standard deviation, and T-value for all variables in all cluster groups for the canopy stratum of 130 plots with more than one stratum.

Character class	Character	X all plots	S all plots	X cl II	T cl II	X cl III	T cl III	X cl IV	T cl IV	X cl V	T cl V	X cl VI a	T cl VI a	X cl VI b	T cl VI b	X cl VI c	T cl VI c	X cl VI d	T cl VI d	X cl VII a	T cl VII a	X cl VII b	T cl VII b	X cl VII c	T cl VII c	X cl VII d	T cl VII d
N		130	130	5	5	7	7	10	10	6	6	14	14	22	22	19	19	10	10	21	21	3	3	6	6	3	3
Woodiness	axylous	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	hemixylous	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	holoxylous	3,00	0,00	3,00		3,00		3,00		3,00		3,00		3,00		3,00		3,00		3,00		3,00		3,00		3,00	
Stem characters	polycormous	0,47	0,72	0,20	-0,38	0,57	0,14	0,80	0,46	0,33	-0,19	0,71	0,34	0,14	-0,46	0,47	0,01	0,00	-0,65	0,71	0,34	0,67	0,28	0,83	0,51	0,00	-0,65
	vertical	2,89	0,34	3,00	0,32	3,00	0,32	2,90	0,02	3,00	0,32	2,93	0,11	3,00	0,32	2,89	0,01	3,00	0,32	2,86	-0,11	2,00	-2,66	2,33	-1,67	3,00	0,32
	diagonal	0,63	0,80	0,00	-0,79	0,14	-0,61	1,20	0,71	0,50	-0,16	0,29	-0,43	0,23	-0,51	0,74	0,13	0,40	-0,29	0,67	0,04	2,00	1,71	2,00	1,71	1,33	0,88
	dead	0,40	0,64	0,20	-0,31	0,43	0,04	0,80	0,62	0,67	0,42	0,50	0,16	0,05	-0,55	0,42	0,03	1,00	0,93	0,43	0,04	0,00	-0,62	0,17	-0,36	0,00	-0,62
Bark characters	green thin smooth	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	green thin rough	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	green thick smooth	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	green thick rough	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	non-green thin smooth	0,62	1,03	0,00	-0,61	1,00	0,37	0,10	-0,51	0,83	0,20	1,64	0,99	0,73	0,10	0,58	-0,04	0,40	-0,22	0,33	-0,28	0,00	-0,61	0,50	-0,12	1,33	0,69
	non-green thin rough	1,32	1,28	0,00	-1,03	1,71	0,30	1,10	-0,17	2,00	0,53	1,14	-0,14	0,27	-0,82	2,05	0,57	0,90	-0,33	1,71	0,30	1,00	-0,25	2,83	1,18	1,67	0,27
	non-green thick smooth	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,45	0,00	-0,09	0,00	-0,09	0,00	-0,09
	non-green thick rough	1,42	1,30	0,00	-1,08	1,14	-0,21	2,40	0,75	0,83	-0,45	0,57	-0,65	2,36	0,73	0,58	-0,64	2,50	0,83	1,52	0,08	1,67	0,19	0,67	-0,57	1,00	-0,32
	non-green very thick rough	0,27	0,80	3,00	3,43	0,43	0,20	0,00	-0,34	0,33	0,08	0,21	-0,07	0,00	-0,34	0,21	-0,07	0,20	-0,09	0,19	-0,10	0,67	0,50	0,00	-0,34	0,00	-0,34
	flaky	0,04	0,26	0,00	-0,15	0,14	0,40	0,00	-0,15	0,33	1,13	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,67	2,40	0,00	-0,15	0,00	-0,15
Roots	tabulate roots	0,04	0,23	0,00	-0,17	0,14	0,45	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,16	0,52	0,10	0,27	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17
	stilt roots	0,42	0,77	0,00	-0,54	0,00	-0,54	0,00	-0,54	0,00	-0,54	0,21	-0,26	0,27	-0,19	0,74	0,42	1,00	0,76	0,52	0,14	0,67	0,33	0,67	0,33	1,33	1,20
	aerial roots	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
Crown volume	restricted to top	0,33	0,75	0,00	-0,44	0,14	-0,25	0,30	-0,04	0,50	0,23	0,00	-0,44	0,09	-0,32	0,53	0,26	0,00	-0,44	0,57	0,32	0,00	-0,44	0,67	0,45	2,00	2,22
	restricted to upper third	2,67	0,80	0,20	-3,08	3,00	0,41	2,60	-0,09	3,00	0,41	2,71	0,06	2,64	-0,04	2,53	-0,18	3,00	0,41	2,86	0,23	3,00	0,41	3,00	0,41	2,67	-0,00
	restricted to upper half	0,38	0,71	0,60	0,32	0,14	-0,33	0,40	0,03	0,17	-0,30	0,64	0,38	0,59	0,30	0,42	0,06	0,10	-0,39	0,24	-0,20	0,00	-0,53	0,33	-0,05	0,00	-0,53
	reaching deeper than half	0,17	0,59	2,40	3,81	0,14	-0,04	0,10	-0,12	0,00	-0,29	0,43	0,44	0,00	-0,29	0,11	-0,11	0,00	-0,29	0,00	-0,29	0,00	-0,29	0,00	-0,29	0,00	-0,29
Crown development	full	2,78	0,51	3,00	0,42	3,00	0,42	2,70	-0,16	2,67	-0,23	2,93	0,28	2,95	0,33	2,42	-0,71	2,80	0,03	2,95	0,33	2,67	-0,23	2,33	-0,88	3,00	0,42
	restricted by neighbours	0,51	0,85	0,80	0,35	0,00	-0,60	0,40	-0,13	0,83	0,38	0,21	-0,35	0,09	-0,49	1,37	1,02	0,40	-0,13	0,10	-0,49	0,00	-0,60	1,67	1,37	0,33	-0,21
	stunted	0,21	0,51	0,00	-0,41	0,29	0,15	0,80	1,16	0,17	-0,08	0,14	-0,13	0,00	-0,41	0,00	-0,41	0,40	0,38	0,38	0,34	0,33	0,25	0,17	-0,08	0,00	-0,41
Crown shape	round	0,46	0,74	0,00	-0,63	0,14	-0,43	0,50	0,05	0,17	-0,40	0,86	0,54	0,59	0,18	0,37	-0,13	0,30	-0,22	0,48	0,02	0,00	-0,63	0,67	0,28	1,00	0,73
	umbrella-shaped	2,09	1,03	0,00	-2,03	3,00	0,88	2,10	0,01	2,33	0,23	2,14	0,05	2,32	0,22	1,79	-0,29	2,00	-0,09	1,95	-0,14	2,33	0,23	2,67	0,56	2,33	0,23
	cylindrical	0,07	0,28	0,00	-0,24	0,14	0,26	0,20	0,46	0,17	0,34	0,14	0,26	0,00	-0,24	0,05	-0,06	0,00	-0,24	0,10	0,09	0,00	-0,24	0,00	-0,24	0,00	-0,24
	conical	0,15	0,60	3,00	4,77	0,00	-0,24	0,00	-0,24	0,17	0,03	0,00	-0,24	0,00	-0,24	0,11	-0,07	0,00	-0,24	0,05	-0,16	0,00	-0,24	0,00	-0,24	0,00	-0,24
	funnel-shaped/umbelliferous	0,22	0,59	0,00	-0,36	0,14	-0,14	0,00	-0,38	0,50	0,47	0,00	-0,38	0,14	-0,15	0,16	-0,11	0,00	-0,36	0,43	0,35	0,00	-0,38	0,67	0,76	2,00	3,02
	fanshaped	0,08	0,31	0,00	-0,28	0,00	-0,28	0,20	0,38	0,00	-0,28	0,07	-0,04	0,00	-0,28	0,05	-0,10	0,00	-0,28	0,10	0,03	0,67	1,90	0,17	0,27	0,33	0,81
	irregular	1,35	1,08	0,80	-0,51	0,57	-0,72	1,90	0,50	2,00	0,60	0,93	-0,39	0,55	-0,75	1,89	0,50	1,90	0,50	1,43	0,07	1,67	0,29	2,00	0,60	1,00	-0,33
Crown overlap	Type 1	0,98	1,18	0,00	-0,83	0,00	-0,83	1,30	0,27	0,83	-0,13	1,29	0,25	1,36	0,32	0,68	-0,25	0,60	-0,33	1,67	0,58	0,67	-0,27	0,17	-0,69	0,67	-0,27
	Type2	1,96	1,14	0,00	-1,73	1,86	-0,09	2,40	0,39	2,33	0,33	2,07	0,10	1,68	-0,25	2,16	0,17	2,80	0,74	1,76	-0,18	2,33	0,33	1,67	-0,26	2,33	0,33
	Type 3	0,88	1,02	3,00	2,08	2,14	1,24	0,70	-0,17	0,67	-0,21	0,93	0,05	0,18	-0,68	1,16	0,28	0,50	-0,37	0,38	-0,49	0,67	-0,21	1,83	0,94	1,00	0,12
Branches	mostly horizontal	0,15	0,44	1,80	3,75	0,00	-0,35	0,20	0,11	0,00	-0,35	0,07	-0,19	0,05	-0,25	0,21	0,13	0,10	-0,12	0,05	-0,24	0,00	-0,35	0,00	-0,35	0,00	-0,35
	mostly diagonal	2,91	0,38	2,20	-1,85	3,00	0,24	2,90	-0,02	3,00	0,24	3,00	0,24	3,00	0,24	3,00	0,24	2,90	-0,02	2,71	-0,51	3,00	0,24	3,00	0,24	3,00	0,24
	mostly vertical	0,14	0,48	0,00	-0,29	0,00	-0,29	0,20	0,13	0,00	-0,29	0,07	-0,14	0,00	-0,29	0,05	-0,18	0,50	0,76	0,33	0,41	0,00	-0,29	0,33	0,41	0,00	-0,29
	dead	2,35	0,81	2,60	0,31	3,00	0,80	3,00	0,80	2,17	-0,23	1,79	-0,71	1,64	-0,89	2,32	-0,05	2,50	0,18	2,62	0,33	3,00	0,80	3,00	0,80	2,33	-0,03
	missing	0,22	0,56	0,00	-0,40	0,14	-0,14	0,00	-0,40	0,33	0,20	0,07	-0,27	0,09	-0,24	0,11	-0,21	0,00	-0,40	0,52	0,54	0,00	-0,40	0,67	0,79	2,00	3,17
Branching pattern	Type 1	1,52	1,14	0,00	-1,33	2,43	0,80	0,30	-1,06	1,83	0,28	2,36	0,74	2,68	1,02	1,26	-0,22	0,60	-0,80	1,00	-0,45	0,00	-1,33	2,00	0,42	2,00	0,42
	Type 2	1,80	1,10	3,00	1,09	1,71	-0,08	2,60	0,73	2,17	0,33	1,29	-0,47	0,45	-1,22	2,21	0,37	2,90	1,00	1,52	-0,25	3,00	1,09	2,00	0,18	2,33	0,48
	Type 3	0,72	0,97	0,00	-0,74	0,14	-0,59	1,50	0,81	0,17	-0,57	0,14	-0,59	0,36	-0,36	0,42	-0,30	0,60	-0,12	1,86	1,18	0,00	-0,74	1,00	0,29	1,00	0,29
Leaf shape	simple	2,68	0,79	0,00	-3,39	2,57	-0,14	2,80	0,15	3,00	0,41	2,71	0,04	2,50	-0,23	2,95	0,34	3,00	0,41	2,76	0,19	3,00	0,41	3,00	0,41	2,67	-0,02
	narrow leaved	0,22	0,65	3,00	4,27	0,00	-0,34	0,00	-0,34	0,00	-0,34	0,07	-0,23	0,00	-0,34	0,21	-0,02	0,00	-0,34	0,19	-0,05	0,00	-0,34	0,67	0,68	0,33	0,17
	palmately lobed	0,55	0,82	0,00	-0,68	1,29	0,90	0,40	-0,19	1,17	0,75	0,93	0,46	0,59	0,05	0,58	0,03	0,60	0,06	0,19	-0,44	0,00	-0,68	0,17	-0,47	0,67	0,14
	compound	0,48	0,76	0,00	-0,63	0,14	-0,44	1,30	1,08	0,67	0,25	0,21	-0,35	0,27	-0,27	0,32	-0,21	0,30	-0,23	0,62	0,19	0,00	-0,63	0,83	0,47	2,00	2,01
	ether	0,02	0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,05	0,24	0,05	0,30	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12
	with drip-tip	0,77	0,84	0,00	-0,92	1,57	0,95	0,80	0,04	0,67	-0,12	0,71	-0,07	1,36	0,71	0,84	0,09	1,10	0,39	0,14	-0,75	0,67	-0,12	0,33	-0,52	0,33	-0,52
	absent	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
Leaf consistency	hymenophyll	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	malacophyll	1,85	1,28	3,00	0,89	3,00	0,89	0,60	-0,98	2,83	0,76	2,71	0,67	2,27	0,33	2,89	0,81	2,80	0,74	0,05	-1,41	0,00	-1,45	0,33	-1,19	1,00	-0,67
	semi-sclerophyll	1,52	1,30	0,00	-1,17	0,00	-1,17	2,90	1,07	0,67	-0,66	0,64	-0,67	1,32	-0,15	0,63	-0,68	0,80	-0,55	3,00	1,15	3,00	1,15	3,00	1,15	3,00	1,15
	sclerophyll	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,45	0,00	-0,09	0,00	-0,09	0,00	-0,09
	semi-succulent	0,18	0,57	0,00	-0,33	0,00	-0,33	0,20	0,03	0,17	-0,03	0,00	-0,33	0,00	-0,33	0,00	-0,33	0,00	-0,33	0,67	0,85	0,33	0,26	0,33	0,26	0,67	0,85
	succulent	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	

Table A: (continued) Mean value, standard deviation, and T-value for all variables in all cluster groups for the canopy stratum of 130 plots with more than one stratum.

Character class	Character	X all plots	S all plots	X cl II	T cl II	X cl III	T cl III	X cl IV	T cl IV	X cl V	T cl V	X cl VI a	T cl VI a	X cl VI b	T cl VI b	X cl VI c	T cl VI c	X cl VI d	T cl VI d	X cl VII a	T cl VII a	X cl VII b	T cl VII b	X cl VII c	T cl VII c	X cl VII d	T cl VII d
Leaf colour	green	2,95	0,21	3,00	0,22	3,00	0,22	3,00	0,22	3,00	0,22	3,00	0,22	3,00	0,22	3,00	0,22	3,00	0,22	2,95	-0,01	3,00	0,22	2,17	-3,74	3,00	0,22
	red	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	bicoloured	0,31	0,67	0,00	-0,46	0,29	-0,03	0,20	-0,16	0,67	0,54	0,14	-0,25	0,00	-0,46	0,21	-0,15	0,10	-0,31	0,52	0,32	0,00	-0,46	2,00	2,53	0,67	0,54
Tree phenology	evergreen	2,95	0,37	3,00	0,12	3,00	0,12	3,00	0,12	3,00	0,12	3,00	0,12	2,86	-0,24	2,84	-0,30	3,00	0,12	3,00	0,12	3,00	0,12	3,00	0,12	3,00	0,12
	deciduous	0,02	0,26	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,14	0,43	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09
Leaf size	sub-leptophyll	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	leptophyll	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	nanophyll	0,24	0,67	3,00	4,13	0,00	-0,36	0,30	0,09	0,17	-0,11	0,07	-0,25	0,00	-0,36	0,16	-0,12	0,00	-0,36	0,24	-0,00	0,00	-0,36	0,33	0,14	0,00	-0,36
	nano-microphyll	0,48	0,88	0,00	-0,54	0,00	-0,54	0,80	0,37	0,67	0,22	0,00	-0,54	0,18	-0,33	0,05	-0,48	0,20	-0,31	1,52	1,19	0,00	-0,54	0,83	0,40	0,67	0,22
	microphyll	0,57	0,96	0,00	-0,60	0,14	-0,45	0,70	0,14	0,33	-0,25	0,64	0,08	0,32	-0,26	0,21	-0,38	0,40	-0,18	1,14	0,60	0,00	-0,60	1,83	1,32	1,33	0,80
	micro-mesophyll	1,28	1,13	0,00	-1,13	0,14	-1,00	2,10	0,73	1,33	0,05	0,93	-0,31	1,91	0,56	1,47	0,17	1,60	0,28	0,62	-0,58	2,33	0,93	1,50	0,20	1,00	-0,24
	mesophyll	1,08	1,08	0,00	-0,99	2,14	0,98	1,00	-0,07	1,83	0,70	1,14	0,06	0,77	-0,28	1,47	0,37	1,80	0,67	0,48	-0,55	1,33	0,24	0,33	-0,69	1,33	0,24
	macrophyll	0,83	0,92	0,00	-0,90	0,86	0,03	0,50	-0,36	1,33	0,54	1,07	0,26	0,45	-0,41	1,05	0,24	1,00	0,18	0,67	-0,18	0,00	-0,90	2,17	1,44	1,00	0,18
	megaphyll	0,40	0,75	0,00	-0,53	1,29	1,18	0,20	-0,27	0,50	0,13	0,36	-0,06	0,23	-0,23	0,42	0,03	0,10	-0,40	0,33	-0,09	0,00	-0,53	0,67	0,35	2,00	2,12
Leaf length	<1cm	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,45	0,00	-0,09	0,00	-0,09	0,00	-0,09
	up to 2cm	0,12	0,39		-0,31	0,00	-0,31	0,50	0,96	0,00	-0,31	0,07	-0,13	0,00	-0,31	0,05	-0,18	0,00	-0,31	0,29	0,41	0,00	-0,31	0,33	0,53	0,00	-0,31
	up to 5cm	0,72	1,02	0,00	-0,71	0,00	-0,71	0,90	0,17	0,83	0,11	0,00	-0,71	0,23	-0,49	0,16	-0,55	0,60	-0,12	2,14	1,39	0,00	-0,71	1,83	1,09	1,67	0,93
	up to 10cm	1,48	1,14	0,00	-1,29	0,14	-1,17	2,20	0,63	1,83	0,31	1,43	-0,04	2,23	0,66	1,42	-0,05	1,80	0,28	0,86	-0,54	2,33	0,75	1,67	0,17	1,33	-0,13
	up to 20cm	1,35	1,05	3,00	1,57	2,00	0,62	1,10	-0,24	1,33	-0,02	1,50	0,14	0,68	-0,64	1,53	0,16	2,00	0,62	0,81	-0,52	1,33	-0,02	1,67	0,30	1,67	0,30
	up to 50cm	0,62	0,83	0,00	-0,75	0,86	0,28	0,40	-0,27	1,33	0,86	0,93	0,37	0,36	-0,31	1,05	0,52	0,70	0,09	0,19	-0,52	0,00	-0,75	0,67	0,05	1,00	0,45
	>50cm	0,39	0,76	0,00	-0,51	1,29	1,17	0,10	-0,38	0,50	0,14	0,29	-0,14	0,32	-0,10	0,26	-0,17	0,10	-0,38	0,43	0,05	0,00	-0,51	0,67	0,36	2,00	2,11
Leaf width	<1cm	0,25	0,69	3,00	4,01	0,00	-0,37	0,20	-0,08	0,17	-0,13	0,07	-0,27	0,00	-0,37	0,16	-0,14	0,00	-0,37	0,24	-0,02	0,00	-0,37	0,83	0,85	0,33	0,12
	up to 2cm	0,36	0,78	0,00	-0,46	0,00	-0,46	0,80	0,56	0,33	-0,04	0,14	-0,28	0,09	-0,35	0,11	-0,33	0,00	-0,46	0,95	0,76	0,00	-0,46	0,67	0,39	0,33	-0,04
	up to 5cm	1,16	1,17	0,00	-1,00	0,14	-0,87	2,10	0,80	1,17	0,00	0,43	-0,63	0,09	-0,92	1,58	0,36	1,70	0,46	1,95	0,68	2,33	1,00	1,83	0,58	2,00	0,72
	up to 10cm	1,40	1,17	0,00	-1,19	2,00	0,51	1,30	-0,09	1,50	0,09	1,79	0,33	2,41	0,86	1,32	-0,07	1,80	0,34	0,43	-0,83	1,33	-0,06	0,33	-0,91	1,33	-0,06
	up to 20cm	0,62	0,85	0,00	-0,73	0,57	-0,05	0,20	-0,49	1,00	0,45	0,93	0,37	0,36	-0,30	0,58	-0,04	0,50	-0,14	0,48	-0,16	0,00	-0,73	2,17	1,83	0,67	0,06
	up to 50cm	0,58	0,82	0,00	-0,71	0,29	-0,36	0,20	-0,46	1,33	0,93	0,86	0,34	0,45	-0,15	0,89	0,39	0,60	0,03	0,57	-0,01	0,00	-0,71	0,17	-0,50	1,00	0,52
	>50cm	0,28	0,66	0,00	-0,42	1,29	1,53	0,10	-0,27	0,50	0,34	0,29	0,01	0,23	-0,08	0,21	-0,10	0,10	-0,27	0,05	-0,35	0,00	-0,42	0,67	0,59	1,33	1,60
Leaf angle	mainly hanging down	0,54	0,84	3,00	2,94	0,74	0,24	0,60	0,07	0,67	0,15	0,79	0,30	0,00	-0,64	0,84	0,36	0,10	-0,52	0,14	-0,47	0,67	0,15	0,00	-0,64	1,67	1,35
	mainly horizontal	1,11	1,04	0,00	-1,07	2,43	1,27	0,70	-0,39	1,17	0,06	1,43	0,31	1,50	0,38	1,68	0,56	1,10	-0,01	0,14	-0,93	0,00	-1,07	0,50	-0,59	1,33	0,22
	mainly horizontal <45°	2,16	1,02	0,00	-2,12	1,71	-0,44	2,90	0,73	2,67	0,50	1,86	-0,30	2,00	-0,16	1,84	-0,31	2,80	0,63	2,52	0,36	2,33	0,17	2,50	0,33	2,67	0,50
	mainly steeper than 45°	0,25	0,66	0,00	-0,38	0,00	-0,38	0,20	-0,08	0,00	-0,38	0,14	-0,17	0,00	-0,38	0,05	-0,30	0,00	-0,38	0,95	1,05	0,67	0,62	0,83	0,87	0,00	-0,38
Spinescence	spines on stem	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,45	0,00	-0,09	0,00	-0,09	0,00	-0,09
	spines on branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	spines on leafs	0,03	0,21	0,00	-0,14	0,14	0,53	0,00	-0,14	0,00	-0,14	0,00	-0,14	0,05	0,07	0,00	-0,14	0,00	-0,14	0,00	-0,14	0,00	-0,14	0,00	-0,14	0,67	2,98
Hairiness	hairs on stems	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	hairs on branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	hairs on leafs	0,08	0,34	0,00	-0,22	0,00	-0,22	0,30	0,65	0,50	1,23	0,00	-0,22	0,05	-0,09	0,00	-0,22	0,00	-0,22	0,14	0,19	0,00	-0,22	0,00	-0,22	0,00	-0,22
Epiphytic lichens	crustose lichens	1,92	2,15	0,60	-0,62	1,57	-0,16	2,30	0,18	2,17	0,11	1,50	-0,20	0,00	-0,90	2,47	0,26	1,50	-0,20	2,81	0,41	3,00	0,50	3,00	0,50	2,00	0,04
	foliose lichens	1,22	1,23	**0,20**	-0,83	0,00	-0,99	2,10	0,71	1,50	0,22	1,07	-0,12	0,09	-0,92	1,58	0,29	0,80	-0,34	1,95	0,59	2,67	1,17	2,00	0,63	2,00	0,63
	shrubby lichens	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	beard-like lichens	1,00	1,26	0,20	-0,64	0,14	-0,68	2,30	1,03	0,33	-0,53	0,36	-0,51	0,00	-0,80	0,53	-0,38	0,10	-0,72	2,62	1,29	2,33	1,06	2,83	1,46	2,00	0,80
Epiphytic mosses	on stem	2,77	0,68	0,40	-3,50	3,00	0,34	3,00	0,34	2,83	0,09	2,14	-0,93	2,91	0,21	2,95	0,26	2,90	0,19	3,00	0,34	3,00	0,34	3,00	0,34	3,00	0,34
	on branches	2,47	0,90	0,40	-2,30	2,71	0,27	2,90	0,48	2,33	-0,15	1,21	-1,40	2,68	0,24	2,68	0,24	2,80	0,37	2,76	0,33	3,00	0,59	2,33	-0,15	3,00	0,59
Epiphytic ferns	on stem	1,79	1,03	0,00	-1,74	2,43	0,62	2,50	0,69	1,67	-0,12	0,43	-1,32	1,95	0,16	1,89	0,10	2,00	0,20	1,62	-0,17	3,00	1,17	2,33	0,52	3,00	1,17
	on branches	1,01	0,94	0,00	-1,07	1,00	-0,01	1,80	0,84	0,67	-0,36	0,21	-0,84	1,36	0,38	1,47	0,49	0,80	-0,22	0,62	-0,41	2,33	1,40	0,33	-0,71	2,33	1,40
Woody epiphytes	on stem	1,15	1,11	0,00	-1,03	0,57	-0,52	2,40	1,13	1,17	0,02	0,07	-0,97	0,00	-1,03	1,26	0,11	1,90	0,68	1,95	0,73	2,67	1,37	1,83	0,62	2,00	0,77
	on branches	0,65	0,97	0,00	-0,67	0,14	-0,52	2,30	1,70	0,83	0,19	0,07	-0,59	0,00	-0,67	0,68	0,04	0,80	0,16	1,10	0,46	2,33	1,74	0,00	-0,67	0,67	0,02
Epiphytic Araceae	on stem	0,55	0,80	0,00	-0,69	1,14	0,74	0,10	-0,57	0,33	-0,28	0,21	-0,43	0,00	-0,69	1,11	0,69	1,40	1,06	0,38	-0,22	1,67	1,39	0,67	0,14	0,67	0,14
	on branches	0,11	0,38	0,00	-0,28	0,14	0,09	0,00	-0,28	0,17	0,16	0,21	0,28	0,00	-0,28	0,21	0,27	0,20	0,24	0,00	-0,28	0,33	0,60	0,00	-0,28	0,67	1,48

Table A: (continued) Mean value, standard deviation, and T-value for all variables in all cluster groups for the canopy stratum of 130 plots with more than one stratum.

Character class	Character	X all plots	S all plots	X cl II	T cl II	X cl III	T cl III	X cl IV	T cl IV	X cl V	T cl V	X cl VI a	T cl VI a	X cl VI b	T cl VI b	X cl VI c	T cl VI c	X cl VI d	T cl VI d	X cl VII a	T cl VII a	X cl VII b	T cl VII b	X cl VII c	T cl VII c	X cl VII d	T cl VII d
Epiphytic bromeliads	on stem	1,84	0,97	0,00	-1,89	2,00	0,17	1,60	-0,25	1,83	-0,01	1,36	-0,50	2,09	0,26	1,68	-0,16	2,70	0,89	2,00	0,17	1,67	-0,18	2,00	0,17	2,67	0,85
	in branching	0,98	0,88	0,00	-1,10	0,29	-0,78	1,70	0,82	0,83	-0,16	0,79	-0,22	0,91	-0,08	0,95	-0,03	1,10	0,14	1,19	0,24	2,00	1,16	0,83	-0,16	1,00	0,03
	in vertical branches	0,38	0,76	0,00	-0,51	0,00	-0,51	0,20	-0,24	0,00	-0,51	0,29	-0,13	0,82	0,57	0,58	0,26	0,00	-0,51	0,38	-0,00	0,00	-0,51	0,67	0,37	0,00	-0,51
	on diagonal branches	1,56	0,95	0,00	-1,65	1,00	-0,59	1,80	0,25	1,83	0,29	1,14	-0,44	0,68	-0,93	2,16	0,63	1,80	0,25	2,05	0,51	2,67	1,17	2,00	0,46	1,67	0,11
	on horizontal branches	0,44	0,80	0,00	-0,55	0,00	-0,55	0,20	-0,30	0,50	0,08	0,07	-0,46	0,77	0,42	0,58	0,18	0,20	-0,30	0,33	-0,13	0,00	-0,55	1,83	1,75	0,00	-0,55
	on dead branches	0,98	0,90	0,00	-1,08	0,14	-0,92	1,40	0,47	1,00	0,03	0,50	-0,53	0,91	-0,08	1,00	0,03	1,00	0,03	1,38	0,45	1,67	0,76	1,33	0,40	1,00	0,03
	on organic ground material	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
Epiphytic orchids	on stem	1,79	1,08	0,00	-1,65	1,57	-0,20	1,80	0,01	2,67	0,81	0,71	-1,00	2,23	0,40	1,89	0,09	1,50	-0,27	2,00	0,19	2,33	0,50	2,33	0,50	2,67	0,81
	in branching	0,60	0,82	0,00	-0,73	0,57	-0,03	1,30	0,85	0,33	-0,32	0,14	-0,56	0,50	-0,12	0,53	-0,09	0,10	-0,61	1,10	0,60	1,00	0,49	0,33	-0,32	1,00	0,49
	on vertical branches	0,27	0,64	0,00	-0,42	0,00	-0,42	0,20	-0,11	0,00	-0,42	0,00	-0,42	0,64	0,57	0,32	0,07	0,00	-0,42	0,29	0,03	0,67	0,62	0,33	0,10	0,00	-0,42
	on diagonal branches	1,30	1,04	0,00	-1,25	1,43	0,12	2,00	0,67	0,83	-0,45	0,64	-0,63	0,55	-0,73	1,42	0,12	1,60	0,29	1,90	0,58	2,33	0,99	1,67	0,35	1,67	0,35
	on horizontal branches	0,32	0,70	0,00	-0,46	0,00	-0,46	0,40	0,11	0,33	0,01	0,07	-0,36	0,41	0,12	0,47	0,22	0,10	-0,32	0,43	0,15	0,00	-0,46	0,67	0,49	0,00	-0,46
	on dead branches	0,78	0,91	0,00	-0,86	1,14	0,39	1,70	1,00	0,67	-0,13	0,29	-0,55	0,64	-0,16	0,53	-0,28	0,40	-0,42	1,10	0,34	1,33	0,60	1,00	0,24	1,33	0,60
Mixed accumulation of epiphytes	on stem	0,82	1,21	0,00	-0,67	0,00	-0,67	1,00	0,15	0,50	-0,26	0,00	-0,67	1,00	0,15	1,68	0,72	1,00	0,15	0,38	-0,36	1,67	0,70	1,50	0,56	2,33	1,25
	in branching	0,76	1,13	0,00	-0,67	0,29	-0,42	1,90	1,00	0,50	-0,23	0,14	-0,55	0,50	-0,23	0,74	-0,02	1,20	0,39	1,14	0,34	1,67	0,80	0,50	-0,23	0,67	-0,08
	on vertical branches	0,05	0,31	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,09	0,12	0,16	0,33	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17
	on diagonal branches	0,25	0,70	0,00	-0,36	0,00	-0,36	0,60	0,50	0,00	-0,36	1,43	1,69	0,09	-0,23	0,26	0,01	0,30	0,07	0,19	-0,09	0,67	0,59	0,00	-0,36	1,33	1,55
	on horizontal branches	0,10	0,50	0,00	-0,20	0,00	-0,20	0,00	-0,20	0,00	-0,20	0,00	-0,20	0,32	0,44	0,32	0,44	0,00	-0,20	0,00	-0,20	0,00	-0,20	0,00	-0,20	0,00	-0,20
	on dead branches	0,14	0,55	0,00	-0,25	0,00	-0,25	0,40	0,47	0,00	-0,25	0,00	-0,25	0,14	-0,00	0,11	-0,06	0,50	0,65	0,14	0,01	0,00	-0,25	0,00	-0,25	0,00	-0,25
Sum of vascular epiphytes	none	0,40	0,90	3,00	2,88	0,00	-0,44	0,10	-0,33	0,17	-0,26	1,29	0,98	0,50	0,11	0,11	-0,33	0,10	-0,33	0,10	-0,34	0,00	-0,44	0,17	-0,26	0,00	-0,44
	some	1,93	1,19	0,00	-1,62	2,86	0,78	1,10	-0,70	3,00	0,90	1,79	-0,12	2,32	0,33	1,95	0,01	2,60	0,56	1,57	-0,30	0,67	-1,06	2,33	0,34	2,33	0,34
	many	1,38	1,26	0,00	-1,09	0,86	-0,41	2,60	0,97	0,67	-0,56	0,43	-0,75	0,64	-0,59	1,63	0,20	1,30	-0,06	2,19	0,65	2,67	1,02	2,00	0,49	2,00	0,49
Connecting elements	lianas on stem	1,37	1,09	0,40	-0,89	1,43	0,05	1,40	0,03	1,67	0,27	1,00	-0,34	1,73	0,33	2,11	0,68	1,50	0,12	0,38	-0,91	2,33	0,89	1,33	-0,03	2,00	0,58
	lianas in tree crown	0,97	0,96	0,20	-0,80	1,57	0,63	1,40	0,45	1,33	0,38	0,93	-0,04	0,55	-0,44	1,89	0,97	1,00	0,03	0,19	-0,81	1,67	0,73	1,33	0,38	0,33	-0,67
	lianas connecting stems	0,33	0,77	0,00	-0,43	0,29	-0,06	0,40	0,09	0,33	0,00	0,50	0,22	0,05	-0,37	1,21	1,14	0,00	-0,43	0,10	-0,31	0,00	-0,43	0,33	0,00	0,00	-0,43
	lianas connecting crowns	0,39	0,78	0,00	-0,50	1,14	0,96	0,40	0,01	0,67	0,35	0,57	0,23	0,05	-0,44	1,05	0,84	0,20	-0,25	0,10	-0,38	0,33	-0,08	0,17	-0,29	0,00	-0,50
	bamboo on stem	1,10	1,12	0,00	-0,98	0,57	-0,47	2,80	1,52	1,50	0,36	0,93	-0,15	0,77	-0,29	1,05	-0,04	1,00	-0,09	0,33	-0,68	2,33	1,10	2,50	1,25	2,00	0,80
	bamboo in tree crown	0,47	0,84	0,00	-0,56	0,57	0,12	1,10	0,75	0,83	0,44	0,57	0,12	0,09	-0,45	0,63	0,19	0,00	-0,56	0,19	-0,33	1,33	1,03	1,83	1,63	0,00	-0,56
	bamboo connecting stems	0,54	0,94	0,00	-0,57	0,29	-0,27	1,60	1,13	1,17	0,67	0,36	-0,19	0,00	-0,57	0,58	0,04	0,20	-0,36	0,10	-0,47	2,00	1,55	2,50	2,08	0,67	0,14
	bamboo connecting crowns	0,26	0,71	0,00	-0,37	0,00	-0,37	0,50	0,34	0,67	0,57	0,29	0,03	0,00	-0,37	0,37	0,15	0,00	-0,37	0,64	0,54	0,67	0,57	1,83	2,21	0,00	-0,37
Conspiciuos life-forms	climbers	0,93	1,08	0,20	-0,68	2,29	1,25	1,30	0,34	1,17	0,22	0,86	-0,07	0,00	-0,86	0,58	-0,33	1,80	0,81	0,67	-0,24	2,67	1,61	1,83	0,84	2,00	0,99
	stranglers	0,15	0,49	0,00	-0,31	0,00	-0,31	0,00	-0,31	0,17	0,03	0,21	0,12	0,00	-0,31	0,63	0,98	0,20	0,09	0,10	-0,12	0,00	-0,31	0,00	-0,31	0,00	-0,31
	Arecaceae	0,21	0,55	0,00	-0,38	0,00	-0,38	0,00	-0,38	0,33	0,23	0,00	-0,38	0,05	-0,29	0,16	-0,09	0,00	-0,38	0,52	0,57	0,00	-0,38	0,67	0,83	2,00	3,24
	Araceae	0,02	0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,05	0,30	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12
	Cyatheaceae	0,05	0,24	0,00	-0,19	0,14	0,40	0,00	-0,19	0,50	1,85	0,00	-0,19	0,05	-0,00	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19
	Cyclanthaceae	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	

Table B: Mean value, standard deviation, and T-value for all variables in all cluster groups for the undergrowth stratum of 130 plots with more than one stratum.

Character class	Character	X all plots	S all plots	X cl II	T cl II	X cl III	T cl III	X cl IV	T cl IV	X cl V	T cl V	X cl VI a	T cl VI a	X cl VI b	T cl VI b	X cl VI c	T cl VI c	X cl VI d	T cl VI d	X cl VII a	T cl VII a	X cl VII b	T cl VII b	X cl VII c	T cl VII c	X cl VII d	T cl VII d
N		130	130	5	5	7	7	10	10	6	6	14	14	22	22	19	19	10	10	21	21	3	3	6	6	3	3
Woodiness	axylous	0,36	0,67	0,00	-0,54	0,00	-0,54	0,00	-0,54	0,17	-0,29	0,00	-0,54	0,00	-0,54	0,37	0,01	0,10	-0,39	1,14	1,17	0,67	0,46	0,67	0,46	2,00	2,44
	hemixylous	0,85	0,80	0,20	-0,81	1,57	0,90	1,20	0,44	0,50	-0,43	0,43	-0,52	0,82	-0,03	0,95	0,13	1,90	1,31	0,24	-0,76	1,33	0,61	0,67	-0,22	1,00	0,19
	holoxylous	2,89	0,31	3,00	0,35	3,00	0,35	2,80	-0,30	3,00	0,35	3,00	0,35	2,86	-0,09	2,90	0,02	2,70	-0,62	2,90	0,04	2,67	-0,72	3,00	0,35	2,67	-0,72
Stem characters	polycormous	1,16	0,82	1,80	0,77	1,14	-0,02	0,60	-0,68	0,50	-0,80	1,14	-0,02	0,64	-0,64	1,16	-0,00	1,00	-0,20	1,62	0,56	2,00	1,02	2,00	1,02	1,67	0,61
	vertical	2,83	0,38	2,20	-1,68	2,86	0,07	2,90	0,18	2,83	0,01	2,93	0,26	2,95	0,33	2,79	-0,11	3,00	0,45	2,86	0,07	2,33	-1,32	2,50	-0,88	3,00	0,45
	diagonal	1,23	0,75	1,60	0,49	1,14	-0,12	0,50	-0,97	1,50	0,36	0,79	-0,59	0,95	-0,37	1,63	0,53	1,30	0,09	1,19	-0,05	2,00	1,02	1,83	0,80	2,00	1,02
	dead	0,94	0,84	0,80	-0,16	1,43	0,58	0,70	-0,28	0,67	-0,32	0,36	-0,69	0,55	-0,47	1,11	0,20	0,20	-0,88	1,67	0,86	2,00	1,26	1,00	0,07	2,00	1,26
Bark characters	green thin smooth	0,95	0,82	0,20	-0,91	1,14	0,23	1,10	0,18	0,67	-0,35	0,43	-0,64	0,91	-0,05	1,26	0,38	1,80	1,03	0,62	-0,41	0,67	-0,35	0,67	-0,35	1,67	0,86
	green thin rough	0,04	0,23	0,00	-0,17	0,00	-0,17	0,10	0,27	0,00	-0,17	0,00	-0,17	0,09	0,23	0,11	0,29	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17
	green thick smooth	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	green thick rough	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	non-green thin smooth	1,70	0,97	2,60	0,93	2,00	0,31	1,40	-0,31	2,00	0,31	2,57	0,90	1,95	0,26	1,16	-0,56	2,10	0,41	1,24	-0,48	1,33	-0,38	0,67	-1,07	2,00	0,31
	non-green thin rough	1,59	1,18	1,00	-0,50	0,29	-1,11	1,90	0,26	2,00	0,35	0,64	-0,81	0,55	-0,89	2,47	0,75	0,90	-0,59	2,62	0,87	2,67	0,91	2,83	1,05	2,33	0,63
	non-green thick smooth	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	non-green thick rough	0,58	0,81	0,00	-0,72	2,14	1,91	0,50	-0,10	0,33	-0,31	0,71	0,16	0,95	0,45	0,11	-0,59	0,70	0,14	0,43	-0,19	0,33	-0,31	0,00	-0,72	0,00	-0,72
	non-green very thick rough	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	flaky	0,05	0,24	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,33	1,17	0,21	0,69	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,05	0,01	0,00	-0,19	0,00	-0,19	0,00	-0,19
Roots	tabulate roots	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	stilt roots	0,29	0,64	0,00	-0,46	0,00	-0,46	0,00	-0,46	0,33	0,06	0,21	-0,12	0,00	-0,46	0,42	0,20	0,80	0,79	0,38	0,14	0,00	-0,46	0,50	0,32	1,33	1,63
	aerial roots	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
Crown volume	restricted to top	1,43	0,81	0,00	-1,77	2,14	0,88	1,00	-0,53	1,50	0,09	0,86	-0,71	1,45	0,03	1,58	0,18	1,40	-0,04	1,71	0,35	2,00	0,71	1,50	0,09	2,00	0,71
	restricted to upper third	2,18	0,71	3,00	1,14	2,00	-0,26	2,30	0,16	2,83	0,91	2,00	-0,26	1,77	-0,58	2,00	-0,26	2,50	0,44	2,52	0,48	2,00	-0,26	2,00	-0,26	2,00	-0,26
	restricted to upper half	1,21	0,79	0,40	-1,02	0,71	-0,62	1,60	0,49	0,33	-1,10	1,71	0,64	1,09	-0,15	1,32	0,14	1,40	0,24	1,19	-0,02	0,67	-0,68	1,83	0,79	1,33	0,16
	reaching deeper than half	0,52	0,68	0,00	-0,76	0,43	-0,14	0,20	-0,47	0,33	-0,28	0,79	0,38	0,27	-0,37	0,53	0,00	0,80	0,40	0,57	0,07	1,33	1,18	0,83	0,45	1,00	0,70
Crown development	full	2,08	0,69	0,80	-1,85	2,14	0,08	2,30	0,31	2,00	-0,12	2,43	0,50	1,95	-0,19	2,26	0,26	2,50	0,60	1,95	-0,19	2,00	-0,12	1,33	-1,08	2,33	0,36
	restricted by neighbours	1,74	0,74	2,80	1,43	1,71	-0,03	1,60	-0,19	1,67	-0,10	1,36	-0,51	1,27	-0,63	1,89	0,21	1,50	-0,32	2,14	0,54	2,00	0,35	2,33	0,80	1,67	-0,10
	stunted	0,37	0,59	0,00	-0,63	0,71	0,59	0,00	-0,63	0,50	0,22	0,07	-0,51	0,27	-0,16	0,21	-0,27	0,10	-0,46	0,71	0,59	1,00	1,08	1,00	1,08	1,00	1,08
Crown shape	round	0,58	0,75	0,20	-0,51	0,14	-0,58	0,80	0,30	0,17	-0,55	0,71	0,18	0,23	-0,47	0,74	0,21	0,40	-0,24	0,86	0,38	1,00	0,57	1,00	0,57	1,00	0,57
	umbrella-shaped	1,15	0,85	0,80	-0,41	0,43	-0,84	1,40	0,30	0,67	-0,56	1,29	0,16	0,82	-0,38	1,11	-0,05	0,90	-0,29	1,90	0,89	0,67	-0,56	1,67	0,61	1,33	0,22
	cylindrical	1,10	0,75	0,20	-1,21	1,00	-0,13	1,60	0,67	1,00	-0,13	1,14	0,06	1,05	-0,07	0,89	-0,28	1,40	0,40	1,19	0,12	1,33	0,31	0,83	-0,36	2,00	1,21
	conical	0,23	0,52	0,20	-0,06	0,14	-0,17	0,50	0,52	0,00	-0,44	0,00	-0,44	0,14	-0,18	0,42	0,36	0,20	-0,06	0,29	0,11	0,00	-0,44	0,50	0,52	0,00	-0,44
	funnel-shaped/umbelliferous	1,42	0,81	0,00	-1,74	2,14	0,89	1,00	-0,51	1,50	0,10	1,00	-0,51	1,41	-0,01	1,53	0,14	1,40	-0,02	1,62	0,25	2,00	0,72	1,67	0,31	2,00	0,72
	fanshaped	0,28	0,63	0,60	0,50	0,43	0,23	0,40	0,18	0,00	-0,45	0,07	-0,34	0,00	-0,45	0,11	-0,29	0,20	-0,14	0,29	0,00	1,33	1,68	1,00	1,14	2,00	2,74
	irregular	2,15	0,57	2,60	0,79	1,86	-0,51	1,60	-0,95	2,83	1,20	2,07	-0,13	1,95	-0,34	2,11	-0,07	2,50	0,62	2,14	-0,01	2,33	0,33	2,50	0,62	2,00	-0,26
Crown overlap	Type 1	0,63	0,85	2,20	1,86	0,14	-0,58	1,60	1,15	0,83	0,24	0,43	-0,24	0,27	-0,42	0,58	-0,06	0,70	0,08	0,48	-0,18	0,33	-0,35	0,50	-0,15	1,00	0,44
	Type2	2,01	0,76	1,40	-0,80	2,00	-0,01	2,00	-0,01	2,50	0,65	1,50	-0,67	2,50	0,65	2,00	-0,01	2,10	0,12	1,90	-0,13	2,00	-0,01	1,50	-0,67	2,00	-0,01
	Type 3	1,86	0,89	0,00	-2,10	2,29	0,48	1,40	-0,52	1,17	-0,78	2,14	0,32	1,45	-0,46	2,00	0,16	2,20	0,38	2,29	0,48	2,67	0,91	2,33	0,53	1,33	-0,60
Branches	mostly horizontal	0,45	0,74	0,20	-0,33	0,14	-0,41	0,30	-0,20	0,00	-0,61	0,07	-0,51	0,05	-0,54	1,16	0,97	0,40	-0,06	0,62	0,23	0,67	0,30	0,67	0,30	1,33	1,20
	mostly diagonal	2,89	0,34	3,00	0,32	2,86	-0,11	2,80	-0,28	3,00	0,32	2,93	0,11	2,91	0,05	2,79	-0,31	3,00	0,32	2,86	-0,11	2,67	-0,67	3,00	0,32	3,00	0,32
	mostly vertical	0,13	0,44	0,00	-0,30	0,00	-0,30	0,00	-0,30	0,00	-0,30	0,14	0,03	0,00	-0,30	0,05	-0,18	0,00	-0,30	0,62	1,11	0,00	-0,30	0,17	0,08	0,00	-0,30
	dead	1,42	0,74	2,20	1,05	1,14	-0,37	1,60	0,25	1,00	-0,56	0,86	-0,75	0,77	-0,86	1,47	0,08	1,10	-0,42	2,05	0,85	2,00	0,78	2,33	1,23	1,67	0,34
	missing	1,54	0,75	0,00	-2,05	2,14	0,81	1,60	0,09	1,50	-0,05	1,00	-0,72	1,41	-0,17	1,53	-0,01	1,90	0,49	1,89	0,47	2,00	0,62	1,67	0,17	2,00	0,62
Branching pattern	Type 1	2,08	0,74	1,80	-0,39	3,00	1,24	2,10	0,02	2,33	0,34	1,79	-0,41	1,55	-0,73	2,42	0,46	2,20	0,16	2,10	0,01	2,00	-0,11	2,00	-0,11	2,33	0,34
	Type 2	1,71	0,70	2,00	0,42	0,71	-1,42	2,10	0,56	1,67	-0,06	1,71	0,01	1,27	-0,62	1,58	-0,18	1,90	0,28	2,00	0,42	2,00	0,42	2,17	0,66	2,00	0,42
	Type 3	0,58	0,78	0,00	-0,74	0,14	-0,56	0,50	-0,10	0,00	-0,74	0,57	-0,01	1,36	1,01	0,21	-0,47	0,00	-0,74	1,24	0,85	0,00	-0,74	0,17	-0,53	0,00	-0,74
Leaf shape	simple	2,67	0,50	3,00	0,66	2,57	-0,19	3,00	0,66	2,83	0,33	2,86	0,37	2,18	-0,97	2,74	0,13	3,00	0,66	2,71	0,09	2,67	-0,00	2,33	-0,67	2,00	-1,33
	narrow leaved	0,25	0,60	0,00	-0,42	0,00	-0,42	0,10	-0,26	0,00	-0,42	0,00	-0,42	0,00	-0,42	0,11	-0,25	0,00	-0,42	1,05	1,32	0,33	0,13	0,67	0,69	1,00	1,24
	palmately lobed	0,72	0,73	0,00	-1,00	0,14	-0,80	0,80	0,11	0,33	-0,54	0,57	-0,21	0,59	-0,18	0,58	-0,20	0,90	0,24	1,05	0,45	1,00	0,38	1,67	1,30	1,33	0,84
	compound	1,49	0,79	0,00	-1,89	2,14	0,82	1,10	-0,50	1,50	0,01	0,93	-0,71	1,55	0,07	1,58	0,11	1,50	0,01	1,81	0,40	2,00	0,64	1,67	0,22	2,00	0,64
	other	0,39	0,68	0,00	-0,58	0,00	-0,58	0,10	-0,43	0,17	-0,33	0,00	-0,58	0,00	-0,58	0,42	0,04	0,20	-0,28	1,29	1,32	0,33	-0,09	0,67	0,41	2,00	2,38
	with drip-tip	1,53	0,68	1,20	-0,48	1,71	0,27	1,20	-0,48	1,17	-0,53	1,21	-0,46	1,45	-0,11	2,00	0,69	1,80	0,39	1,29	-0,36	2,00	0,69	2,00	0,69	2,00	0,69
	absent	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,45	0,00	-0,09	0,00	-0,09	0,00	-0,09
Leaf consistency	hymenophyll	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	malacophyll	2,35	0,83	3,00	0,79	3,00	0,79	2,50	0,18	2,83	0,59	2,43	0,10	2,14	-0,25	2,89	0,66	3,00	0,79	1,33	-1,22	2,00	-0,42	1,33	-1,22	2,67	0,38
	semi-sclerophyll	1,43	1,11	0,00	-1,29	0,00	-1,29	1,60	0,15	0,33	-0,99	0,93	-0,45	1,82	0,35	0,95	-0,43	0,70	-0,66	2,86	1,28	2,67	1,11	2,33	0,81	1,00	-0,39
	sclerophyll	0,04	0,23	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,00	-0,17	0,19	0,66	0,00	-0,17	0,17	0,56	0,00	-0,17
	semi-succulent	0,37	0,71	0,00	-0,52	0,00	-0,52	0,40	0,04	0,33	-0,05	0,00	-0,52	0,00	-0,52	0,05	-0,45	0,10	-0,38	1,38	1,43	0,33	-0,05	1,33	1,37	0,67	0,42
	succulent	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	

Table B: (continued) Mean value, standard deviation, and T-value for all variables in all cluster groups for the undergrowth stratum of 130 plots with more than one stratum.

Character class	Character	X all plots	S all plots	X cl II	T cl II	X cl III	T cl III	X cl IV	T cl IV	X cl V	T cl V	X cl VI a	T cl VI a	X cl VI b	T cl VI b	X cl VI c	T cl VI c	X cl VI d	T cl VI d	X cl VII a	T cl VII a	X cl VII b	T cl VII b	X cl VII c	T cl VII c	X cl VII d	T cl VII d
Epiphytic bromeliads	on stem	1,42	1,43	0,00	-0,99	2,14	0,51	0,50	-0,64	2,00	0,41	0,43	-0,69	0,82	-0,42	1,42	0,00	1,50	0,06	2,29	0,61	2,00	0,41	3,00	1,10	2,67	0,87
	in branching	0,08	0,34	0,00	-0,22	0,00	-0,22	0,00	-0,22	0,00	-0,22	0,00	-0,22	0,05	-0,09	0,00	-0,22	0,00	-0,22	0,43	1,02	0,00	-0,22	0,00	-0,22	0,00	-0,22
	in vertical branches	0,04	0,26	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,05	0,03	0,00	-0,15	0,00	-0,15	0,19	0,58	0,00	-0,15	0,00	-0,15	0,00	-0,15
	on diagonal branches	0,26	0,67	0,00	-0,39	0,00	-0,39	0,20	-0,09	0,00	-0,39	0,00	-0,39	0,05	-0,32	0,05	-0,31	0,00	-0,39	1,38	1,68	0,00	-0,39	0,00	-0,39	0,33	0,11
	on horizontal branches	0,04	0,26	0,00	-0,15	0,29	0,95	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,14	0,40	0,00	-0,15	0,00	-0,15	0,00	-0,15
	on dead branches	0,25	0,64	0,00	-0,39	0,14	-0,16	0,20	-0,07	0,00	-0,39	0,07	-0,27	0,00	-0,39	0,05	-0,30	0,00	-0,39	1,05	1,26	0,00	-0,39	0,00	-0,39	0,67	0,66
	on organic ground material	0,77	1,10	0,00	-0,70	0,00	-0,70	0,70	-0,06	1,00	0,21	0,00	-0,70	0,05	-0,66	0,21	-0,51	0,40	-0,33	2,52	1,59	1,33	0,51	2,00	1,12	2,00	1,12
Epiphytic orchids	on stem	1,32	1,44	0,00	-0,92	3,00	1,16	0,70	-0,43	1,00	-0,22	0,00	-0,92	0,95	-0,26	0,95	-0,26	0,60	-0,50	2,57	0,87	2,67	0,93	2,83	1,05	2,67	0,93
	in branching	0,02	0,20	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,00	-0,12	0,05	0,11	0,00	-0,12	0,00	-0,12	0,10	0,37	0,00	-0,12	0,00	-0,12	0,00	-0,12
	on vertical branches	0,01	0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,05	0,43	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09	0,00	-0,09
	on diagonal branches	0,20	0,64	0,00	-0,31	0,14	-0,09	0,20	0,00	0,50	0,47	0,00	-0,31	0,05	-0,24	0,00	-0,31	0,00	-0,31	0,76	0,88	0,67	0,73	0,00	-0,31	0,33	0,21
	on horizontal branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	on dead branches	0,12	0,50	0,00	-0,25	0,00	-0,25	0,30	0,36	0,00	-0,25	0,21	0,18	0,00	-0,25	0,00	-0,25	0,00	-0,25	0,38	0,52	0,00	-0,25	0,00	-0,25	0,67	1,09
Mixed accumulation	on stem	0,09	0,49	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,00	-0,19	0,57	0,98	0,00	-0,19	0,00	-0,19	0,00	-0,19
of epiphytes	in branching	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	on vertical branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	on diagonal branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	on horizontal branches	0,00	0,00	0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00		0,00	
	on dead branches	0,06	0,41	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,00	-0,15	0,24	0,43	0,00	-0,15	0,00	-0,15	1,00	2,30
Sum of vascular	none	2,56	0,70	3,00	0,62	1,86	-1,00	2,80	0,34	2,67	0,15	3,00	0,62	2,73	0,24	2,47	-0,12	3,00	0,62	2,10	-0,66	2,67	0,15	2,17	-0,56	2,33	-0,32
epiphytes	some	1,22	1,06	0,00	-1,16	2,14	0,87	0,90	-0,31	1,33	0,10	0,14	-1,02	0,55	-0,64	1,58	0,34	0,60	-0,59	2,19	0,91	2,00	0,73	2,00	0,73	2,00	0,73
	many	0,08	0,32	0,00	-0,24	0,00	-0,24	0,00	-0,24	0,00	-0,24	0,00	-0,24	0,05	-0,10	0,00	-0,24	0,00	-0,24	0,29	0,65	0,00	-0,24	0,33	0,80	0,33	0,80
Connecting elements	lianas on stem	1,26	0,85	0,40	-1,01	1,14	-0,14	1,10	-0,19	1,17	-0,11	0,93	-0,39	1,36	0,12	1,63	0,44	0,90	-0,43	1,19	-0,08	2,00	0,87	2,00	0,87	2,00	0,87
	lianas in tree crown	1,21	0,83	0,40	-0,97	1,43	0,27	1,20	-0,01	1,67	0,55	1,29	0,09	1,00	-0,25	1,37	0,19	0,90	-0,37	1,00	-0,25	2,00	0,95	2,00	0,95	1,33	0,15
	lianas connecting stems	0,62	0,84	0,00	-0,74	0,00	-0,74	0,60	-0,03	0,00	-0,74	0,79	0,19	0,59	-0,04	1,05	0,51	0,40	-0,27	0,38	-0,29	1,33	0,85	1,33	0,85	1,33	0,85
	lianas connecting crowns	0,84	0,90	0,20	-0,71	1,43	0,66	0,60	-0,27	0,17	-0,75	1,14	0,34	0,32	-0,58	1,11	0,30	0,60	-0,27	0,81	-0,03	2,00	1,30	1,50	0,74	1,33	0,55
	bamboo on stem	1,37	1,06	0,00	-1,29	0,29	-1,02	2,90	1,44	2,50	1,06	1,07	-0,28	1,27	-0,09	1,16	-0,20	1,50	0,12	0,95	-0,39	2,00	0,59	2,17	0,75	1,67	0,28
	bamboo in tree crown	1,20	1,05	0,00	-1,14	0,29	-0,87	2,80	1,52	2,17	0,92	0,86	-0,33	1,14	-0,06	0,89	-0,29	1,40	0,19	0,81	-0,37	2,00	0,76	2,17	0,92	0,67	-0,51
	bamboo connecting stems	1,04	1,03	0,00	-1,00	0,29	-0,73	2,70	1,61	1,83	0,77	0,57	-0,45	0,59	-0,43	1,05	0,01	1,10	0,06	0,67	-0,36	2,00	0,93	2,17	1,09	0,67	-0,36
	bamboo connecting crowns	0,98	1,03	0,00	-0,96	0,29	-0,68	2,60	1,57	1,50	0,50	0,64	-0,33	0,55	-0,43	0,74	-0,24	1,10	0,11	0,81	-0,17	2,00	0,99	2,17	1,15	0,67	-0,31
Conspiciuos life-forms	climbers	0,63	0,88	0,00	-0,72	2,00	1,55	0,70	0,08	1,17	0,61	0,57	-0,07	0,00	-0,72	0,32	-0,36	1,70	1,21	0,43	-0,23	0,33	-0,34	1,17	0,61	0,67	0,04
	stranglers	0,10	0,33	0,00	-0,31	0,00	-0,31	0,30	0,61	0,00	-0,31	0,00	-0,31	0,05	-0,17	0,16	0,18	0,10	0,00	0,19	0,28	0,00	-0,31	0,00	-0,31	0,00	-0,31
	Arecaceae	0,55	0,71	0,00	-0,79	1,00	0,63	0,00	-0,79	0,83	0,40	0,07	-0,68	0,55	-0,01	0,63	0,11	0,20	-0,50	1,10	0,77	1,00	0,63	0,17	-0,55	1,33	1,11
	Araceae	0,40	0,67	0,00	-0,60	1,00	0,90	0,30	-0,15	0,67	0,40	0,07	-0,49	0,00	-0,60	0,21	-0,28	0,70	0,45	0,71	0,47	0,00	-0,60	0,83	0,65	0,33	-0,10
	Cyatheaceae	1,25	0,86	0,00	-1,44	2,14	1,04	1,00	-0,29	1,00	-0,29	0,86	-0,45	1,27	0,03	1,47	0,26	1,30	0,06	1,19	-0,06	1,67	0,49	1,33	0,10	2,00	0,87
	Cyclanthaceae	0,45	0,75	0,00	-0,61	0,00	-0,61	0,00	-0,61	0,17	-0,38	0,00	-0,61	0,00	-0,61	0,47	0,03	0,40	-0,07	1,52	1,43	0,33	-0,16	1,00	0,73	2,00	2,07

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfmittel verwendet habe.

Ferner erkläre ich, dass ich weder an der Universität Bayreuth noch anderweitig mit oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

(Axel Paulsch) Bayreuth den 10. 12. 2001