

DEVELOPMENT AND APPLICATION OF A
CLASSIFICATION SYSTEM FOR UNDISTURBED
AND DISTURBED TROPICAL MONTANE
FORESTS BASED ON VEGETATION STRUCTURE

Dissertation Thesis

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie
und Geowissenschaften der Universität Bayreuth genehmigten
Dissertation zur Erlangung der Würde eines Doktors der
Naturwissenschaften (Dr. rer. nat.)

vorgelegt von

Diplom-Geoökologe Axel Paulsch

Geb am 24. 2. 1966 in Pforzheim

Erstgutachter:

Prof. Dr. K. Müller-Hohenstein

Zweitgutachter:

Prof. Dr. E. Beck

Promotionsgesuch eingereicht am: 10. 12. 2001

Tag der mündlichen Prüfung: 10. 02. 2002

Alle Rechte vorbehalten.

Das Werk einschließlich aller seiner Teile ist urheberrechtlich geschützt. Jede Verwertung außerhalb der engen Grenzen des Urheberrechtsgesetzes ist ohne Zustimmung des des Autors unzulässig und strafbar. Das gilt insbesondere für Vervielfältigungen, Übersetzungen, Mikroverfilmungen und die Einspeisung und Verarbeitung in elektronischen Systemen.

All rights reserved.

No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, without the prior permission of the author.

CONTENTS / INHALTSVERZEICHNIS

List of Tables	VI
List of Figures	VII
Acknowledgements	IX
Summary	X
Zusammenfassung	XII
Resumen	XIV
Zusammenfassende Übersicht	I
A Einleitung	I
B Material und Methoden	3
B.1 Untersuchungsgebiet	3
B.2 Überblickskartierung	4
B.3 Parzellenscharfe Strukturkartierung genutzter Bereiche	4
B.4 Plotscharfe Strukturkartierung von Waldbereichen	5
B.5 Statistische Auswertung	6
C Ergebnisse und Interpretation	7
C.1 Übersichtskartierung	7
C.2 Parzellenscharfe Strukturkartierung genutzter Bereiche	8
C.3 Plotscharfe Strukturkartierung von Waldbereichen	9
C.3.1 Sekundärvegetation an Straßenböschungen (Cluster I a)	10
C.3.2 Sekundärvegetation auf Rutschungen oder Lichtungen (Cluster I b)	11
C.3.3 Aufforstung mit <i>Pinus patula</i> (Cluster II)	11
C.3.4 Sekundärwald in Mindo (Cluster III)	11
C.3.5 Primärwald in Cajanuma (Cluster IV)	12
C.3.6 Natürliche Waldränder (Cluster V)	12
C.3.7 Sekundärer Schluchtwald (Cluster VI a)	12
C.3.8 Schluchtwald mit Anzeichen menschlicher Einflußnahme (Cluster VI b)	13
C.3.9 Primärer Schluchtwald tieferer Lagen (Cluster VI c) ..	13
C.3.10 Primärer Schluchtwald höherer Lagen (Cluster VI d) .	14
C.3.11 Mikrophyller Gratwald (Cluster VII a)	14
C.3.12 Mesophyller Gratwald (Cluster VII b)	15
C.3.13 Makrophyller Gratwald (Cluster VII c)	15
C.3.14 Megaphyller Gratwald (Cluster VII d)	15

C.4	Reduzierter Merkmalskatalog	16
D	Diskussion	17
D.1	Klassifikationssystem	17
D.2	Verteilung der Waldstrukturtypen	19
D.3	Funktionale Zusammenhänge	21
E	Literatur	22
1	Introduction	28
2	Material and Methods	34
2.1	Investigation area	34
2.2	Mapping structure on a landscape level	36
2.3	Mapping structure on a patch level (land-use areas)	36
2.4	Mapping structure on a plot level (forest areas).....	38
2.5	Statistical interpretation	50
3	Results and Interpretation	53
3.1	Landscape level	53
3.2	Patch level	55
3.3	Plot level	62
3.3.1	Test of classification systems	62
3.3.2	Cluster analysis	65
3.4	Grouping of plots	65
3.4.1	Plots with one stratum	65
3.4.2	Plots with more than one stratum	67
3.4.2.1	Secondary growth after road construction (Cluster I a)	77
3.4.2.2	Secondary growth after landslides or clearing (Cluster I b)	78
3.4.2.3	Plantation of <i>Pinus patula</i> (Cluster II).....	79
3.4.2.4	Secondary forest in Mindo (Cluster III)	80
3.4.2.5	Primary forest in Cajanuma (Cluster IV)	81
3.4.2.6	Forest on edges of natural gaps (Cluster V)	83
3.4.2.8	Ravine forest under human influence (Cluster VI b).....	85
3.4.2.9	Primary ravine forest at lower altitude (Cluster VI c)	87
3.4.2.10	Primary ravine forest at higher altitude (Cluster VI d).....	89
3.4.2.11	Microphyll ridge forest (Cluster VII a)	92
3.4.2.12	Mesophyll ridge forest (Cluster VII b)	94
3.4.2.13	Macrophyll ridge forest (Cluster VII c).....	95

3.4.2.14	Megaphyll ridge forest (Cluster VII d)	97
3.5	Distribution of structural forest types in the investigation area	103
3.6	Frequency of structural characters and correlation between structural characters	107
3.7	Reduced classification system	113
3.8	Proposal for a dichotomous key to the structural forest types of the investigation area	121
4	Discussion	123
4.1	The structural classification system	123
4.1.1	Plot size	123
4.1.2	Plot distribution	123
4.1.3	Structural features	124
4.1.4	Data collection	125
4.1.5	Statistical interpretation	125
4.2	Distribution of forest types and site conditions	128
4.2.1	Altitudinal zonation	128
4.2.2	Wind	131
4.2.3	Soil	131
4.2.4	Light	132
4.3	Disturbance and succession	133
4.4	Functional relationships	135
5	Literature	138
	Maps	145
	Appendices	146

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 Dzedziuch)

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.

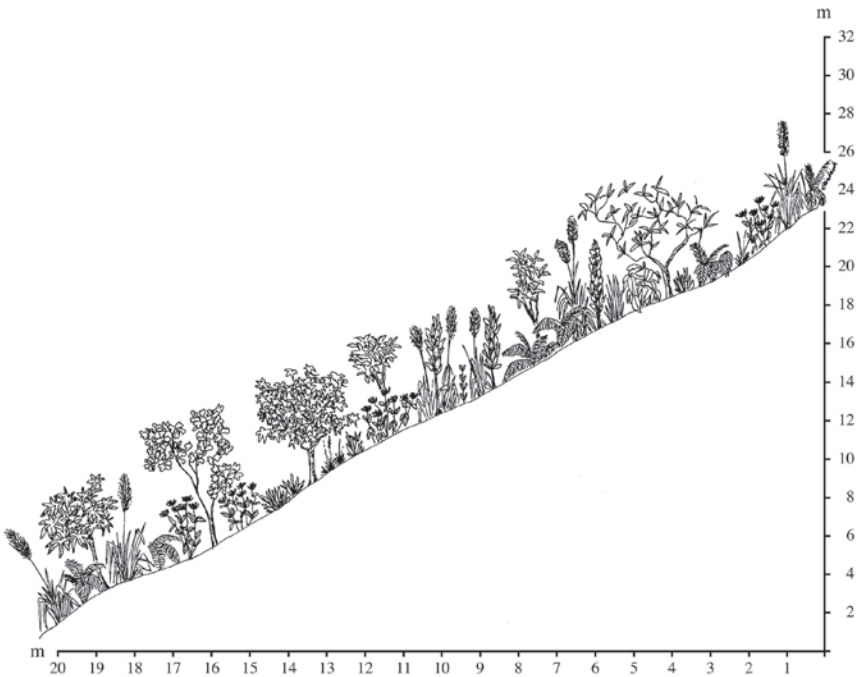


Figure 17: Profile of Secondary growth after landslides or clearing (Cluster I b) of Plot 37 (Illustration by Dzedziuch)

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 Dziedziuch)

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 Dzedziach)

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 leaves 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 Dziedziuch)

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.

3.2 Patch level

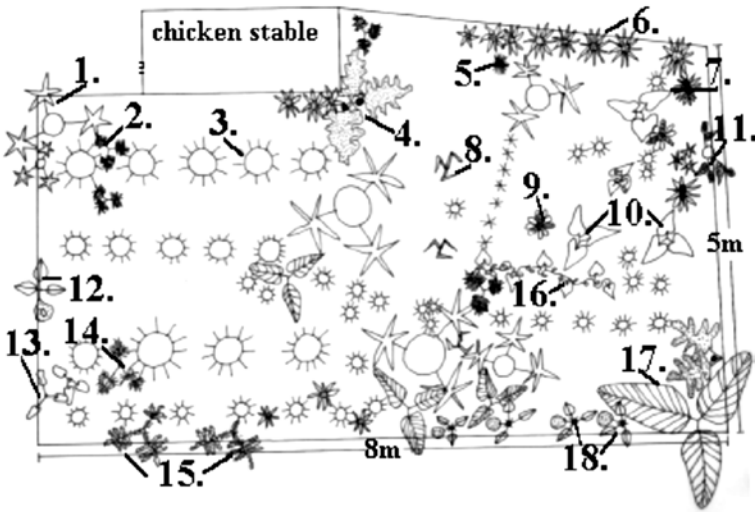
The 12 fincas marked in Figure 6 could be subdivided into 245 patches. These patches were assigned to the following land-use units: forests, reforestations, pastures (with and without trees), groups of trees, bushes, clear cuts, fern dominated patches, farmland, landslides, house gardens, houses, and 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 (<i>Carica papaya</i> L.) | 10. Papachina (<i>Colocasia esculenta</i> (L.) Scholt) |
| 2. Tomato (<i>Lycopersicon esculentum</i> Mill.) | 11. Coffee (<i>Coffea arabica</i> L.) |
| 3. Sugar cane (<i>Saccharum officianum</i> L.) | 12. Avocado (<i>Persea americana</i> Mill.) |
| 4. Naranjilla (<i>Solanum quitoense</i> Lam.) | 13. Chilli (<i>Capsicum chinense</i> N. Jacq.) |
| 5. Hierba luisa (<i>Cymbopogon citratus</i> (Dc.) Stapf) | 14. Carrot (<i>Daucus carota</i> L.) |
| 6. Ornamental plants | 15. Hortiga (<i>Loasa picta</i> Hokk.) |
| 7. Corn (<i>Zea mays</i> L.) | 16. Bean (<i>Phaseolus vulgaris</i> L.) |
| 8. Cariamanga (<i>Poaceae</i>) | 17. Achira (<i>Musaceae</i>) |
| 9. Pea (<i>Pisum sativum</i> L.) | 18. Sweet lemon (<i>Citrus limetta</i> 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.

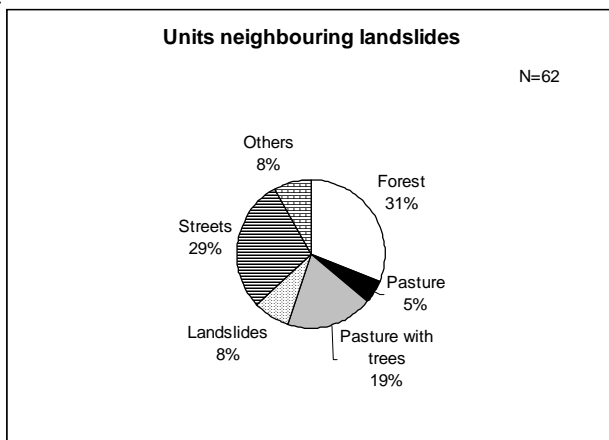


Figure 8a: Distribution of units neighbouring landslides (from SCHNEIDER 2000, modified).

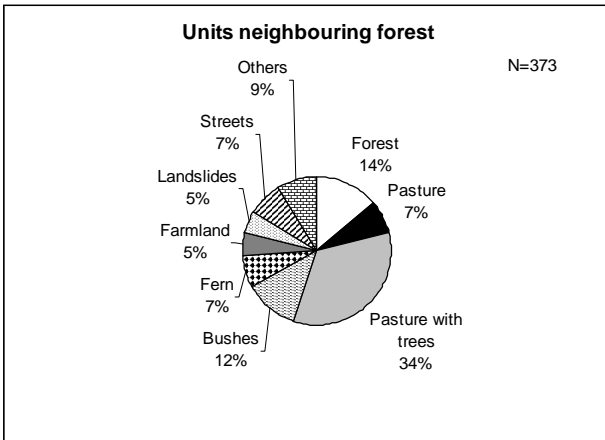


Figure 8b: Distribution of units neighbouring forest patches (from SCHNEIDER 2000, modified).

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.

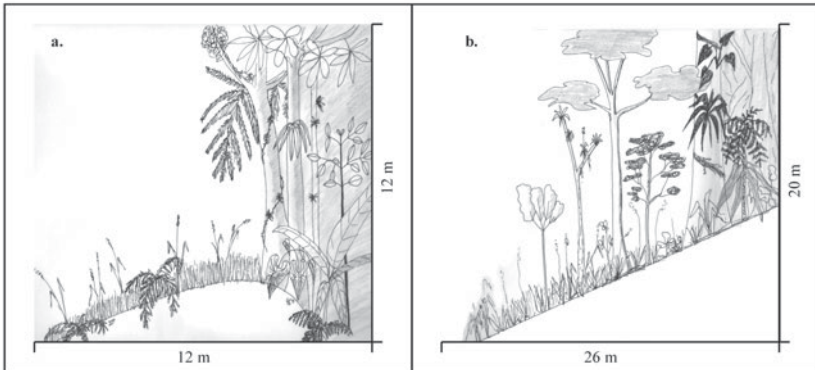


Figure 9: **a.** Sharp boundary between pasture and forest. **b.** Gradual transition between pasture and forest (from SCHNEIDER 2000, modified).

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.

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 Dziedziuch)

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. (*Cyrtillaceae*) 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-succulent 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 Dziejziuch)

3.4.2.12 Mesophyll ridge 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-