Chapter 10.3
Forest Vegetation Structure Along an Altitudinal Gradient in Southern Ecuador

A. Paulsch(✉), D. Piechowski, and K. Müller-Hohenstein

10.3.1 Introduction

Approaches to classify vegetation are numerous but can be divided into two major groups: floristic approaches and physiognomic/structure-based approaches (Beard 1973), both leading to equal results when compared (Brocque and Buckney 1997; Webb et al. 1970; Werger and Sprangers 1982). Floristic systems (e.g. Braun-Blanquet 1928) base on plant species and species composition to classify vegetation within a hierarchical system. They are well established in temperate zones with their surveyable number of plant species (e.g. Dierschke 1994, Sautter 2003). The higher plant diversity in the tropics is well known and especially true for our investigation area (Henderson et al. 1991; Jørgensen and León-Yánez 1999). All floristic surveys in the tropics have to focus on some selected taxa (e.g. Kessler 2002; Krömer et al. 2006), functional groups like trees (e.g. Condit et al. 2002; Phillips et al. 2003) or vascular epiphytes (e.g. Werner et al. 2005) or create a flora for a locally distinct area (e.g. Mori et al. 1997, 2002; Ribeiro et al. 1999). Physiognomic approaches are based on structural parameters of parts of plants (e.g. leaves) or whole plants (e.g. architecture) and can be used without a detailed knowledge of the local flora. The most important structure-based classification systems by Ellenberg and Mueller-Dombois (1967) and Holdridge et al. (1971) are widely used to name vegetation units (formations) of bioms and sub-bioms worldwide (e.g. UNESCO 1973). However, these classifications are not adapted to smaller areas, especially where human influence has largely disturbed the natural vegetation and replaced it by vegetation units, where structural characteristics appear which were not known before (lopped trees, grazed bushes, plantations with one species all of the same age). Several structural approaches are applicable on smaller scales but none of them is useable in the investigation area due to improper characters (Orshan 1986), or the usage of floristic parameters (Halloy 1990; Parsons 1975) or due to the restrictiveness in classic forestry parameters (Condit 1998; Proctor et al. 1988). For a detailed comparison see Paulsch (2002) and Paulsch and Czimczik (2001).

Here we present results of a new structural approach on the basis of systems by Orshan (1986), Parsons (1975), Richards et al. (1940) and Werger and Sprangers

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(1982). We follow Barkman (1979) in defining vegetation structure as the “horizontal and vertical arrangement of vegetation”. The set of 102 structural parameters per stratum used in our system is applicable on a plot level concerning the vegetation, the plant community or a closed mosaic of different plant communities. Additionally, we investigate how the forests examined on plot level are matched into the highly fragmented, anthropogenically altered landscape. We follow the definition of landscape by Forman (1997): “a landscape is a mosaic where the mix of local ecosystems or land-uses is repeated in similar form over a kilometers-wide area”. The objective on this level is to choose and characterize a representative section of the man-made landscape by structural attributes. These attributes are of outstanding importance once the chosen section is regarded as an ecosystem, providing space (an assemblage of biotops) for all living creatures (biocenoses).

Beside the fast and easy application of a structure-based classification, functional relationships on the ecosystem level can be derived. Ewel and Bigelow (1996) stated that: “it is the mix of life-forms, not the mix of species, that exerts major controls over ecosystem functioning”, where life-forms = structural elements.

Special structures are responsible for the uptake of water or nutrients, others are decisive for photosynthesis and again others influence or determine the microclimate. Additionally important are biocenotic connections between animals and plant or vegetation structures. Dziedzioch (2001) showed many relations between more than 20 hummingbird species and different forest types in the investigation area (at plot level).

10.3.2 A New Structure-Based Classification System

The land use patterns of 12 farms (*fincas*) were recorded on the landscape level for parts of the San Francisco valley between Zamora and the ECSF (Fig. 10.3.1). The size and shape of patches were noted, based on the concepts of Forman (1997) and Wiens et al. (1993). The number of neighboring land-use units and the sharpness of boundaries were observed for each of the 245 units as well as e.g. the degree of fragmentation, the size and shape of different vegetation communities, the density of borderlines and the types of linear vegetation units (Table 10.3.1; Müller-Hohenstein et al. 2004) and the density, diameter at breast height (dbh), height and cover of the remaining trees (Paulsch et al. 2001). The grouping of patches into classes of similar characteristics was done with cluster analyses.

The study area reached along an altitudinal gradient from the Bombuscaro section of the Popocarpus National Park via the San Francisco valley and the area of the ECSF to the Cajanuma Section of the Podocarpus Park. Some 34 plots were installed in the Bombuscaro section (960–1090 m a.s.l.) and 19 on the property of the adjacent Finca Copalinga (1030–1580 m a.s.l.). The ECSF area hosted 102 plots (1820–2650 m a.s.l.) and 11 plots were investigated at the Cajanuma section (2750–3100 m a.s.l.).

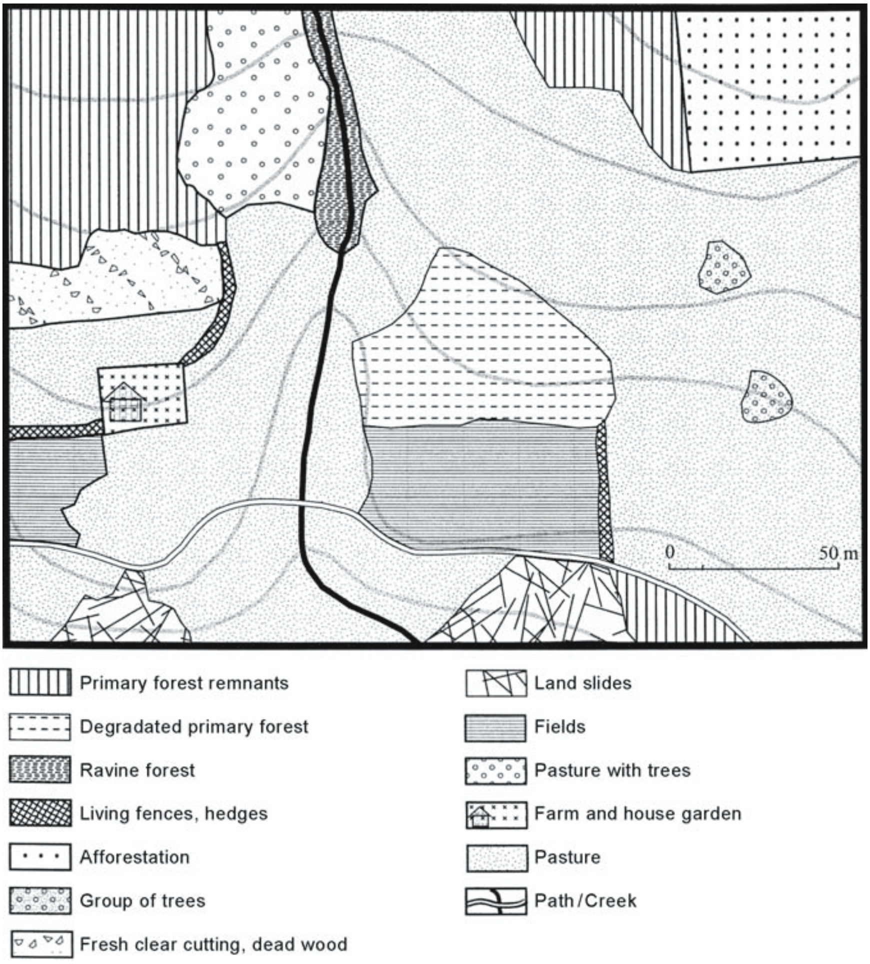

Fig. 10.3.1 Schematic overview of the typically found structural units in the area under land use in the San Francisco valley

Characteristics of forest stands were documented on these 166 plots of 20×20 m each. These plots covered an altitudinal gradient from 960 m to 3100 m. For each stratum of woody vegetation within these plots two groups of character classes were investigated: the first group contained eight parameters on a ratio scale, such as dbh, height of stratum or distance between stems. Data were collected as an average value for the stratum. The second group contained 94 parameters per stratum on an ordinal scale. This scale followed Webb et al. (1970) and had the four categories: absent, rare, abundant and dominant.

These parameters included e.g. leaf size, leaf shape, degree of epiphytic coverage, crown shape and crown development (Table 10.3.1). The complete catalogue

Table 10.3.1 Structural parameters on different levels

Level	Structural parameters
Landscape level: mosaic of vegetation units, natural or man-made	Size and shape of patches, degree of fragmentation, length and density of boundaries, linear structures, land use induced structures like gardens, pastures with or without trees, shade trees, etc.
Plot level: vegetation mosaic in closed stands	Stratification, total cover, distance between stems, distance between crowns, diameter at breast height, abundance of epiphytes, lianas, leaf size, leaf length, leaf width, leaf shape, leaf consistency, thickness and roughness of bark, angle of branches, ramification and branching pattern, crown shape, crown development, height of tree, stem diameter, coverage of mosses, ferns, orchids and bromeliads on stem and branches, etc.

of parameters and the classes within each parameter are given by Paulsch (2002) and Piechowski (2003). Statistical interpretation was carried out by the use of cluster analyses and the Ward algorithm, with the squared Euclidean distance as a distance measure.

To find relationships between the total of 204 parameters for the highest and the lowest strata and altitude the Spearman rank correlation coefficient (r_s) was calculated. To avoid a table-wide false discovery rate only probabilities of $P<0.001$ were considered.

10.3.3 Results and Discussion

Landscape level classification In the majority, the 245 land-use units of the 12 fincas investigated were not regularly shaped but followed geo-morphological features of the terrain (e.g. small valleys, landslides) or human-induced boundaries (e.g. slash and burn destruction of primary forest). Figure 10.3.1 gives a schematic overview of the typical structural units in the area under land use in the San Francisco valley. Pasture is the dominant form of land use and pasture patches can be further differentiated by the presence of trees or groups of trees, by the amount of dead wood still present or the degree of fern (*Pteridium arachnoideum*) invading the grass-dominated patches.

Regular-shaped gardens are found directly around the farm buildings, providing the farmers with fruit, vegetables and medical plants. In some places afforestations with *Pinus* sp. and *Eucalyptus* sp. can be found. Landslides occur typically in the context of road construction. Forest remnants can be found especially along little creeks (*quebradas*) and recently cleared patches border the primary forests at the upper level of the properties. The landscape pattern described by the structural analysis shows attributes of a just recently colonized region: boundaries follow geomorphological structures instead of linear property boundaries, pastures still include dead trees not yet rotten and farms are irregularly distributed in a matrix of primary forest. It can be concluded that the landscape undergoes a dynamic process of land-use changes that will lead to more loss of primary forest (see Chapters 3 and 4 in this volume). The structural classification is an appropriate means of documenting this process.

10.3.3.1 Plot Level Classification and Altitudinal Correlations

The 166 plots were grouped by cluster analyses into 21 forest types of different degree of human interference. Table 10.3.2 assigns the nine primary forest types to the altitudinal range of their occurrence.

The grouping of the plots into structural forest types was based on a multitude of parameters and it is impossible to name only a handful of individual key parameters that would justify the grouping (Paulsch 2002). In order to handle the structural forest types as descriptive units the very obvious parameters of leaf size and topographic situation were used in name-giving, despite the fact that the types are distinguished by the varying occurrence of more than 100 parameters. Thus, the nine types of Table 10.3.2 can be described as follows.

The primary forest of the ridge of Cajanuma was an elfin forest with small stunted trees, with diagonal stems, a high coverage of epiphytic mosses and vascular epiphytes and a high percentage of *Weimannia* species (see Chapter. 10.4). The canopy stratum was only 10–15 m high, 5–25 trees per plot covered 40–50% and the 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. Bamboo was omnipresent, overgrowing young trees and filling gaps.

The canopy stratum of *the primary ravine forest of higher altitudes* 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 individual trees hosted some vascular epiphytes, connecting elements were rare or absent, climbers conspicuous. The percentage of standing dead trees was higher than average and stilt roots were abundant.

The primary ravine forest of lower altitudes 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). In the canopy stratum, 1–5 individual trees covered 40–50%. The irregular or umbrella-shaped crowns had a distance of <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 °.

The microphyll ridge forest had the widest altitudinal range of all forest types in the investigation area. It was characterized 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. Compared with 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. The high percentage of semi-sclerophyll leaves corresponded with the dominance of *Purdiaea nutans* Planch. (Cyrillaceae) in the canopy stratum (see Chapter 19). A high percentage of species of the Clusiaceae was responsible for the over-representation of semi-succulent leaves (see Chapters 10.1, 10.4).

Compared with the other forest types, the height of canopy, height of lowest branch and height of main ramification in *the macrophyll ridge forest* were under-represented and the distance between crowns and stems less than average. Ground cover was higher and more crowns than in other forest types were restricted by their neighbors. Bamboo as a connecting element was over-represented in the canopy stratum. The over-representation of macrophyll semi-sclerophyll and bicolored leaves corresponded with the high percentage of species of Melastomataceae (genera *Miconia*, *Graffenrieda*) in the canopy stratum (see Chapters 10.1, 10.4).

Palm trees were over-represented in the canopy stratum of *the megaphyll ridge forest* corresponding with the over-representation of funnel-shaped crowns, a crown volume restricted to the top, a high number of trees without branches and a high percentage of megaphyll compound leaves.

Compared with the canopy strata of other forest types, *the mesophyll ridge forest* was over-represented by diagonal stems, fan-shaped crowns, dead branches, epiphytic ferns, bamboo and connecting lianas. Climbers were conspicuous.

In *the forest with dense canopy* the crowns of neighboring trees grew into each other, the number of trees in the canopy stratum was higher than in other types and climbers and lianas were highly abundant.

The low ridge forest was characterized by a sparse canopy of less than 20 m height, a dbh of 20–30 cm, semi-sclerophyll leaves and a high abundance of vascular epiphytes.

For a closer description of which parameters are most abundant or characteristic for each type, see Paulsch (2002) and Piechowski (2003).

The distribution of structural forest types does not follow a clear altitudinal gradient throughout the investigation area. Instead, two main gradients determine vegetation structure: the degree of destruction mainly caused by humans and the relief. Especially in the lower part of the investigation area between 960 m and 1500 m and in the lower part of the ESCF area (1800–2000 m) the human influence by selective logging or cutting and burning causes different vegetation types at the same altitudinal level. In the mid-elevation part of the ECSF area (2000–2300 m) the distribution of forest types is mainly caused by the heavily inclined relief and the small scale mosaic of deep valleys and steep ridges. Only at an altitude between 2400 m and 3100 m, which is above the steep valleys (in the higher part of the ECSF area, in the Cajanuma section of the Podocarpus National Park) the forest vegetation forms a kind of altitudinal belts.

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 is based on the results of an intense testing of the applicability of several approaches known from the literature (for more details, see Axmacher 1998). 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 extended 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 (Bogh 1992; Finckh and Paulsch 1995; Grubb et al. 1963; Nadkarni 1984). The resulting structural classification approach offers an easy and quick way with only a minimal training requirement to map the vegetation of a distinct area like e.g. a national park. In contrast, a floristic classification would be very time-consuming and require the knowledge of a team of experts for all the different plant taxa.

Highly significant changes ($P \leq 0.001$) in the occurrence of parameters with increasing altitude are e.g. crown development, leaf consistency, leaf size, occurrence of drip-tips and leaf angle: with increasing altitude the percentage of semi-sclerophyll ($r_S = 0.401$) and semi-succulent leaves ($r_S = 0.332$) increases as well as the occurrence of nanophyll ($r_S = 0.294$) and nano-microphyll ($r_S = 0.445$) leaves, while the occurrence of larger leaves (mesophyll $r_S = -0.345$) decreases. Not only the size and consistency of leaves changes, but also the angle in which they are presented. With increasing altitude leaves are less often presented horizontally ($r_S = -0.576$), more at steeper angles ($r_S = 0.681$). All these findings might be explained as adaptations to extreme amounts of radiance at higher elevations that occur in the rare occasions of cloudless days and lead to the danger of drought stress, especially on the less profound soils on ridges. The decreasing number of drip-tips with increasing altitude ($r_S = -0.696$) might be related to different precipitation patterns: at the lower elevations heavy rains occur regularly, while at higher elevations a main part of the moisture comes from clouds and slight drizzle. Other changes relate to the shape of the trees as a whole: with increasing altitude a higher percentage of crowns in the canopy layer were fully developed ($r_S = 0.658$) and not restricted by neighbors ($r_S = -0.527$). At lower elevations and especially in ravines occurs hard competition for light and trees will fill every gap in a way that allows only some individuals to develop full crowns, whereas at higher elevations the lack of other resources (e.g. nutrients) is determining tree growth. So trees are dispersed more scarcely and crowns in the canopy layer do not outgrow each other in their competition for light.

These examples show that structural features and their changes can be related to the change in environmental conditions.

10.3.3.2 Comparison with Existing Zonation Models

The expression ‘montane rain forest’ is used in different contexts (e.g. Beard 1955; Ellenberg 1975; Gradstein and Frahm 1987; Grubb et al. 1963; Lauer and Erlenbach 1987; Richards 1952). Table 10.3.2 places nine of the primary structural forest types according to their altitudinal range and the relief position. It can be observed that the altitudinal zonation of structural forest types does not contradict the established zonation systems and confirms a change in forest formations at about 2200 m a.s.l.; moreover, it allows further distinction of forest types which would be assigned to one single formation in the traditional classification systems.

10.3.3.3 Functional Relationships

The classification of structural forest types was meant as a basis for the 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 a 1-ha transect in the lower part of the ECSF investigation area. Her data revealed that the distribution of hummingbird-visited plant species and plant individuals reflected the structural forest types. 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. D. Paulsch used the structural forest types in the ECSF area as a basis for his investigations of bird communities and also found relationships (see Chapter 11.1 in this volume). The structural classification system thus provides a solid basis for further investigation of functional relationships.

Table 10.3.2 Structural forest types

Altitude (m a.s.l.)	Structural classification system	
4000	–	
	Shrub and grass páramo	
3000	Primary forest Cajanuma	
2000	Primary ravine forest at higher altitude	Microphyll ridge forest
	Primary ravine forest at lower altitude	Macrophyll ridge forest
		Megaphyll ridge forest
		(Mesophyll ridge forest)
1000	Forest with dense canopy	Low ridge forest
0		

10.3.4 Conclusion

The newly developed and tested structural classification approach offers an easy and quick way with only a minimal training requirement to map the vegetation of a distinct area like e.g. a national park. The altitudinal zonation of the resulting structural forest types does not contradict the established zonation systems and confirms a change in forest formations at about 2200 m a.s.l. in the investigation area. Moreover, it allows further distinction of forest types which would all be assigned to one single formation in the traditional classification systems. Investigation of functional relationships shows that the classification of structural forest types can 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. Thus, the system provides a solid basis for further investigation of functional relationships.