Tree species composition and forest structure of the premontane rain forest in the Reserva Biológica Alberto Brenes, Costa Rica

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Abstract

Spatial variation of tree species composition and forest structure was studied in the Reserva Biológica Alberto Brenes in north-central Costa Rica. Within 13 permanent plots of 400 m² we inventoried all trees with a dbh ≥ 5 cm and investigated some additional site parameters. 147 tree species from 54 plant families were found. Based on similarity in species composition the plots could be divided into three distinct topographical vegetation types. These forest types show not only differences in tree compositions, but also in structural features as crown cover, canopy height and tree stature. In comparison to the often-used one hectare inventories the applied method gives a fast impression of alpha- and beta-diversity of the trees of an area.

Introduction

In this study we tried to find topographical vegetation units from data about tree species composition and forest structure in permanent plots. Topography is one important factor affecting spatial variability of vegetation structure and diversity by providing (micro-)habitat heterogeneity (e.g. Clark et al. 1999, Harms et al. 2001, Lieberman et al. 1985a, Phillips et al. 2003, Takyu et al. 2002, Webb et al. 1999). It is a complex variable, composed of factors as e.g. elevation, hydrology, nutrient dispersion, soil structure and exposure, what it makes difficult to understand its contribution to maintain the high tropical tree species diversity.

In most of the studies on tropical tree diversity and vegetation structure plots of one hectare or bigger are inventoried to describe forest sites (e.g. Lieberman et al. 1985a, Valencia et al. 1994, Wattenberg & Breckle 1995). This study shows an alternative method based on smaller plots, which allows the differentiation of forest types on a smaller scale. Plots are grouped by statistical means based on tree species composition. As results we get information about the alpha- and beta-diversity of the study area.

Study area

This study was carried out in the Reserva Biológica Alberto Manuel Brenes (RBAMB) which is located on the Atlantic slope of the Cordillera de Tilarán (Fig. 1). The RBAMB is part of the province of Alajuela in north-central Costa Rica.

The area shows a mountainous relief, with altitudes ranging between 550 m and 1650 m. Mean annual rainfall reaches about 4100 mm at the biological station (860 m, data from the last twelve years), in few years one or two drier month (precipitation < 100 mm) occur between January and April.

Most of the protected area of 7800 ha is covered with primary forest, which can be classified as tropical premontane wet forest according to Holdridge et al. (1971) and Hartshorn (1983) or as bosque tropical húmedo premontano (tropical premontane wet) forest after Kappelle (2001).

The alpha-diversity is high, in the so far investigated area around the biological station more than 1000 species of higher plants were found (Breckle 1998, Gómez-Laurito & Ortiz 1996, 2004). A more detailed description of the RBAMB is given by Salazar Rodriguez (2000).

Fig. 1: Map of Costa Rica with the location of the Reserva Biológica Alberto Manuel Brenes (RBAMB).

Material and methods

Within the project "Gap dynamics and growth dynamics of tree species from montane tropical rain forests in South Ecuador and Costa Rica" tree species composition and forest structure at the RBAMB was investigated. In the study area 13 permanent plots of 400 m² were installed between 850 and

1210 m of elevation in different topographical situations from the bottom of the Rio San Lorencito valley to the nearby ridge (Fig. 4). These plots are situated in homogeneous, mature vegetation without visible recent disturbances (e.g. tree fall) within an area of ca. 1 km². In the plots a complete inventory of all stems with a diameter at breast height (dbh) of 5 cm or bigger was carried out. All trees were marked with aluminium tags, height, dbh and positions within the plots were measured. From all unknown species herbarium specimens were prepared and deposited at the herbaria of the Universidad de Costa Rica, San José (USJ), Instituto Nacional de Biodiversidad (INB) and University of Bielefeld (BIEL). Profile diagrams of sections of three selected plots were drawn (20 m x 5 m). Crown cover in the plots was estimated with a spherical densitometer (Lemmon 1956). From the resulting data about tree species composition we calculated similarity of the plots with three different indices (Morisita, NESS m_{max} and Soerensen). For ordination nonmetric multidimensional scaling (NMDS) and correspondence analysis were applied. For a more detailed description of the inventory, the statistical methods and the similarity indices see Homeier (2004).

Results

In the 13 permanent plots we inventoried 541 tree individuals (without tree ferns) of 147 tree species (97 with a dbh $\geq$ 10 cm) from 54 plant families. The most important families were Rubiaceae (14 species), Fabaceae (including Mimosoideae, 13), Lauraceae (11), Melastomataceae (10) and Moraceae (9). Species richest genera were *Inga* (7 species), *Ocotea* (7) and *Miconia* (4). As most frequent species we found the two palms *Cryosophila warscewiczii* (43 individuals) and *Iriartea*

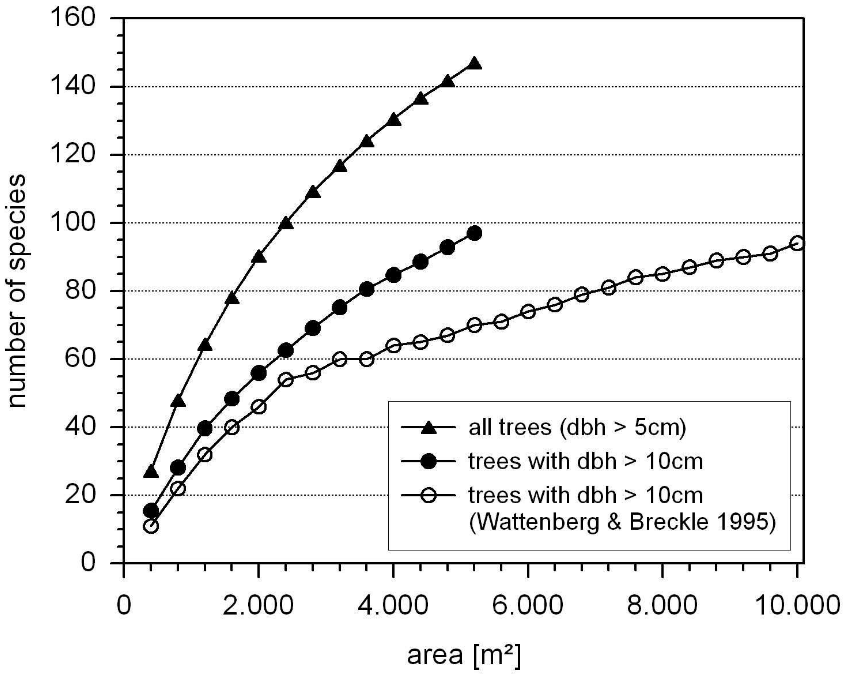


Fig. 2: The figure shows the number of tree species in relation to the plot area. The two upper curves (black symbols) show the species increment for this study (plots are randomly pooled), the lower curve (open symbols) shows the results from a study (Wattenberg & Breckle 1995) worked out at the same area on a one-hectare plot.

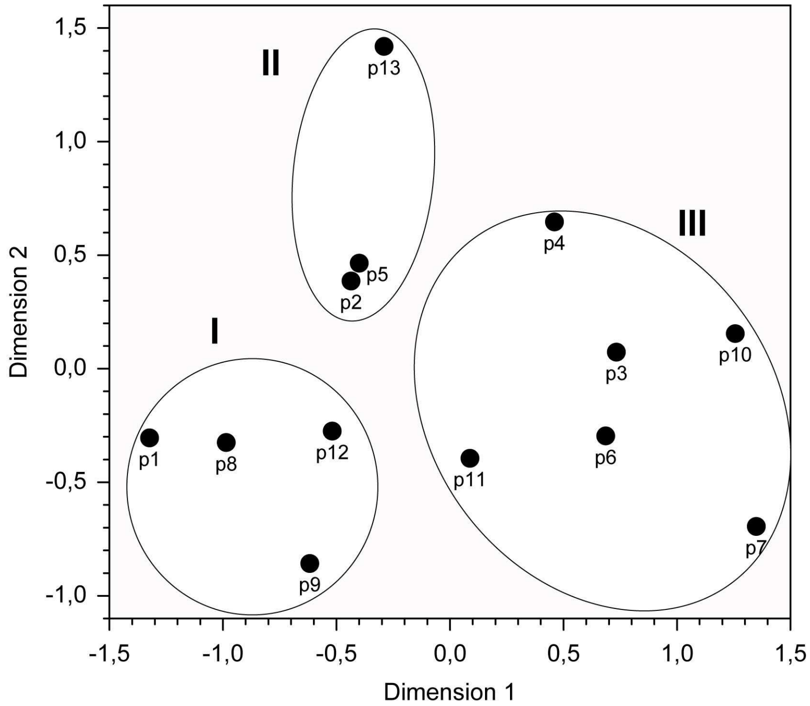


Fig. 3: Nonmetric multidimensional scaling plot (two dimensions) of tree species similarity (based on NESS m_{max} index) of the investigated permanent plots.

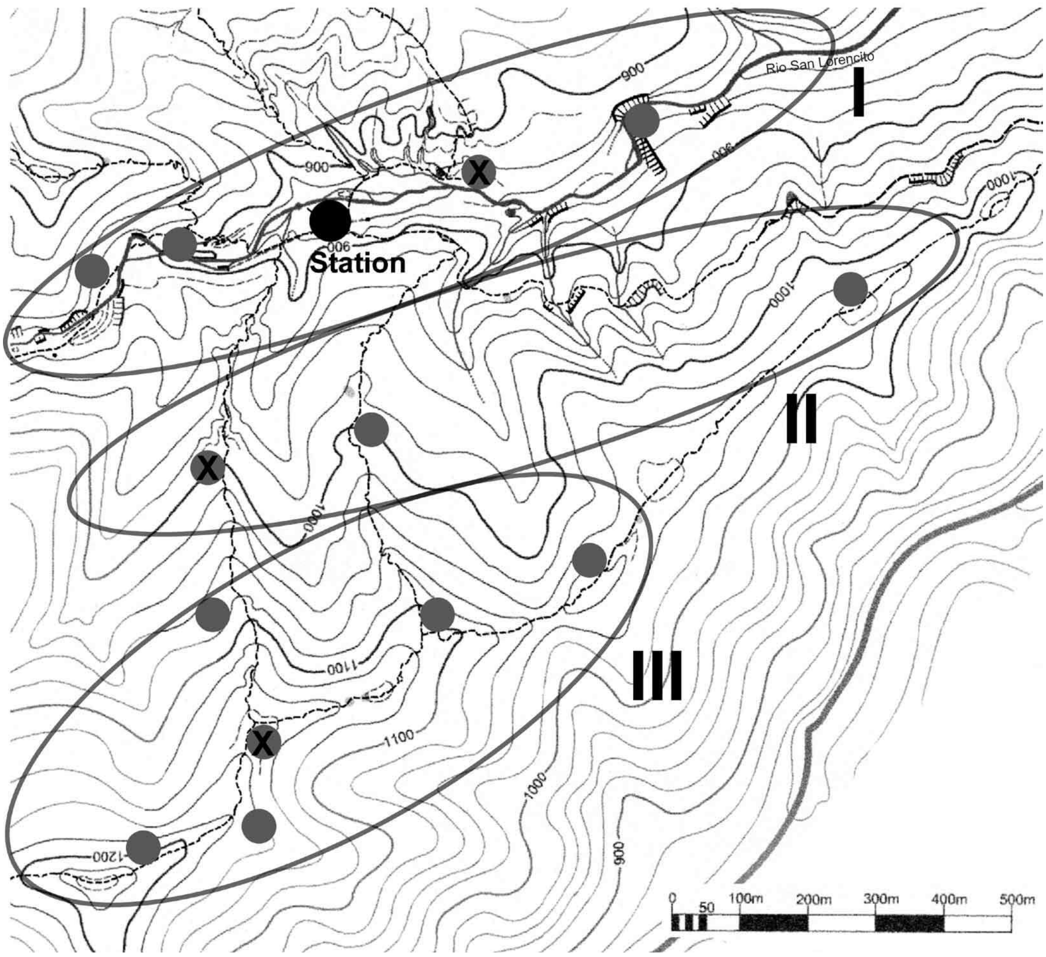


Fig. 4: Investigation area with location of the permanent plots. The three distinct forest types are marked, Type I: forest of the Rio San Lorencito valley, Type II: slope forest, Type III: forest on upper slopes and ridges. The three plots with an "X" are shown in the profile diagrams of Fig. 6.

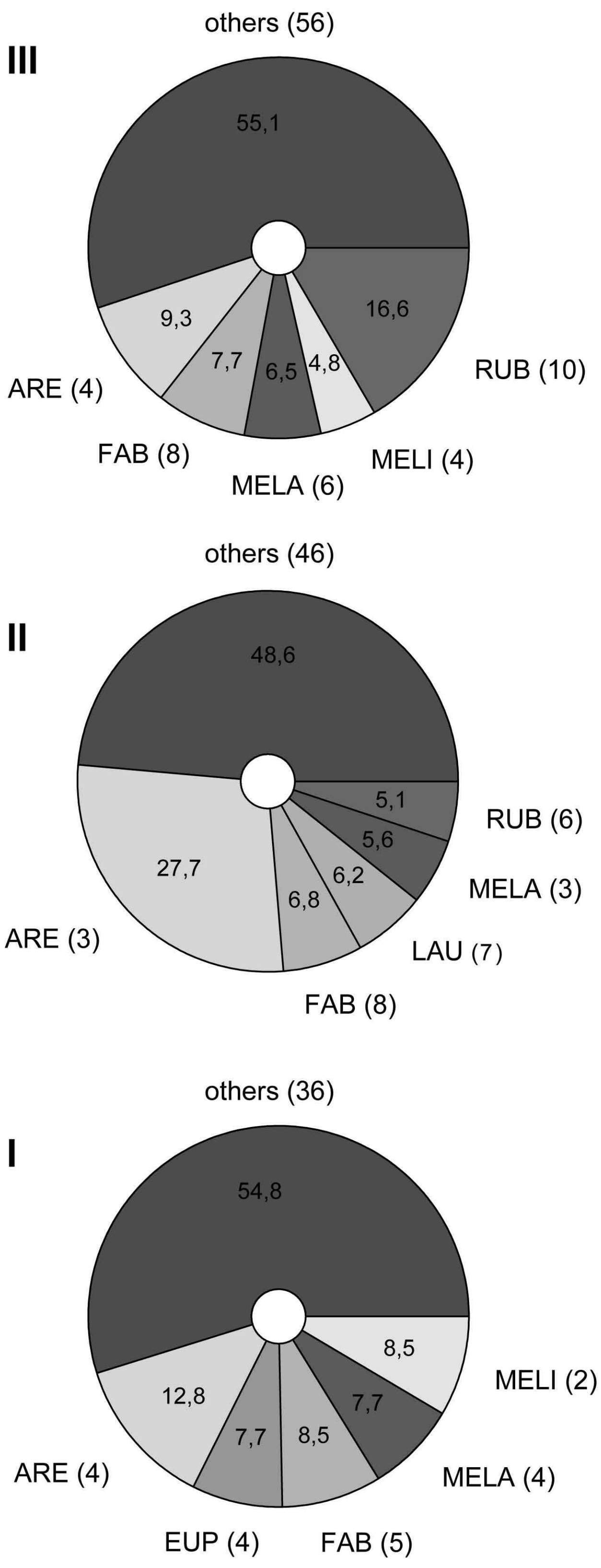


Fig.5: Family composition of the trees in the three forest types. ARE Arecaceae, EUP Euphorbiaceae, LAU Lauraceae, MELA Melastomataceae, MELI Meliaceae, MIM Mimosaceae, RUB Rubiaceae.

deltoidea (18) and the Rubiaceae *Elaeagia auriculata* (20).

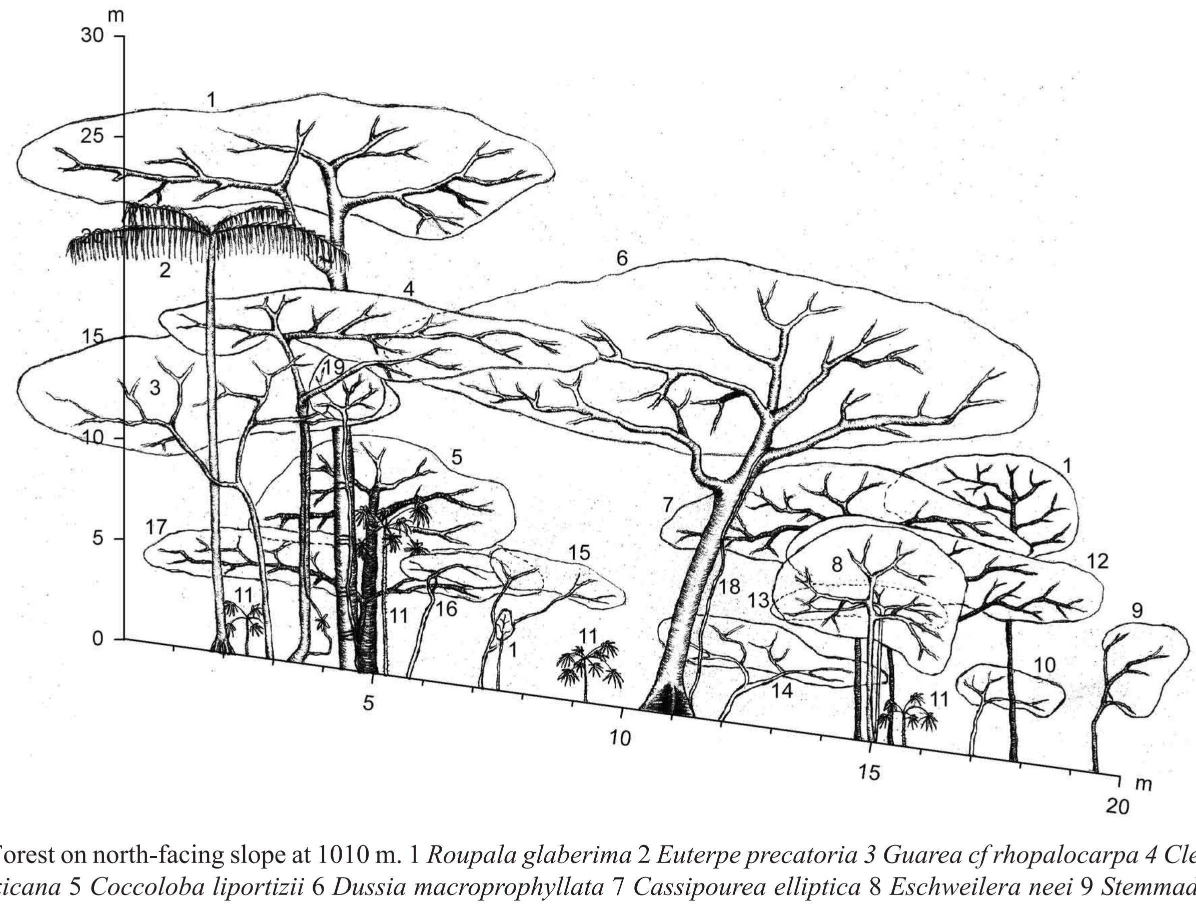
The number of tree species is increasing with increasing sampling area (Fig. 2) and an area of 0.5 or 1.0 hectare seems to be not enough to get all tree species of the investigated forest. In comparison to the study of Wattenberg & Breckle (1995), who inventoried a (rather homogenous) hectare plot at the same site, the increment of the species number is steeper. We found more tree species (dbh ≥ 10 cm) in half the area (accumulated plot area) of the former study.

Figure 3 shows an example for the ordination with NMDS based on similarity of tree species composition in the permanent plots. The ordination divides the plots into three groups which we define as forest types. The same groups we got from three other applied methods (correspondence analysis based on species abundance and NMDS with results from the indices Soerensen and NESS, Homeier 2004).

These three types represent different topographic microhabitats in the study area (Fig. 4). Type I (Fig. 5, 6a) is found at the bottom of the San Lorencito valley, represented by four of our permanent plots. Along the river the tallest forest occurs with up to 30 m height and some emergent trees reaching over 40 m. The most frequent species is *Iriartea deltoidea* (Arecaceae), other common species are *Alchornea glandulosa* (Euphorbiaceae), *Guarea glabra* (Meliaceae) and the shrub *Spathacanthus hoffmannii* (Acanthaceae).

The second type (Fig. 5, 6b) is found on slopes between 900 and 1050 m of elevation where it reaches up to 25 m. It is characterized by the high frequency of *Cryosophila warscewiczii* (Arecaceae), a small palm tree. The palms make up more than one quarter of all trees. Other important families are Lauraceae,

Fig. 6a-c: Profile diagrams of the forest types in the altitudinal gradient. Depth of the profiles is 5 m.
a) Forest in the valley of the Rio San Lorencito at 850 m. 1 *Iriartea deltoidea* 2 *Bunchosia veluticarpa* 3 *Guarea glabra* 4 *Inga leonis* 5 *Trophis mexicana* 6 *Sorocea pubivena* 7 *Warszewiczia uxpanapensis* 8 *Hasseltia floribunda* 9 *Capparis frondosa* 10 *Plinia salticola* 11 *Chamaedorea tepejilote* 12 *Spathacanthus hoffmannii* 13 *Cordia croati* 14 *Ardisia nigropunctata* 15 *Mucuna urens*



b) Forest on north-facing slope at 1010 m. 1 *Roupala glaberima* 2 *Euterpe precatoria 3 Guarea cf rhopalocarpa 4 Clethra mexicana* 5 *Coccoloba liportizii* 6 *Dussia macroprophyllata* 7 *Cassipourea elliptica* 8 *Eschweilera neei* 9 *Stemmadenia alfari* 10 *Psychotria elata* 11 *Cryosophila warscewiczii* 12 *Sorocea pubivena* 13 *Cordia croati* 14 *Hybanthus denticulatus* 15 indet. 16 *Microtropis occidentalis* 17 *Chrysophyllum hirsutum* 18 liana 19 *Ficus spec.*

c) Forest on ridge at 1160 m. 1 *Ocotea insularis* 2 *Pterocarpus hayesii 3 Licania kallunkii 4 Panopsis costaricensis* 5 *Calatola costaricensis* 6 *Eugenia austin-smithii* 7 *Ocotea paulii* 8 *Plinia salticola* 9 *Faramea occidentalis* 10 *Pachira aquatica* 11 *Clusia spec.* 12 *Prestoea acuminata* 13 *Chrysochlamys psychotrifolia* 14 *Chamaedorea tepejilote* 15 *Malvaviscus arboreus* 16 *Hybanthus denticulatus* 17 *Neea pittierii* 18 *Drymonia conchocalyx* (epiphytic)

Melastomataceae, Mimosaceae and Rubiaceae. *Billia rosea* (Hippocastanaceae) and *Eschweilera neei* (Lecythidaceae) are two of the biggest trees from this forest type with heights up to 35 m and stem diameters to over 60 cm.

Type III (Fig. 5, 6c) occurs on the upper slopes and ridges between 1050 and 1250 m. The canopy reaches not much more than 20 m. Rubiaceae is the most important tree family in species and individual numbers. Common trees are *Elaeagia auriculata* (Rubiaceae), the small palm *Geonoma interrupta*, *Licania kallunkii* (Chrysobalanaceae) and *Calatola costaricensis* (Icacinaceae).

The three types are not only different in species composition, but also in structural appearance which is illustrated in the figures 6 a-c.

Mean crown cover (Fig. 7) is decreasing from type I (91.2 %) over type II (90.1%) to type III (87.7 %), variability is increasing in the same order. In comparison with type I the two other types show well-developed undergrowth vegetation.

Canopy height is decreasing within the gradient valley-slope-ridge (Fig. 6). The relation of dbh to tree height is declining with altitude (Fig. 8), what means that trees of the same height have a larger diameter at higher elevations.

There was no difference found in basal area between the forest types, mean basal area (dbh ≥ 5 cm) was 1.55 m² per plot (respectively 38.8 m² per ha). Stem numbers were ranging from 16-31 (dbh ≥ 10 cm) per plot, highest densities occurred on the slopes (type II) with an average of 27.0 stems per plot in comparison to 20.3 in type I and 19.3 in type III.

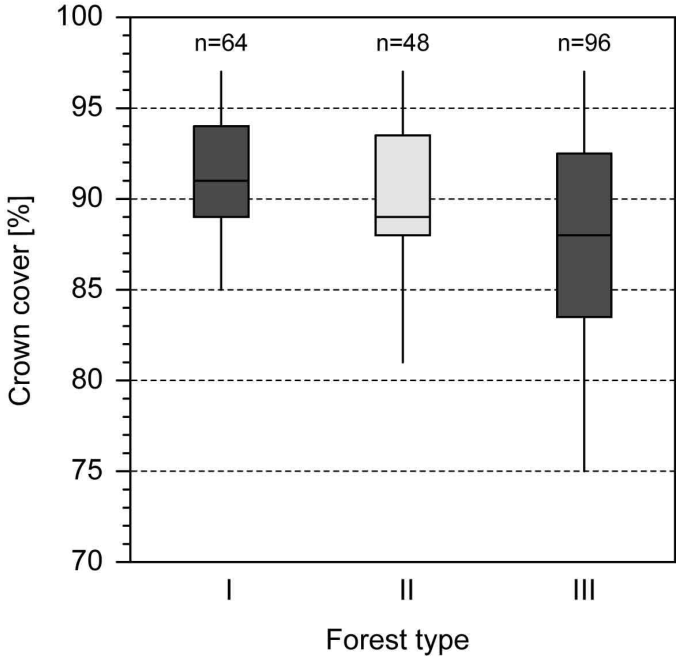


Fig. 7: Box-Whisker-plot of the proportional crown cover in the three forest types. Total number of measurements (16 per plot) per forest type is given in the diagram.

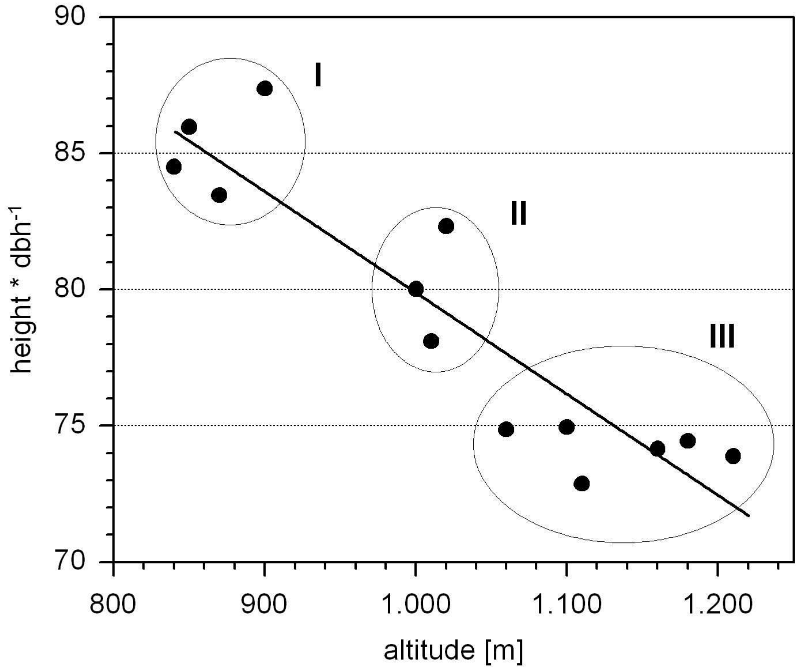


Fig. 8: The figure shows the relation of tree height to tree diameter (means for the 13 permanent plots) within the altitudinal gradient and the forest types. The correlation with altitude is highly significant ($r = 0.91$, $p < 0.001$).

Discussion

The species number of 97 (dbh ≥ 10 cm) is within the range of Costa Rican forests at the comparable elevations (Lieberman et al. 1996: 82 to 125 tree species with dbh ≥ 10 cm per ha at Volcan Barva between 750 and 1250 m, Haber 2000: 104 at Peñas Blancas, 750 m) and does not reach the diversity of Costa Rican lowland forests (e.g. Golfo Dulce, Weissenhofer et al. 2001: 120-190) or Amazonian

forests (Cuyabeno in Ecuador, Valencia et al. 1994: 307; Yanamono in Peru, Gentry 1988:283).
Hartshorn & Hammel (1994) found the following five plant families to be the most important in the lowland forest of La Selva, Costa Rica: Fabaceae, Lauraceae, Rubiaceae, Euphorbiaceae and Moraceae. In the RBAMB some typical lowland families like Annonaceae, Euphorbiaceae, Moraceae and Sapotaceae (Gentry 1990) are well represented, but they seem to be more common in the lower parts of the reserve and in the valleys (type I). According to Haber (2000) Lauraceae, Rubiaceae, Melastomataceae, Fabaceae and Myrtaceae are the families with the highest number of tree species in the montane forest of Monteverde (adjacent to the RBAMB in the northwest) above 1200 m. Melastomataceae and Myrtaceae are among the most diverse tree families in the RBAMB too, therefore the investigated premontane forest can be interpreted also floristically as a transition forest between lowland and montane forests (see Burger 1991).

The investigated forest seems to be a highly dynamic mosaic in space and time of different phases of development, where no distinct layers or strata can be found. The lesser crown density of types II and III permit a better developed understorey, whereas type I with its taller trees and denser canopy is more comparable to lowland sites.

In their large-scale altitudinal gradient Lieberman et al. (1996) found a decreasing canopy height and a decreasing index of slenderness (relation of dbh to height of a tree) with increasing altitude. They discussed the influence of temperature, mineral nutrition and wind. Reasons for the decreasing index of slenderness in our study could be the higher static requirements due to stronger wind impact on the ridge and better nutrient availability close to the river, where sediments and organic material are accumulated (Breckle 1997).

The basal area is a little higher than that of similar forests from Costa Rica, Hartshorn & Peralta (1988) found 32.5-36.9 m^2 ha^{-1} between 1000 and 1260 m, Lieberman et al. (1996) 27.4 m^2 ha^{-1} at 1000 m. Higher stem densities on slopes as we found them were reported from La Selva by Lieberman et al. (1985b).

Wattenberg & Breckle (1995) found *Iriartea deltoidea* to be the most frequent tree species at their hectare, which is situated on a slope. This study shows that frequencies of the dominating species are highly depending on topography. *Iriartea deltoidea* is found with high individual numbers in the forest along the river and on lower slopes (types I and II), whereas the species on the upper slopes and ridges does not occur that often.

The steeper increase of species number with plot area and the higher total number of species in comparison to Wattenberg & Breckle (1995) can be explained by the inclusion of different topographical units and their species in our study. However, it seems not to be possible to determine a minimum area and therefore phytosociological methods and syntaxonomy are not applicable in such a diverse ecosystem.

In comparison to the often used one-hectare-inventories the here applied inventory method seems to be more suitable to get an idea of tree diversity of an area and its small-scale heterogeneity in tree species composition and forest structure. With a higher number of smaller plots it seems to be possible to get more information of an area.

The application of similarity indices based on species abundance followed by ordination methods shows clearly that vegetation types can be determined with statistical methods. Plot replication permits the representative consideration of all obvious vegetation types in an area and the assessment of effects influencing vegetation, like topography.

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