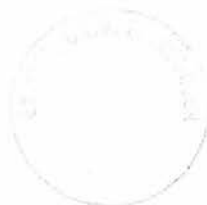


**Ecology and Biogeography of a Atlantic Montane Forest in
Southeastern Brazil**

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1998**



Declaration

I am responsible for composing this dissertation. It represents my own work and where the work of others has been used it is duly acknowledged.

Edinburgh, 27/11/1998

Claudio Belmonte de Athayde ~~Bohrer~~

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Abstract

The Brazilian Atlantic forest is considered an area of highest priority for conservation. This present study concentrates on the Macaé de Cima Reserve of Nova Friburgo, state of Rio de Janeiro. The research aim is to characterise the variations in the structure and floristic composition of the forest and to investigate their relationships with the physical environment at local and regional scales.

The local analysis is based on vegetation and soil data collected in ten 20x20 m (400m²) plots established at different sites within the Reserve. An analysis at a regional level was also carried out, comparing floristic and environmental data from 51 areas within the Atlantic forest domain. Both analyses are based on multivariate techniques. Aerial photographs, Landsat TM satellite imagery and other spatial data are analysed through digital image processing and geographical information system software.

The Reserve is covered mainly by dense primary and old growth secondary tropical forest. Montane forest is the dominant vegetation type, covering slopes up to 1500m altitude. The high montane forest occurs on top-slopes, in restricted mountain ridge areas. Secondary forests occur mainly on medium and lower slopes. The forest as a whole has an average density of 1108 trees/ha, and an average basal area of 43 m²/ha. The average total height is 14m, and the average wood volume reaches 171.3 m³/ha. A total of 445 trees were measured in the sampling plots, representing a total of 164 species. Myrtaceae has the greatest number of species, followed by Lauraceae, Leguminosae, Melastomataceae, Monimiaceae, Rubiaceae, Clusiaceae, Moraceae and Sapindaceae. The ten species with highest IVI are *Euterpe edulis*, *Licania kunthiana*, *Ocotea indecora*, *Vochysia saldanhae*, *Calycorectes* sp.1, *Dendropanax trilobium*, *Kielmeyera insignis*, *Cryptocarya moschata*, *Meriania robusta*, and *Clethra scabra*. The TWINSPAN classification reveals the occurrence of at least two distinct types of forest. The first axis of the DCA ordination is related to an altitudinal gradient.

PCA analysis of forest structural, environmental, geographical and soil data revealed high correlation between altitude and Al, basal area and K, number of species and %C, clay content and slope. The CCA ordination reveals a correlation between altitude, height and canopy and the first axis, while slope, number of species, P, Ca+Mg, H+Al and CEC are correlated with the second axis. CCA also shows a relief gradient along two axes. The ordination and classification results support the hypothesis of a local mosaic composed by different plant communities that can be related to site and relief characteristics, with variations on the forest structure and composition, and site conditions strongly related to altitude, location on the relief and slope. Forest plots are classified into two main forest

types. The first type is related to the montane forest formation. The remaining plots represent a transition between the montane and the high-montane forest or cloud forests.

The floristic patterns demonstrated by the classification (UPGMA, TWINSpan) and ordination (DCA, CCA) of the 51 forest areas are strongly related to climatic and geographical variables. Köppen climatic types are shown to be good predictors of similarities between the areas. CCA reveals a clear gradient from low latitude, lowland warm areas with high rainfall to higher latitude and altitude, colder and drier areas. All methods distinguish the semideciduous from the coastal moist forests, with the occurrence of a transitional montane ecotone between the two main forest types. High altitude areas also indicate floristic links with the *Araucaria* mixed forests, which might be related both to current climate and historical biogeographical events.

Past (1970) and current land cover maps were produced, with results from the analysis at both local and regional scales used as surrogate information on the classification. A conceptual model for the Atlantic forest vegetation in southeastern Brazil is proposed, based on the relationships discovered between the forest vegetation and the physical environment.

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CHAPTER 1. Introduction

1.1. Research Context

Tropical forests are a vital human resource. They host a great part of the earth's biological diversity and are both home for a large population and source of food and materials. However, despite their importance, the total area covered by tropical forests has been continuously reduced since the first human impacts.

Until a few decades ago, little was known about tropical forest ecosystems. Difficulties of access and a strong centralisation of science in northern temperate countries, among others, were important reasons for this situation. This has changed dramatically over the last decades, as great advances in both pure and applied science have led to a much better knowledge of the overall patterns and related processes that occur in tropical forest ecosystems, and greater recognition of impacts at the global scale.

Most of tropical forest research has been concentrated on lowland areas, which are often regarded as more important in terms of their extent, biodiversity and management potential. However, in many parts of the tropics, mountain areas are also of great importance. They protect the headwaters of important rivers, they are the source of several forest products, and also possess a high biodiversity, which sometimes can be comparable or even greater than many lowland areas. Tropical mountain forests also contain a large number of endemic species, and in many areas are the only remaining forests of any significance. Despite their importance, tropical mountain forests have received relatively little attention, either for research or for conservation purposes.

The Atlantic forest, which covered most of Brazilian eastern coast, is one of the most endangered tropical forest areas of the Neotropics, or indeed of the whole world (Olson & Dinerstein, 1998). Despite having a relatively long history of colonisation by European and African settlers, Rio de Janeiro State still possesses a considerable forest area. Most of the remaining forests are located on the wet Atlantic-facing slopes of its coastal mountain range, with small fragments occurring

in the coastal lowlands and the drier inter-montane valleys. Little is known about the structure and composition of the different types of forest ecosystems.

In this study an investigation will be made into the structure and floristic composition of a tropical mountain forest environment, and its relationships with the physical environment at different spatial scales. This will be carried out by means of a case study, concentrated in a mountain forest area located in central-eastern part of Rio de Janeiro. The study will analyse the extent to which forest structure and composition varies across the local landscape and will assess the influence of related environmental factors. The role of environmental factors at a broader scale and the floristic relationships of this forest with other forest areas across SE Brazil will also be examined. Finally, the results are summarised in a conceptual model of the forest-physical environment relationships, which could be expanded to other SE Brazil Atlantic forests.

1.2. Aims

The objective of this research project is to investigate how the forest structure and composition varies in a tropical mountain forest area, and to distinguish the main environmental factors related to the ecological variation at different spatial scales. More specifically, the research will attempt to answer to following questions:

1. Is it possible to identify and characterise the main relationships between Atlantic forest communities and environmental gradients at a local (site) scale?

This question can be answered by investigating the vegetation patterns, including the identification of possible boundaries between different forest types, in a specific forest area. The objective is to search for patterns of relationships between the forest structure and composition and the local physical environment, including the role of human activities. The forest structure, its floristic composition and its variation along the landscape will be addressed in Chapter 5. The role of the environmental factors in the variation of forest structure and composition will be addressed in Chapter 6.

2. Is it possible to identify and characterise the main relationships between forest composition and factors of the physical environmental gradients at broader (regional) scales?

This question can be answered by investigating the relationships between different Atlantic forest sites and related environmental gradients. The objective is to search for patterns of relationships between the floristic composition and the physical environment across the Atlantic forest area in SE Brazil. The degree of similarity between different forest areas and their relationship with the main aspects of the physical environment will be addressed in Chapter 7.

3. Are the variations of the forest across the landscape (spatial distribution of the forest resources) related to variations of other environmental variables?

This question can be answered through an analysis of the spatial patterns of the landscape, at different spatial scales. The objective is to analyse if, and to what degree, the heterogeneity of the forest structure and composition in an Atlantic montane forest area can be related to the heterogeneity of the physical landscape. The spatial aspects of the Atlantic mountain forest environment will be addressed in Chapter 8.

4. Can the relationships between the forest and the physical environment be summarised in a spatial model that could predict the potential vegetation in the Atlantic forest region?

This question can be answered by organising the links and relationships between the forest vegetation and aspects of the physical environment at different spatial scales systematically. The objective is to summarise the forest-physical environment relationships in a spatial conceptual model of the Atlantic forest vegetation that could be implemented through a computer system. This model could be used to predict the potential vegetation of any given area, as well as to investigate

rates and trends of changes in the landscape structure in a temporal scale. This question will be addressed in Chapter 9.

5. How can the ecological knowledge of the spatial aspects of the Atlantic forest ecosystem be used for the implementation of better forest conservation and management?

This question can be answered by the identification and assessment of the information needs, its availability, accuracy and adequacy, and by establishing the important information gaps for appropriate management of the Atlantic mountain forest ecosystem. The objective is to assess the potential role of an integrated landscape approach on the evaluation of possible impacts resulting from forest management policies. Aspects such as type of the data needed, presentation of the research results, and the possibilities for integration of remote sensing and geographic information systems capabilities into the decision-making process will be addressed in Chapters 6-9, as well as in the conclusion (Chapter 10).

CHAPTER 2. Concepts and Methods

2.1. Introduction

This chapter assesses the main concepts and methods used in the analysis of the composition and structure of tropical forest and its relationship to the physical environment. The objective is to evaluate the suitability of such procedures for use in the study of the Atlantic forest ecosystem, as a way to support planning, with the ultimate goal of conservation and sustainable forest management. The chapter presents an overview of possible methodologies, from which the specific practices adopted in the research will be drawn.

2.2. Forest Management and Conservation Planning

Land-use planning seeks to promote and maintain the sustainable use of natural resources. Land evaluation and assessment procedures are an important part of the planning process, where the capability or suitability of the land for alternative uses is assessed based on specific criteria (Carpenter, 1981). Most land evaluation methods adopted in land-use planning normally emphasise the potential of the soil for agricultural uses (Davidson, 1992; FAO, 1976). However, land-use planning should also take into account other options for use of the land, based on the knowledge of processes and interactions that occur in the landscape. Furthermore, it should consider the total economic value of the land, including the direct and indirect, current and future uses and benefits provided by the land resources (Pearce & Moran, 1994; WRI, 1992).

Forest evaluation procedures concentrate mainly on the potential for timber production (FAO, 1984; Heindijk, 1975). However, the value of non-timber products, the indirect environmental and social benefits of the forest, and the importance of forests in regional and global climatic processes are also being increasingly considered (Bushbacher, 1990; Oldeman, 1991; Peters *et al.*, 1989; Sample, 1994; Solomon & Shugart, 1993). Efforts have also been directed towards the integration of forest management and conservation objectives (Blockhus *et al.*, 1992; Wilcox, 1995). The ultimate goal is to find a balance between the economic

and social benefits from the exploitation of forest products and the maintenance of the diversity and variability of the forest.

Forest management deals with the procedures involved in the decision-making process (Carpenter, 1981). Management decisions are normally made in relation to management units or stands, which may or not be related to the environmental heterogeneity of the land (Blockhus, 1992; FAO, 1984; Kleine & Heuvelop, 1993). Forest management units can be considered as homogeneous production systems characterised by a mixture of plant community, ecosystem and landscape entities, depending on the heterogeneity of the major environmental determinants. The identification and characterisation of discontinuities, e.g., discrete vegetation communities along more or less continuous environmental gradients, can have a great value for forest management. With management units closely related to the spatial patterns of the environment, decisions could be made on a sounder environmental and ecological basis.

A current paradigm of ecological science emphasises the role of natural disturbance on the structure and functions of ecological systems (Picket *et al.*, 1992). As a consequence, the focus in conservation planning has changed to the rational utilisation of land resources, aiming at the maintenance of essential processes and life-supporting systems (MacKinnon *et al.*, 1986). Emphasis has been shifting from the establishment of protected areas surrounded by incompatible land-uses to a greater integration between conservation and other land-use types, involving consideration of the biological and technical aspects and of the local socio-economic and political environment (Blockhus *et al.*, 1992; Spelleberg, 1992).

Conservation biology deals basically with the selection of priority areas for protection, avoiding extinctions, and restoring areas with ecological damage (Fiedler & Jain, 1992; Western, 1989). It aims to provide conservation principles, identify problems, establish corrective procedures, and to establish a bridge between science and management. It tries to establish common criteria for recognising biological boundary limits, identifying endangered species or ecosystems, and distinguishing critical ecological processes and keystone species (Western, 1989). A good knowledge of the ecology and natural history of the species or ecosystems considered, and of the possible impacts resulting from the adoption of different land

management strategies is fundamental for the achievement of conservation objectives (Fiedler & Jain, 1992; Shrader-Frechette & McCoy, 1993).

2.3. Ecological Concepts

Ecology studies the relationships between organisms and their environment (Colinvaux, 1992). There is not yet an accepted 'universal theory' of ecology, with general principles that apply to both plant and animal species and ecological systems. Some of the theoretical problems that still concern ecological science might be related to the concepts themselves (Shrader-Frechette & McCoy, 1993). Widely used concepts such as community, ecosystem, population, formation, stability, steady state, etc., can have different definitions and uses by different ecologists (Allen & Hoekstra, 1992), which is a serious constraint to their full adoption into the planning process.

Conventionally, ecological concepts have been ordered in a kind of a hierarchy: biosphere, biome, landscape, ecosystem, community, population, organism and cell. However, this hierarchy does not always correspond to the levels defined by the scale of the observed phenomena or systems, e.g. the different concepts or levels are not strictly related hierarchically (Allen & Hoekstra, 1992). The ecological concepts that are more relevant to this investigation, landscape, ecosystem, and community, are described briefly below:

Landscape

The landscape concept has been adopted with different meaning and definitions by different disciplines. More recently, it has been adopted by ecologists as a new level of analysis and also as way to unify or to link the different concepts in terms of both space and time (Turner & Gardner, 1991). The natural landscape can be defined as: 'a part of the space on the earth's surface, consisting of a complex of systems, formed by the activity of rock, water, air, plant, animals and man, and recognised as a unit by its physiognomic forms' (Zonneveld, 1995). Forman & Godron (1986) defined landscape as 'a heterogeneous land area composed of recognisable and spatially repetitive clusters of interacting ecosystems'. The use of

the landscape concept in ecology and environmental management, and its relevance for the present investigation is further explored in Section 2.5.

Ecosystem

An ecosystem is 'an assembly of homogeneous natural elements on a specific area of land, with its own specific interrelationships among those components' (Waring & Shlesinger, 1985). Ecosystem ecology studies the circulation, transformation and accumulation of matter and energy through organisms and their activities, focusing on the identification of pathways (ecosystem structure), how they work (ecosystem function), and on the quantification of processes (biomass production, energy transfer, nutrient cycling). While the vertical boundaries of terrestrial ecosystems are the atmosphere and the soil, the horizontal boundaries are normally defined according to the objectives of the study (Zonneveld, 1995). Studies at ecosystem level have been increasingly incorporated into the planning process and in the investigation of global climatic changes (Likens & Bormann, 1995; Sample, 1994; Waring & Running, 1998).

Community

A community can be defined as 'the integration of the complex behaviour of the biota in a given area, producing a cohesive and multifaceted whole', or simply as the collection of individuals from different species (Greig-Smith, 1983). Community structure relates to the patterns of resource allocation among the species, and to their spatial and temporal abundance. Over a region, groups of species may occur repeatedly in space (community types), while other areas may contain a mix of species from adjacent communities (transition or ecotone).

Concepts of plant community of relevance to the present study include the 'organismic concept' of Clements (1928), the 'individualistic concept' of Gleason (1926), the 'continuum' concept (McIntosh, 1967), and the 'climax pattern hypothesis' of Whittaker (1953) and Whittaker & Levin (1977). The latter suggested the existence of a mosaic of different communities with repeating patterns at a regional scale, correlated with controlling environmental factors. The 'hierarchical continuum' concept (Collins *et al.*, 1993) derives from a combination of the

individualistic distribution of species, hierarchical assemblage structure, and the core-satellite hypothesis (Hanski, 1982, 1991). The hierarchy relates to different responses by plant species to the environmental gradients. Core species combine high abundance and density over a broad gradient, while satellite species have low densities within a small gradient.

The difficulties in establishing a general conceptual model of plant species and communities response to environmental gradients might be related to different scales of patterns, processes, and observation involved (Allen & Hoekstra, 1992). The hierarchical continuum model (Collins *et al.*, 1993) could be combined with the single environment model (Whittaker, 1953), although both models are based on a single environmental gradient, instead of the multiple gradient reality (Austin & Smith, 1989). The concept of vegetation continuum forms the main theoretical basis of the ordination methods employed in the analysis of relationships between plant communities and environmental gradients (Kent & Coker, 1992, Noy-Meir. & Whittaker, 1977; see Section 2.4.4).

Scale

Scale in ecology is related to both time and size. Ecological systems are scale-dependent, but concepts such as the community and organism, and ecological processes and types of ecological structures are independent of scale (Allen & Hoekstra, 1992). The identification of the spatial patterns of both environmental and biological heterogeneity is a first step in the identification and understanding of the processes that occur in the natural environment (Austin, 1987; Greig-Smith, 1983). Although these processes can vary continuously along environmental gradients, the complex combination of the physical environment, ecological interactions and the human influence at a specific moment could result in the occurrence of more homogeneous landscape units or elements, or plant community types (Jongman *et al.*, 1995; Whittaker, 1978). Human actions may accentuate natural boundaries, as they can also be affected by local environmental factors (Kent *et al.*, 1997). As a result, different plant community types can often be mapped and linked to a specific landscape or factor of the physical environment (Zonneveld, 1995).

Austin & Smith (1989) suggest the existence of three types of environmental gradients, each producing a different response by different plant species. *Indirect gradients* (or a complex of environmental factors) are site specific and cannot be extrapolated (e.g. altitude). *Resource gradients* are related to varying resources consumed for growth (nutrient, water, and light). *Direct gradients* have a direct physiological impact on growth, but are not consumed (temperature, pH, water table). The interactions between gradients at different spatial and temporal scales reflect on the scales of the ecological heterogeneity.

The identification of boundaries between different plant communities and their relationships with the physical environment is related to the spatial variation of the main environmental factors across the landscape. Therefore, the selection of an appropriate scale of analysis must take into account the scales of variation of both vegetation and environmental patterns, as well as the objectives of the investigation. The integration of the community, ecosystem and landscape levels of analysis might provide the best approach for the classification and characterisation of relatively homogeneous land units, as a basis for forest management and conservation planning. Relevant methods and techniques that can be adopted in such analyses will be discussed in the next sections.

2.4. Analysis of Tropical Forest Vegetation

Vegetation science is dedicated to the description, explanation and prediction of the distribution patterns of plant populations, species and vegetation units in space and time (Austin, 1986; Greig-Smith, 1983; Wiegleb, 1989). It studies processes which determine the patterns of composition and the emergent properties observed, such as species richness, degrees of dominance and biomass (Austin & Smith, 1989; Burrows, 1990). It tries also to qualify, quantify and to model the complex interactions between the components of plant communities and the physical environment, in order to understand the underlying factors that affect the vegetation patterns seen in nature (Greig-Smith, 1983; Mueller-Dombois & ElleMBERG, 1974).

Quantitative estimates of vegetation factors can be used to estimate the overall floristic composition of the vegetation of an area. They can be adopted for comparisons with other areas, to investigate the internal variation of the vegetation

within the area, or to correlate changes in vegetation with one or more environmental parameters (Greig-Smith, 1983; Shimwell, 1971).

2.4.1. Vegetation Sampling

Sampling procedures are necessarily adopted for gathering vegetation data, due to the impossibility of measuring all of the population over relatively large areas. The selection of an adequate sampling strategy, according to the survey objectives, is one of the first steps that need to be taken into account in any vegetation study.

Sampling Design

Sampling procedures are adopted in most vegetation studies, in order to provide a quantitative and/or qualitative description of vegetation stands (Kent & Coker, 1992). The objective is to give an accurate picture of the overall characteristics of the population with the least number of measurements compatible with the desired accuracy, and to increase the speed in the information gathering (de Vries, 1986; Greig-Smith, 1983). The sampling plots can also be used as control points (ground truth), which can serve as fixed references for the delineation of vegetation or land cover maps (Zonneveld, 1988f).

The choice of the sampling design will depend greatly on the objectives of the study, the features to be measured, the simplicity and speed of measurements, and on the characteristics of the vegetation. The location of sampling plots can be made by a subjective assessment, with selection of a single sample that gives the impression of being fairly representative of the stand or community type. However, as the selection of a 'typical' site depends on the observer's pre-conceived ideas of the character of the vegetation, the data cannot be considered an unbiased estimate of the vegetation of the area (Greig-Smith, 1983). Alternatively, a multiple plot method can be adopted, with a series of quadrats scattered through a stand type, where the overall properties are considered to represent the stand or community.

The sampling methods commonly employed in the study of vegetation can be divided basically into random and non-random sampling. In random sampling all sampling units have an equal chance to be chosen. The estimate of the precision of the means (standard error of the mean) can be used to compare different areas

(Cochran, 1963). In a stratified random sampling, the population is divided into homogeneous sub-populations or strata, with one or more random sample being taken in each stratum. It can increase the precision in the estimation of data for the whole population, as a heterogeneous population is divided into more homogeneous strata, but the precision is dependent on an adequate stratification. The stratification of vegetation can be made using remote sensing images, topographic maps, or based on a previous knowledge of the vegetation variation (Zonneveld, 1988a,c).

Plot size and shape

Different plot sizes and shapes can be used in the sampling of tropical vegetation (Greig-Smith, 1983; Kent & Coker, 1992; Kershaw & Looney, 1985; Mueller-Dombois & Elleberg, 1974), and the choice varies according to purpose. Most vegetation sampling plots have a regular square shape, known as a quadrat. Rectangular samples are considered to be more efficient due to the non-randomness of vegetation (Greig-Smith, 1983). The choice of the plot size will depend mainly on the variability of the population. Most vegetation studies adopt the minimal area concept, with the minimal area chosen to represent the true characteristics of a plant community (Mueller-Dombois & Elleberg, 1974). The selection is normally based on the species-area relationship (Crawley, 1986; Greig-Smith, 1983; Mueller-Dombois & Elleberg, 1974). However, in highly heterogeneous forests, this could lead to very large sampling units (>1 ha), which in many cases are impracticable (Campbell, 1989).

An alternative is the use of a plotless sampling strategy (Campbell, 1989; Mueller-Dombois & Elleberg, 1974). Plotless sampling methods are based on the concept that the distribution of distances can be converted into an estimate of density (Cottam & Curtis, 1956). Plotless methods include the Closest Individual, the Nearest Neighbour, the Random Pairs, and the Point-Centred Quarter (PCQ) method (Clark & Evans, 1954). Their main advantage is that as there is no need for delimitation of an area, a greater speed in the measurements is achieved. They permit a broader sampling of micro-habitats and species per number of individuals sampled, and can also give accurate information in the assessment of distribution patterns of the different species (Campbell, 1989; Payandesh, 1970; Pielou, 1959). The main

criticism is that they assume a random distribution of individuals, which is rare in natural forests (Kershaw & Looney, 1985). The results are also difficult to compare with other studies done with different sampling intensity or based on area sampling.

Any estimate of minimal sampling area is just an approximation, subjectively based on whether the sample area is large enough to represent the characteristic structure of a plant community. Austin *et al.* (1972) considered that the minimal area should be the area that provides an adequate sample of the environmental heterogeneity of the habitat, rather than being based only on the forest composition. Sampling plots with 0.1-0.3 ha could provide enough data to characterise the structure and diversity of tropical forests (Higushi *et al.*, 1982; Scolforo *et al.*, 1993). Several studies made in forest areas in Brazil were based on a single 1 ha rectangular plot, or alternatively with use of smaller plots varying from 0.02-0.2 ha, added to form a total sample area of at least 0.5-1 ha (Martins, 1990; Oliveira-Filho *et al.*, 1994e). The PCQ method has also been widely used in both savanna and forest areas (Lobão & Souza, 1993; Mantovani *et al.*, 1989; Milliken & Ratter, 1989; Ratter *et al.*, 1973; Silva & Leitão-Filho, 1982). The Botany Program from CNPq adopted the 1 ha rectangular plot as a standard, to allow comparisons between different forest areas (Guedes-Bruni *et al.*, 1997).

2.4.2. Structural Analysis

The quantitative description and analysis of vegetation allows an objective assessment of the community composition and of the importance of individual species within the community (Campbell, 1989; Greig-Smith, 1983; Kent & Coker, 1992; Kershaw & Looney, 1985). The use of quantitative data in the definition and classification of the community-types or stands also allows further comparisons between different plant communities (Küchler & Zonneveld, 1988).

The quantitative assessment of forest stands based on structural analysis provides an accurate picture of the horizontal and vertical structure of the forest (Campbell, 1989). This information is fundamental for the design of any management plan for the sustained use of the forest (Lamprecht, 1990; Lobão & Souza, 1993). The main criteria used in the structural analysis of forest stands are

density, cover and frequency, both in absolute figures or relative to the total value of the stand (Finol, 1971; Greig-Smith, 1983).

The density or abundance value represents the number of individuals of each species per unit of area. It is measured by the account of the individuals of each species at each plot. For its simplicity, it is widely used to describe the vegetation structure, or to compare different stands or communities (Greig-Smith, 1983).

Cover or dominance represents the proportional area of ground occupied by the individuals of a particular species, or the area of coverage of the foliage of the species (vertical projection of the crown). It can be measured with a perpendicular projection of the crown on the ground. In woody vegetation, the basal area can be used as an estimate of cover (Greig-Smith, 1983).

Frequency refers to the chance of recording a species in any single sampling plot or the distribution of the individual species over the area. It is normally measured by counting the occurrence of the species in sub-plots of a main plot or transect. Frequency values are highly influenced by plot size, by the individual plant size and also by the pattern of spatial distribution of the species (Greig-Smith, 1983).

A number of indices have been developed to report on quantitative structural information. The Importance Value Index (IVI) is a relatively arbitrary mode of combining the different structural variables. It is normally estimated as the sum of relative frequency, relative density, and relative cover (Mueller-Dombois & Elleberg, 1974). The IVI values must be used critically, as different species situations (a few large individuals versus many small ones) may give the same combined value (Kershaw & Looney, 1985). The Importance Cover Index (IC), which is estimated by the sum of relative cover and density of each individual, can be used as an alternative.

Ecological dominance occurs when one or more species limits the performance of others by exhibiting superior biomass and greater competitive ability (Cain & Castro, 1959). Dominance-diversity relationships of plant communities can be estimated by ranking the component plant species according to their importance values (Whittaker, 1975). A subjective assessment of abundance can also be adopted. In the Braun-Blanquet method, species abundance can be classified in five classes: dominant, abundant, frequent, occasional and rare (Küchler & Zonneveld, 1988a).

Vegetation could also be described by using higher taxonomic units (genera, family, order) rather than species, especially in the analysis of data from a wide geographical or habitat range (Dale & Clifford, 1976). This approach is based on the assumption that the morphological similarities between members of a higher order taxon are likely to be associated with physiological similarities.

Other types of indices have been developed in order to measure the diversity of plant communities (Whittaker, 1975). They allow comparison between different stands and can also be used for numerical vegetation classification (Goodal, 1978). Indices commonly adopted in vegetation studies include the Simpson index of dominance and the Shannon- Wiener indices of diversity and equitability (Whittaker, 1975; Greig-Smith, 1983). They make use of two elements, species richness and equitability. Species diversity or richness (S) is based on the number of species in the community. The Shannon-Wiener or information index measures the evenness of the contribution of different species to the community. The two indices are combined into the concept of heterogeneity (H'), which measures the functional apparent number of species within the community.

2.4.3. Vegetation Classification

Vegetation classification attempts to identify natural groupings of species or plant communities (Küchler, 1988b; Whittaker, 1978). It involves arranging stands into classes, in which members have one or more characteristics in common setting them apart from the members of other classes. As vegetation varies continuously in space, except on geological or other environmental or historical discontinuities, sharp or clear boundaries between different vegetation types normally cannot be easily recognised (Whittaker, 1975).

Plant communities are groups of species with similar environmental limits of tolerance (Greig-Smith, 1983). Plant community types are distinct and definable units of the natural landscape, with any kind of shared characteristics (Whittaker, 1978). Boundaries of community-types are often arbitrary as they are influenced by the choice of the characteristics used in the classification (Shimwell, 1971; Whittaker, 1978). Criteria used in the classification of plant communities include the floristic composition, measures of species abundance, performance of individuals

species, plant growth-forms or life-forms, vegetation physiognomy, patterns of the constituent species, or constants and indices derived directly or indirectly from other criteria (Whittaker, 1978).

Most vegetation classification systems or methods can be grouped in two main approaches, floristic or physiognomic (Kershaw & Looney, 1985; Kùchler, 1988b; Whittaker, 1978). Other approaches include quantitative or numerical procedures, and ecological or landscape oriented systems, based on the characteristics of the environment, such as climate, soils and topography (Kùchler, 1988b).

Physiognomic Analysis and Classification

The vegetation physiognomy is defined by the structural types of plants or growth-forms that dominate or are most conspicuous in the plant community (Shimwell, 1971; Whittaker, 1978). Structure relates to the spatial distribution pattern of growth or life form in a plant community, defined by three main components: vertical (stratification), horizontal (spatial distribution of individuals), and abundance of each species (Kershaw & Looney, 1985).

The concept of formation is a basic feature of most physiognomic systems. A formation can be considered as a community type on a given continent defined by growth-forms dominance and major features of environment. A group of similar formations occurring in similar climate of the different continents is a formation-type (Whittaker, 1978).

Physiognomic methods analyse the stratification of individuals in layers and the arrangement and density within these layers. Location, trunk diameter, total height, height to first main branch, lower limit of crown and crown width of tree data can be used for the preparation of profile diagrams, which are useful to compare similar formation-types (Richards *et al.*, 1940; Beard, 1955; Proctor *et al.*, 1983).

Beard (1946, 1955) proposed a physiognomic-structural system for the classification of tropical American vegetation, with use of the formation-series concept, which relates the vegetation physiognomy to environmental gradients. The formations are considered as stages in a continuous gradient, with the rainforest as a kind of central control or highest type of vegetation possible, from which several

formation-series radiate in response to environmental gradients. The classification groups the formations at three levels: (a) a floristic grouping (association); (b) a physiognomic grouping (formation); and (c) a habitat grouping (formation-series). The approach relates structural characteristics of communities to the qualities of environment to which these characteristic are physiologically adapted (Beard, 1978).

Fosberg (1961) and Eiten (1968) proposed the adoption of structural features only, independent of environmental and floristic features. The life-zones system (Holdridge, 1971) relates physiognomy to climate, classifying the world vegetation into a system of compartments defined by temperature and moisture. The system does not consider the influence of local environmental factors such as soils, which limits its application at more detailed scales, but it has been widely applied in the classification of tropical American vegetation (Lamprecht, 1990; Milano *et al.*, 1987). More recently, it has been used also in climate change modelling research (Cramer & Leeman, 1993)

A physiognomic-structural system was developed for UNESCO, primarily for use in vegetation maps at 1:1,000,000 scale (Ellemberg & Mueller-Dombois, 1967; UNESCO, 1973). The system adopts the Raunkiaer's life-form classes, modified and enlarged by the authors, with additional physiognomic features employed to characterise the vegetation. It is based on a hierarchy of formations (class, subclass, group, formation, subformation and facies), and also includes environmental features (UNESCO, 1973).

The UNESCO's classification system was adapted for the vegetation mapping of Brazil at 1:1,000,000 scale, carried out by the RADAMBRASIL project (Velooso & Góes-Filho, 1982). This system has been reviewed, with a characterisation of the hierarchy for different scales of mapping (Velooso *et al.*, 1991), and was adopted in the vegetation map of Brazil at 1:5,000,000 scale (IBGE, 1993a).

Floristic Analysis and Classification

The floristic analysis of vegetation relies exclusively on its composition. The Braun-Blanquet method of plant association (Küchler & Zonneveld, 1988a) considers the full species composition of the community as an expression of the environment. It is based on the concept of association, which is considered to

represent a vegetation community with a determined floristic composition under uniform environmental conditions (Kent & Coker, 1992; Moore, 1962). The method uses diagnostic species as indicators of particular relationships (Küchler & Zonneveld, 1988a).

The field sampling is based on a choice of a uniform area for physiognomic description, based on the "homogeneity" of the stand. The resulting association table shows the structure of the association, the diagnostic species, and its sub-units, as well as ecological information, which can be used as a working hypothesis to be checked in additional studies (Kent & Coker, 1992). The method has been employed in the vegetation mapping of both temperate and tropical vegetation (Loth & Prins, 1986; Zonneveld, 1988c; Zonneveld & Surasana, 1988), and can also be used in combination with physiognomic data (van Gils & Wijngaarden, 1984; Küchler & Zonneveld, 1988a).

The choice of a physiognomic or floristic classification approach will depend on the objectives of the study and also on the knowledge of the vegetation composition. Perhaps the best solution is to combine both, especially in areas where the floristic composition of different vegetation types is far from being well known.

2.4.4. Multivariate Analysis

Multivariate analysis methods can deal with complex data attributes, such as most ecological data, where each sampling unit can be characterised by many attributes. The quantification of relations between species and environmental variables can be used to model and/or predict species abundance from observed environmental data, or conversely, to predict values for environmental variables from observed species data (Jongman *et al.*, 1995).

Multivariate classification (discrete) and ordination (continuous) techniques are important tools in the description of the community structure. Classification can be based both on floristic characteristics such as species composition or dominance, or on physiognomic characteristics (Kent & Coker, 1992; Webb *et al.*, 1970). Ordination techniques allow analysis of the variation of vegetation according to composition along continuous environmental gradients, independent of spatial contiguity (Austin, 1985; Greig-Smith, 1983; Kent & Coker, 1992; Whittaker, 1967).

They permit the study of the spatial patterns of vegetation in relation to environmental factors by reducing the multi-species data to a few relatively homogeneous clusters of both species and communities along a few axes, representing environmental gradients (Ter Braak, 1987; Noy-Meir & Whittaker, 1977; Whittaker, 1973).

Both ordination (direct/indirect gradient analysis) and cluster classification can be useful to determine vegetation/ecosystem units, and/or in the exploratory phase of ecological classifications (Jongman *et al.*, 1995). Ordination and classification methods can also provide information on the sharpness of the transition between two different communities (Kent *et al.*, 1997).

Numerical Classification - Cluster Analysis

Numerical classifications or cluster analyses are based directly on measurements of relative similarity of either the distribution of species or the composition of samples. They are considered to be more objective than traditional floristic or physiognomic methods, as the use of standard procedures provides an objective measure of similarity (Greig-Smith, 1983). Numerical classification techniques operate either by grouping stands together on subjective assessment of similarities, or by dividing the whole set of stands into two or more groups on the basis of the presence of one or few dominant or indicator species. Ecological groups and characteristic species groups are primarily arbitrary groupings of species by similarity of distributional relationships. The resultant output is either a non-hierarchical or hierarchical arrangement of samples or species (Gauch, 1982).

Many classification procedures have no statistical element and can be regarded as a way to generate hypotheses. If the data contain a discontinuity they can serve as a basis for a 'natural' classification. Ordination enables visualisation of the continuity or discontinuity of the data, and also gives information on the number of clusters to be recognised. Among the advantages of numerical classification are the speed, the use of less skilled labour, its objectivity, the identification and use of natural discontinuities, and the adoption of optimisation procedures (Goodal, 1978).

Variables most commonly used in the classification are floristic variables (presence/absence) or importance values (abundance, IVI, cover, basal area). In

heterogeneous stands the species presence can be an appropriate variable, with quantitative measures adding little value to the classification (Kershaw & Looney, 1985). Physiognomic characteristics (Webb *et al.*, 1976), or environmental factors associated with the vegetation could also be used as variables (Goodal, 1978). Weighting can be used, especially in unstandardised quantitative data (Webb *et al.*, 1967ab).

Clustering can be done by calculating a matrix of indices of similarities between pairs of stands. Numerical procedure leads to an arrangement of the samples in a hierarchical pattern, which can be expressed as a dendrogram, reflecting both the successive steps and the presumptive relationships among the clusters distinguished. Rules can be established to define a point beyond which distal branches of the dendrogram will be regarded as members of the same class (Goodal, 1978; Greig-Smith, 1983).

Indicator Species Analysis is a divisive polythetic method that uses reciprocal averaging ordination to reflect the most important vegetation gradient in the first axis (Hill *et al.*, 1975). The stands are divided into two groups at the centroid, the mean value of the stand scores. Species whose occurrences are most nearly confined to stands on one or the other side of the division are identified as 'differential species' or 'pseudo-species'. These species are used to refine the initial ordination of stand, dividing the stands into two groups. The procedure is repeated again for each subgroup (van Tongeren, 1995). TWINSpan (for Two-Way Indicator Species ANalysis), a program developed for this approach makes use of "pseudo-species" with differential indicator value at different levels of abundance (Hill, 1979a).

In rainforest stands, classification of just a part of the species composition can be sufficient to draw conclusions about the interrelationships of the stands, with reduction of redundant species (Austin *et al.*, 1972; Webb *et al.*, 1967b). Non-taxonomic or physiognomic criteria can also be used. Webb *et al.* (1976) developed a *pro-forma* based on selected physiognomic-structural features of tropical forest vegetation, designed to facilitate collection of data by non-botanists. It was successfully tested in the classification of species-rich rainforests in Australia. Quantitative (e.g. canopy height), qualitative (e.g. presence/absence of lianas),

ordered multi-state (e.g. leaf-size), or unordered multi-state (e.g. bark type) types of data can be employed in the classification (Webb *et al.*, 1976).

Ordination of Vegetation - Gradient Analysis

Ordination of plant communities aims to generate hypotheses about the relationships between the vegetation composition and environmental factors (Jongman *et al.*, 1995). It can be used as a framework on which values of any environmental factor can be plotted, and the resulting distribution of values examined for evidence of existence of correlation. Ordination methods use non-standardised procedures that reduce the multi-species data to a few relatively homogeneous clusters distributed along a few axes (Ter Braak, 1987). The main value of ordination is selecting from the indefinite number of possible important influencing factors, those that are worthy of further investigation.

Gradient analysis relates the gradients to one another on three levels: environmental factors, species population and community characteristics. It makes it possible to visualise the vegetation as a pattern of populations and communities corresponding to a pattern of environment (Whittaker, 1975). Direct gradient analysis is used to display the distribution of organisms along gradients of important environmental factors (Whittaker, 1973). The species selected along the gradient are given weightings according to their position, with the weightings used with the amount of the species in a stand to obtain a more precise placing of that stand on the gradient.

In the indirect gradient analysis or ordination *sensu strictu*, there is a comparison among vegetation samples. It organises community data, leaving the environmental interpretation to a subsequent, independent step. The result is an arrangement of species and samples in a low-dimensional space such that similar entities are close by and dissimilar entities are far apart (Gauch, 1982).

Principal Component Analysis (PCA)

Traditional ordination techniques include Polar Ordination, Factor Analysis and Principal Component Analysis (PCA). Factor Analysis is concerned with the part of variability in the data that is accounted for by correlation between the variables

(Greig & Smith, 1983). Principal Component Analysis determines the axis or component which accounts for the maximum variance at each stage (Orloci, 1966). It operates on data centred by species, changing the reference axes to a new orthogonal set, concentrating the variability in the successive axes derived. The starting point is a square matrix of similarities between species. The outputs are a series of eigenvalues, which are proportional to the variation accounted for by each axis. These are associated to eigenvectors that give the loadings or the spatial coordinates of each plot or species on the axes (Greig-Smith, 1983).

Limitation of PCA includes a rigid data requirement and inappropriate mathematical properties. The use of orthogonal axes constrains the interpretation of the resultant ordination and the axes cannot always be directly or simply related to ecological parameters (Kershaw & Looney, 1985). It also demands normally distributed data and complete linearity between species relationships (Kent & Coker, 1992; Kershaw & Looney, 1985).

Reciprocal Averaging (RA) and Detrended Correspondence Analysis (DCA)

Reciprocal Averaging or Correspondence Analysis (CA) is an eigen analysis technique where the axes have sequentially decreasing eigenvalues (Hill, 1973). The stand score can be used to give a corrected species score, as the average score for the stand in which a species occurs. The new species score is then re-scaled and is used to recalculate stand scores. Successive cross-calibration converges to a unique set of values, providing a simultaneous one-dimensional ordination of species and stands. The species-score is based on the average of scores for stands in which the species occurs, re-scaled to constant total range, while the stand score is based on the average of scores for species occurring in the stand. The eigenvalue gives the importance value of the axis in the ordination, and can be referred as the percentage of variance accounted for by the axis sites (Kershaw & Looney, 1985).

This one-dimensional ordination is equivalent to the first axis of the PCA, with both samples and species ranked along the matrix diagonal. CA can be applied either to presence/absence or quantitative data. It is considered efficient for heterogeneous data, with the double standardisation giving emphasis on rare species and poorer sites (Kershaw & Looney, 1985). The main disadvantage is that it shows

the so-called 'arch effect' (Gauch et al., 1977; Kent & Coker, 1992). The extent of the arch-distortion can exceed the eigenvalue of a secondary environmental gradient. Another disadvantage is that the equivalent differences in composition are not represented by the same differences in the first axis position (Greig-Smith, 1983).

Detrended Correspondence Analysis (DCA) is an evolution of Correspondence Analysis (Hill & Gauch, 1980). DCA eliminates the arch effect by adjusting loadings on the second axis centring them to a zero mean value within predefined segment of axis, thus removing the non-linear dependence between the axes. The DCA ordination eliminates doubtful groupings, and the clarity of the grouping is essentially maintained (Kershaw & Looney, 1985).

Canonical Correspondence Analysis (CCA)

Canonical Correspondence Analysis is an eigenvector technique that combines aspects of regular ordination with aspects of direct gradient analysis (Ter Braak, 1986). It is considered as an extension of the Correspondence Analysis. CCA identifies an environmental basis for community ordination by detecting the patterns of variation in community composition that can best be explained by the environmental variables. The ordination diagram shows the main pattern of variation in community as accounted for by the environmental variables and, in an approximate way, the distribution of each species or stand along each environmental variable (Ter Braak, 1988).

Classification and Ordination of Tropical Forest Vegetation

Multivariate classification and ordination techniques are currently widely used in vegetation science (Kent & Coker, 1992). Ordination methods have been applied to floristic data in both temperate and tropical forest vegetation (Austin *et al.*, 1972; Greig Smith *et al.*, 1967; Oliveira-Filho & Ratter, 1995; Webb *et al.*, 1967a,b). In more heterogeneous vegetation, qualitative (presence/absence) data can be effectively used (Williams *et al.*, 1973). Austin & Greig-Smith (1968) consider that less than 25% of the flora can give an efficient ordination. Hall & Swaine (1976) considered that the use of all species occurring in the plots has given better results in the reciprocal averaging analysis of tropical forest stands in Ghana.

Oliveira-Filho & Ratter (1995) applied both classification and ordination procedures to analyse the similarities among several forest sites in Central Brazil, adopting the IBGE (1993a) vegetation classification system as an environmental background. They used three different techniques (DCA, TWINSpan and UPGMA, an agglomerative hierarchical classification based on the Sørensen index of similarity) in order to seek for common patterns. Their work supported the utility of adopting a standard classification system to compare different sites. They also found similar results in all three techniques.

Silva-Jr *et al.* (1996) used both ordination (CCA) and classification (TWINSpan, UPGMA) to analyse gallery forest communities in central Brazil. They also applied a PCA ordination to soil parameter data in order to reduce the variation and auto-correlation among the variables. The results confirmed the existence of a gradient of soil fertility, texture and moisture related to the floristic composition of the forest. Rodrigues & Shepherd (1992) used PCA to investigate the relationships between montane forest communities and soils along an altitudinal gradient in SE Brazil. They found that changes in both soils parameters and the community structure were related to differences in altitude and landform.

Bowman *et al.* (1991) applied ordination to 144 forest plots in NW Australia. Although a moisture continuum gradient related to rainfall was identified, they considered the use of indirect gradient analysis as more appropriated, because of the occurrence of patches of wet sites not linked to the regional climate. Floristic patterns showed a relationship with surface soil physical and chemical characteristics. A unidimensional ordination recovered a major environmental gradient (dry fertile > infertile waterlogged soils), with species showing a continuously varying sequence of unimodal curves along the ordination axis.

Despite some limitations (McCune, 1997; Økland, 1996; Westfall, 1997), TWINSpan, DCA and CCA are well established as standard tools for the analysis of vegetation variation and its relationship with environmental variables (Jongman *et al.*, 1995; Palmer, 1993). Their relative robustness as well as the easy access to software that perform the analyses are some of the main reason for the increasingly adoption of these techniques among ecologists (Kent & Coker, 1992; McCune & Mefford, 1997; Økland, 1996). The combined use of TWINSpan classification and

both direct (CCA) and indirect (DCA) ordinations can provide a useful basis for the investigation of vegetation patterns and their relationships with environmental variables.

2.5. Landscape Ecology

Landscape Ecology (LE) studies broader scale relationships between phenomena and processes in the landscape, including communities of plants, animals and men, through the analysis of its structure, functions and changes (Forman & Godron, 1986). It searches for an understanding of the spatial relationships in a heterogeneous land area, composed by a combination of interacting ecosystems, the flow of species, energy and material, and the ecological dynamics of the landscape mosaic (Forman, 1995; Jongman *et al.*, 1995).

LE concepts can be used to stress the interrelationships between the physical, biological and cultural aspects of ecological systems, by mapping and describing landscape patterns (descriptive approach). LE can also focus on the factors which control the locations and actions of organisms in space and time (analytical approach), and on the influence of organisms on landscape patterns (Turner & Gardner, 1991).

2.5.1. Landscape Analysis

Landscape analysis is based on the study of the interactions between the biota, soils and landforms, and the classification of ecosystems on the basis of plant/animal communities (Zonneveld, 1995). Quantitative methods can be used to analyse patterns, to determine the importance of the spatially explicit processes and to develop landscape models applicable to ecological data at multiple spatial-temporal scales (Turner & Gardner, 1991).

LE focuses on three main characteristics of the landscape: *structure*, or the distribution of energy, materials and species (spatial relationships); *functions*, the flow of energy, material and species (interactions among spatial elements); and *change* (alteration in structure and functions over time). The main structural elements for landscape analysis are patches, corridors and the matrix (Forman, 1995). Patches are non-linear surface areas differing in appearance from their surroundings. They

vary widely in size, shape, type, heterogeneity and boundary characteristics, being often embedded in a surrounding area (matrix), with different species structure or composition. Patches can originate from disturbance, environmental heterogeneity or human action (Forman & Godron, 1986).

Corridors are narrow strips of land that differ from the matrix on either side (Forman & Godron, 1986). Corridors can have an effect on dispersal across landscapes, or act as habitats or sources of environmental/biological effects on their surroundings (Forman, 1995). They belong to higher levels of organisation than the patches they connect, allowing interactions of the parts of large-scale communities and ecosystems (Allen & Hoekstra, 1992).

The matrix refers to the more extensive and connected landscape type, playing a dominant role in the functioning of the landscape (Forman & Godron, 1986). It is larger in total area, enclosing other landscape elements, and exerts a dominant influence on the dynamics of the landscape as a whole (Forman, 1995). Most landscapes contain highly diverse proportions and spatial configuration of patches, corridors and matrices. Lines and strip corridors and networks increase with human disturbance regimes, while patches, stream corridors and matrix characteristics are abundant in natural vegetation (Godron & Forman, 1983).

Landscape analysis can also be based on the identification and description of homogeneous parts or units of the landscape, through the adoption of a hierarchy of landscape units. An ecotope/geotope is the smallest holistic land unit with specific ecological conditions, characterised by the homogeneity of at least one land attribute, and with small variations in other attributes (Zonneveld, 1995). Other units include land facies/geofacies and land systems (Tricart & KiewietdeJonge, 1992). An alternative typology includes 'natural', 'semi-natural', 'agricultural' or 'cultural' landscapes, depending on the degree of human influence (Zonneveld, 1995).

The analysis of landscapes as a system attempts to measure the degrees of correlation between its various components (Zonneveld, 1995). The approach studies the vertical (topological) relationships between the elements of the ecological community and their spatial distribution. It also takes into account the flow of energy and materials, and changes in time that indicate a certain evolution of the landscape (Tricart & KiewietdeJonge, 1992).

The CSIRO Land Systems approach uses transects to establish land terrain units and elements and their interrelationships, and the relationships between land patterns (Davidson, 1992). Land systems are chorographic units determined by climate/palaeoclimate, lithology and geomorphic history. Land units are more homogeneous areas that recur repeatedly, with the land facet corresponding to elements of landform. Coincidences in the spatial extent of different environmental components are considered to express correlation between them. The approach has been widely adopted for land surveys in Australia and other tropical areas (Davidson, 1992; Zonneveld, 1995).

A hierarchical approach that integrates the ecosystem and landscape concepts was proposed for use in the ecological classification of land (Klijn & de Haes, 1994). It can be related to the CSIRO and other similar systems of land classification, as well as to ecological or phytogeographic classifications, in a hierarchy from eozones, ecoprovinces, ecoregions, ecodistrict, ecosection, ecoseries, ecotope and eco-element.

2.5.2. Landscape Ecology and Conservation

Concepts based on island biogeography, population dynamics and extinction processes have been applied in the design and management of nature reserves (Kupler, 1995). The management of spatial aspects is considered important to maximise the number of species, or to minimise the rate of extinction (Harris, 1984). Reserves can be considered as discrete patches of suitable habitats within a matrix of less suitable land-uses, so it is important to characterise and understand the ties between the reserve and the surrounding ecosystems, and also the linkages among different reserves (Bridgewater, 1993; Forman, 1995; Kupler, 1995).

Metapopulation theory conceptualises a species in terms of a series of discrete sub-populations, linked at a larger spatial scale by dispersal, with dynamic patterns of local extinction and recolonisation (Fiedler & Jain, 1992). Non-equilibrium dynamics at patch scale could be compensated by a dynamic equilibrium at landscape level, and the gene flow or migration among sub-populations in different habitats or patches could help to avoid extinction of the entire population. Reserve distribution, shape, landscape corridors, and boundary dynamics are factors

that need to be addressed. Reserve functioning is also an important factor that stresses the importance of ecosystem management, with conservation of processes at ecosystem level, including natural disturbance regimes (Bridgewater, 1993; Forman & Godron, 1986; Harris & Silva-Lopez, 1992; Kupler, 1995).

Concepts and methods related to LE can provide both the framework and the tools to investigate how spatial aspects of the environment affect the internal structure of the vegetation community (Turner & Gardner, 1991). Methods of vegetation analysis can be combined with the analysis of the spatial aspects of the environment, providing the basis for an ecological classification of the land (Jongman *et al.*, 1995). Both approaches can also be adopted to analyse how spatial aspects of the landscape affect diversity levels of different types of communities, an important information for conservation purposes. The integration of community, ecosystem and landscape concepts in a common framework can also provide a strong basis for the study of environmental changes.

2.6. Tropical Forests and the Spatial Heterogeneity

Most vegetation surveys made in tropical forest areas have been based on the physiognomic mapping of the vegetation combined with forest inventory field sampling, which have mainly emphasised estimates of the timber volume. Studies with more detailed sampling, covering the floristic composition of the forest, including components of different synusia (trees, liana, epiphytes, ferns), are normally confined to a few restricted areas, which is due mainly to infrastructure problems and the high costs involved. Examples of well studied areas in the Neotropics include Barro Colorado Island in Panama, Estación La Selva in Costa Rica (McDade *et al.*, 1994), Luquillo Forest in Puerto Rico (Lugo & Lowe, 1995), and Maracá Island in Brazilian Amazonia (Milliken & Ratter, 1998). A few Atlantic forest areas like the Poço das Antas Biological Reserve in Rio de Janeiro (JBRJ, 1993), Juréia Ecological Station and Serra do Japi in São Paulo (Mantovani, 1993; Morellato, 1992a) have also been subject to detailed multidisciplinary study.

The results of studies at population, community and ecosystem levels made in the last decades, have contributed to a much better understanding of the structure of tropical forest ecosystem and related processes. However, the limited range of the

areas studied so far constrains the understanding of these processes at wider spatial scales (e.g. landscape and regional levels). Although studies that address the spatial scales involved in the ecological processes have received increasing attention in temperate areas, very few studies so far have addressed this problem in the tropics. The high diversity of species and habitats makes extrapolations even more difficult.

The need for a better understanding of the spatial dimension of ecological phenomena in tropical regions has been emphasised by the increasing awareness of the global scale of environmental problems such as climatic changes and high deforestation rates, with imminent loss of valuable biodiversity, at genetic, species or habitat levels. As an example, the role of tropical forests as sinks for CO₂ and the impacts of deforestation on this process are still far from being well established. The estimates of the spatial variation in the amount of carbon stored in tropical forest ecosystems, an essential input for global climatic models, can vary considerably (Brown, 1996).

2.6.1. Spatial Forest Modelling

The use of environmental models at regional or continental levels highlights the necessity for better methods to model ecological phenomena at different scales. In recent years, several types of forest models have been developed, and there have been already some attempts to link different types of models (Solomon & Shugart, 1993; Waring & Running, 1998). A common approach used to model forest dynamics at regional scales is by connecting forest growth models, developed for use at stand level, to a Geographic Information System (Acevedo *et al.*, 1993; Urban *et al.*, 1991).

Geographic Information Systems (GIS) are computer systems that can be used to store, retrieve and analyse spatial data. GIS are especially suitable for use in environmental and resource planning, as they can handle many layers of information relating to an area, each layer describing a different aspect of its geography, such as geology, soils, land cover, species distribution, and human population characteristics (Burrough, 1986).

GIS have been increasingly used in the field of environmental modelling (Goodchild *et al.*, 1993). They can provide a database structure for storing and

managing ecological data for large regions, enabling aggregation and disaggregation of data between regional, landscape and plot scales. GIS can help to link the understanding of ecological processes and mechanisms from site-specific and organism studies with ecosystem models at several scales (Waring & Running, 1998).

The hierarchical nature of ecosystem structure and processes suggests a stronger basis for moving between different scales (Allen & Hoekstra, 1992). The link of processes and fluxes between scales is a necessary step for the understanding of the dynamics of ecosystems at regional, continental and global levels, in order to build predictive models of the environmental consequences of climatic changes or human actions (Solomon & Shugart, 1993; Waring & Running, 1998). GIS is a valuable tool to operate such inter-scales studies, linking data and models obtained and developed at different spatial scales.

The assessment of patterns of ecosystem structure and function are based on spatially distributed ecological data, recorded at a variety of spatial and temporal scales. GIS can be exploited for analyses that compare the ecological structure between positions in a landscape or between regions (Sample, 1994; Stow, 1993). GIS support the numerical modelling of spatially distributed ecosystem processes, supplying input data variables and modelling parameter data (Acevedo *et al.*, 1993; Goodchild *et al.*, 1993; Haynes-Young *et al.*, 1993). GIS data can also be used to assist the processing and analysis of remote sensing images, especially in estimates of terrestrial ecological variables (Haynes-Young *et al.*, 1993; McCloy, 1995; Sample, 1994; Solomon & Shugart, 1993).

The identification of clear relationships between plant species and communities and key aspects of the environment can be used as a basis for the development of models of the plant-environment dynamics. The analysis of spatial and temporal patterns of the landscape can support the development of a 'conceptual model', based on key environmental factors identified in the analyses, which could be later tested and calibrated against new empirical data. Further refinements could allow predictions, at certain confidence intervals, of which plant species or communities are more likely to occur in specific sites, or which types of physical

environment are characterised by the occurrence of indicator species or vegetation types (Jongman *et al.*, 1995).

The spatial patterns of forest communities and other landscape elements can be analysed by use of both aerial photographs and remote sensing images (Kalliola & Syrjanen, 1991; K uchler & Zonneveld, 1988b; Mertes *et al.*, 1995). The landscape heterogeneity can be measured directly from satellite images, by use of several indices, based on the spectral response from different landscape elements (Hall *et al.*, 1991; Haynes Young *et al.*, 1993; Rey-Benayas & Pope, 1995; Turner & Gardner, 1991). The integrated use of both remote sensing and GIS can help to develop and test hypotheses regarding the effects of scale on ecological relationships and processes (Bridgewater, 1993; Goodchild, 1994; Gregg, 1994).

The availability of remote sensing imagery from different years and seasons allows the analysis of the landscape dynamics. The spatial distribution of the landscape elements in different years can be compared, in order to detect if there were significant changes in the overall structure of the landscape (Turner & Gardner, 1991). Alternative scenarios of landscape evolution, based on the implementation of different conservation and management options, can be evaluated through the development of models of landscape dynamics (Hall *et al.*, 1991). Concepts and criteria from conservation and landscape ecology, forest ecology and forest management could be integrated into a single model, in order to identify priority areas for intervention (Acevedo *et al.*, 1993; Botkin, 1993; Ritters *et al.*, 1997; Sample, 1994; Turner & Gardner, 1991; Vanclay, 1995).

2.6.2. Predictive Vegetation Mapping

Traditional vegetation maps are usually digitised and used in a GIS as a data source, to be combined with other spatial environmental data (Franklin, 1995). The representation of spatial data (polygons, geometry, topology) in a GIS are artefacts of the data modelling process, as real geographic variation is complex and continuous (Goodchild, 1994). This is a factor that is often neglected when digital vegetation maps are used in environmental planning or modelling.

Predictive vegetation mapping attempts to predict the vegetation composition across a landscape from mapped environmental variables related to topography

(elevation, aspect/exposure, slope, curvature, position), climate (annual rainfall, temperature, radiation), soils (type, properties, water chemistry), geology (parent material), hydrology (catchment area, groundwater, drainage, runoff), or satellite spectral data (Busby, 1991; Davis & Goetz, 1990; Franklin, 1995; Kirby, 1995; Mackey, 1993b; Neilson, 1995).

The realised niche concept or species ecological response curve, reflected by species distribution patterns (Austin, 1985), is basic to predictive mapping. It assumes that vegetation distribution can be predicted from the spatial distribution of environmental variables that correlate or control plant distributions. The plant community is essentially a spatial concept dependent on landscape pattern. Therefore, communities and ecotones are geographic entities that could be predictively mapped (Franklin, 1995). The conceptual vegetation model includes relationships between direct gradients (nutrients, moisture, temperature), the environmental determinants (climate, geology, topography), potential/actual vegetation and land cover (Franklin, 1995).

Predictive vegetation models can be viewed as static models, based on the assumption of a 'quasi-equilibrium' between vegetation and climate. They have been developed mainly at biome or continental scales, by correlating plant functional types (e.g. life form) distribution to climate variables (Busby, 1991; Neilson, 1995). Predictions of species or functional type distributions are considered to be more powerful than of biome or plant communities, whose composition can vary over geologic time (Franklin, 1995).

A spatial hierarchy of environmental controls on plant distribution can be devised, with physiologically based climatic variables related to direct gradients exerting control at larger spatial and temporal scales. It is followed by geology, which affects soil chemistry and nutrient availability. Finally, topography, which influences precipitation and temperature, radiation regime and moisture demand, soil development, moisture, and wind exposure (Franklin, 1995).

Digital Terrain Models (DTM) can be used to model direct gradients (solar radiation), to construct indices related to direct gradients (topographic moisture), while topographic attributes (elevation, slope, and aspect) can be used as indirect gradients. Topographic attributes related to vegetation patterns include slope, aspect,

specific catchment area, slope curvature, and litter accumulation and erosion/deposition rates (Davis & Goetz, 1990; Franklin, 1995).

Predictive vegetation modelling can also be related to habitat suitability modelling, as cartographic models where data layers represent environmental or ecological variables. Models for plant communities could be developed in a GIS, based on relationships between communities and mapped environmental variables (Johnston, 1993). Spatial distributions of plant species can be modelled from climatic variables related to direct/resource gradients or physiographical tolerances (Busby, 1991; Mackey, 1993a,b; Scov & Borschsenius, 1997). Dependent variables can be continuous (abundance) or categorical (presence/absence). Independent variables may also be continuous (rainfall, temperature, elevation, multispectral reflectance, slope), grouped into ordinal classes (slope, aspect), or categorical/nominal (soil type, lithology, disturbance type).

2.6.3. Remote Sensing and Vegetation Mapping

Remote sensing refers to a group of techniques for gathering information pertinent to the environment from a distance, without contacting them (Lo, 1986; Reeves *et al.*, 1975). Interpretation is the art of examining images for the purpose of identifying objects and studying their significance (Ester & Simonett, 1975; Zonneveld, 1988b). Interpretation can be used to guide field check and sampling methods, and can be undertaken either manually or using digital or automatic methods. Fieldwork or ground surveys are used to check the preliminary interpretation, based on the different patterns identified in the image (Lee, 1975).

The main features that are analysed in an image are tone (colour, value, chrome), texture (smooth, fine, rough), size and shape (form). Patterns can be related to man-made features, for example crop sites, but changing relationships between organisms and their environment can also produce patterns. Stereoscopic viewing of aerial-photographs helps to identify relief shape and levels, and vegetation height differences (Lo, 1986).

Images of vegetation are usually dominated by energy reflected or emitted from the vegetation canopy, which can be affected by the vegetation phenology in different seasons. Another important factor is the water content of plants and soil.

Criteria for vegetation classification include physiognomy, structure, functional aspects, and Leaf Area Index-LAI (Townshend, 1981).

Remote Sensing Images and Sensors

Aerial-photographs have long been used in vegetation surveys. Types of films used include panchromatic, black-and-white infrared, true colour and colour infrared. Cloud, haze, smoke and dust may affect the quality of the images. Biophysical properties also affect radiation characteristics by the vegetation cover are cellular structure (related to vigour, maturity and water stress), plant life form, pigmentation, and the leaf moisture content (Heller, 1971; Lo, 1986).

Aerial photographs are essential tools in forest inventory, supplying information for exploitation, logistical planning and management. The stereoscopic view can reveals differences in terrain, accessibility, transport possibilities by roads or rivers, drainage and aspects of the vegetation itself. In general, 1:20,000-1:100,000 scales are used for inventories at reconnaissance level, for general land-use classification, and for broad vegetation mapping (Lo, 1986). The main constrain is the high cost of aerial photogrametric surveys.

Radar is an active microwave sensor, emitting its own radiation, the reflection of which is detected and converted into a digital image (Palme *et al.*, 1996). Radar remote sensing enables the observation of differences in vegetation structure, distribution, and orientation (Zonneveld, 1988b). Different vegetation types associated with broad topographic and drainage units can be distinguished mainly on the basis of tone and texture. Leaf size, percentage of ground cover and moisture conditions can affect the radar image tones, while texture is also affected by height variability of vegetation, which can be related to the forest biomass. The technique's main advantage is weather independence, allowing the mapping of continuously cloud-covered areas such as tropical and equatorial humid regions (Furley, 1986; Lo, 1996; Sicco, 1988)

Sidelooking Airborne Radar System (SLAR) images are useful for mapping drainage patterns, through the detection of rivers, lakes, estuaries, swamps, and related features such as gallery forests. Human influences, with detection of tonal differences and abrupt changes in vegetation height, urban areas, roads, agricultural

terraces, and boundaries in large plantation areas can be easily recognised. Physiographic features, such as topographic differences, delineation between flooded wetlands and non-flooded areas, correlation of the relief with species composition and volume may also be visible (Sicco, 1988). A resource survey of Brazil was carried out by use of semi-controlled radar mosaics, at 1:250,000 scale, with the production of final thematic maps (geology, geomorphology, soils, and vegetation) at 1:1,000,000 scale. The image interpretation was complemented with low-level flights and verification at selected ground control points (Furley, 1986).

Space remote sensing provides a large area uniformity of perspective and repetitive coverage of any particular area (Mather, 1987). Other advantages include the possibility of use of both manual and digital analysis, combining the visual elements of shape, texture, pattern and location with the spectral characteristics ('signature') of the image, and also visual presentation to decision-makers.

Landsat satellites provide both MSS and TM images. Each Landsat scene covers an earth surface of nearly 34.2 km² (185x185 km), with a temporal resolution is of 16 days. The Multispectral Scanner System (MSS) operates in four spectral bands (0.3-1.1µm), with a spatial resolution of 80 m. The Thematic Mapper (TM) sensor works with seven spectral bands, with a spatial resolution of 30 m. The bands most commonly used in vegetation mapping are bands 3 and 4 (TM). The band 3 (0.62-0.69 µm) is closely related to chlorophyll absorption, and can provide information on cover percentage and the degrees of maturity of crop canopies. Band 4 (0.76-0.90 µm) values are closely related to LAI and plant biomass (Mather, 1987).

The SPOT satellite sensor covers a scene of 60x60 km. In the panchromatic mode (0.51-0.73 µm), it has a spatial resolution of 10 m. The XS mode operates in three spectral bands, with 20 m of spatial resolution. It uses two identical sensor-systems, each of which can be aimed off nadir over 0-27° from the vertical, allowing the combination of two images from different angles into a stereo model. SPOT has a temporal resolution varying from 3-26 days (Lo, 1986).

Thermal sensors measure radiation emitted the region of 10-12.5 µm. They can be used to measure the surface temperature of vegetation, soil or water bodies and other surfaces. From knowledge of surface temperatures, inferences can be made of the status of soil moisture. Thermal imagery has also been used to derive

ecophysiological information (forest evapotranspiration, seasonal changes), in forest fire monitoring, and it also can be used for crop yield prediction (Lo, 1986; Waring & Running, 1998).

Satellite imagery is considered the main tool in the detection and monitoring of tropical deforestation (Eden, 1986; Gringer, 1984; Skole & Tucker, 1993). Both Landsat TM and SPOT imagery have already a wide use in the land-use planning and vegetation mapping in Brazil (Câmara, 1996; Frohn *et al.*, 1996). The main constraints for their use in moist forest areas and at more detailed scales are the occurrence of clouds, the relative coarse spatial resolution, and the difficulty to relate image spectral signatures to different plant community types (Lewis, 1998).

Digital Image Processing and Classification

Image processing is the activity of transforming 2-D data (numbers) into images, or into geo-data bases or maps. Image processing procedures include radiometer correction, gain and offset correction, correction of atmospheric effects, geometric correction, colour coding, and spectral features extraction.

Remote sensing images in digital format can be used to generate images for visual analysis, or can be used for the delineation of features by computer-assisted recognition of spectral patterns. This procedure permits rapid analysis of spectral patterns, quantitative comparison of spectral responses in data acquired at different times and rapid analysis of spectral differences between targets that are too small to be detected by human eye. Analysis can be done also by overlaying digital thematic data (Mulder, 1988).

Supervised classification requires the user to specify in advance the class definitions, and to provide a training set for the determination of the decisions functions or decisions rules. Steps in the classification sequence include the extraction of the features (spectral, spatial), the definition of a training set or test area maps for training, and the definition of context masks and rules for context reclassification (Mather, 1987; Zonneveld, 1988b).

2.7. Vegetation Mapping and Monitoring in the Atlantic Forest

The potential of remote sensing, computer mapping and GIS technologies for resource management and environmental research has been met by an increasing use of these tools in both developed and developing countries. Remote sensing is particularly valuable in remote tropical areas, where the acquisition of environmental data is constrained by complex terrain and lack of infrastructure, trained personnel and adequate funding. However, the development of local expertise can be constrained by the high cost and the very fast development of related technologies.

Several vegetation surveys, most of them at reconnaissance level, provide data on forest cover in the Atlantic forest region in Brazil. The first surveys, made by use of aerial-photographs, provided data at detailed scales, but with limited spatial coverage. Recent surveys gave a broad picture of the current situation of the Atlantic forest biome (SOS Mata Atlântica, 1990), and of the remaining forest fragments in Rio de Janeiro (IEF, 1994), based on visual interpretation of Landsat TM images

Digital image processing techniques are being increasingly adopted in Brazil. Studies made in the Amazon region show that it is also possible to characterise both natural and secondary forest vegetation through digital processing of Landsat TM images (Corves & Place, 1994; Dargie & Furley, 1993, Foody *et al.*, 1996; Shimakburo *et al.*, 1998). Good correlation between the spectral signature and the tropical vegetation of more specialised habitats such as mangrove, alluvial and seasonal tropical forest areas have also been found (Mertes *et al.*, 1995; Garcia & Alvarez, 1994; Rey-Benayas & Pope, 1995). Such approaches could be used also to classify different vegetation types in the Atlantic forest region, including secondary forest at different successional stages. Ancillary spatial environmental data stored in a GIS could be used to improve the image classification

There have been great advances recently in the implementation of GIS technologies in Brazil, due to the decreasing costs and increasing performance of computer software and hardware. A low-cost system which integrates both digital image processing and GIS functions was locally developed and supported the establishment of RS/GIS laboratories in universities and government agencies (Câmara, 1996). Several initiatives for use of remote sensing and GIS in environmental planning and monitoring in the Atlantic forest region are currently

under development (Japiassu *et al.*, 1992; Lino & Cencig, 1992; SOS Mata Atlântica, 1990).

The development of new sensors with better spatial and spectral resolution points for a greater use of remote sensing in ecological studies. The choice of sensor will depend on the objectives of the study, especially the spatial and temporal scales involved. Local environmental conditions such as vegetation physiognomy, relief, occurrence of clouds, as well as the land use patterns are also important. At the moment, the main choices for the investigation of the spatial patterns of the Atlantic forest are the Landsat TM and SPOT images. Spaceborne radar systems could be used in areas with constant cloud cover, such as southern Bahia. Their use in combination with other spatial environmental data could overcome some of the limitations in terms of spatial and spectral resolution. GIS provide a valuable tool to store several types of remote sensing and spatial environmental data, which could be used for different types of spatial analysis, including vegetation monitoring and spatial environmental modelling.

Summary

No general nor even widely accepted methodological package has been specifically developed for vegetation studies in tropical humid forest areas. A careful assessment of which techniques are more appropriate has to be made according to the objective of the research. Fieldwork might be based on a preliminary stratification, dependent on the interpretation of remote sensing images, with one or several samples established within each stratum. Either quadrat or plotless sampling could be used, according to the time available and the local conditions.

The high diversity of most tropical forests is an obstacle to any vegetation study. The correct identification of all tree species in the field is an almost impossible task for areas over a few hectares. Vouchers from all species should be collected for identification in the herbarium, a difficult and time consuming task in tropical forests. The knowledge of local tree spotters, although often considered inaccurate, can provide a rapid identification of species in the field, at least to family or generic level.

A possible approach is to find a compromise between the positive features of both classification and ordination methods. Both techniques can be applied to the same data set, and can be used together in comparisons among a considerable number of samples. Ordination can help to identify possible correlations between stands or species with environmental variables. It can also help the numerical classification, by revealing the occurrence of clusters of stands along the main environmental axes. The combined use of both techniques can provide a useful basis for the investigation of the vegetation patterns of the Atlantic forest and their relationships with environmental variables.

Forest management and conservation planning deals with land areas of considerable size, from a few to thousands of hectares. It is therefore necessary to understand the spatial patterns of the ecological phenomena and interrelationships. Concepts and methods from vegetation science, conservation biology, soil and forest science can be applied to the study of tropical forests and in the evaluation of land-use alternatives. Landscape ecological concepts and methods can serve as a common framework for the analysis of the spatial aspects of forest-environment relationships.

Tools that deal explicitly with spatial information such as remote sensing and GIS can provide powerful means to handle and combine spatial data in the ecological analysis and evaluation of forest resources. They are also important tools for predictive vegetation modelling, and can be used to provide spatial input data, analytical capabilities, and presentation of the modelling results.

The integration of ecological information obtained from large-scale surveys with data obtained at local (site) scale is a difficult task. There is a clear need for a working framework for the study of the spatial aspects related to the tropical forest heterogeneity, where the necessary scientific knowledge and the steps needed to obtain it are clearly organised and linked. This study aims to provide a basis for the development of such a framework, which is reflected in its methodology (see Chapter 4). This framework could be adopted for ecological and biogeographical analyses and for forest management and conservation purposes in the Atlantic forest region of SE Brazil, as well as for other tropical forest regions.

CHAPTER 3. The Brazilian Atlantic Coastal Forest and the Study Site

3.1. Introduction

This chapter sets on to examine the present situation of the Atlantic forest biome. A brief review will be made of the current state of knowledge about its biogeography, the structure and dynamics of the forest ecosystem, and the management and conservation of the forest, including also related tropical forest issues. The main purpose is to show how the forests of the Rio de Janeiro state, and most particularly this study, relate to the context of the Atlantic forest biome as a whole.

Despite being located near most of the larger cities of Brazil, including its former capital, Rio de Janeiro, where most of the scientific institutions of the country are located, the Atlantic forest, locally known as Mata Atlântica, has received little attention during most of this century (Dean, 1995; Por, 1992). Most of the research efforts were concentrated on the *cerrados* (savanna) in central Brazil and the on Amazon forest. One of the reasons was priority status, due to the almost total lack of previous studies in the latter regions, and the increasing impacts caused by the official land occupation and migration policies. The Atlantic forest was thought to be well studied, at least at the taxonomic level.

However, in the last 10-15 years there has been a renaissance in interest in studying the region, with an increasing concern for the forest and its animal life by the Brazilian society. Although the international public opinion has been much more concerned with the Amazon forest, most Brazilians realised that the Atlantic forest, close to or part of the area where most of the Brazilian population lives, was almost totally lost, with very few remaining areas still covered by extensive forests. Several NGOs were formed, with an increasing pressure on the governments to adopt policies to halt the deforestation process and to protect the remaining forest areas (Dean, 1995).

The emergence of a stronger Brazilian scientific community, fuelled by the establishment of post-graduate courses in areas such as Ecology, Botany, Zoology, Geography and Forestry, in universities located in the densely populated Atlantic

forest region, was another important reason. The proximity and precarious situation of the remaining forest areas has led to the establishment of many research projects in the region (Martins, 1990; Por, 1992). The results of these researches so far have allowed a much clearer picture of the Mata Atlântica ecosystem as a whole. In relation to biodiversity, in some areas it was found that plant diversity was equal or even higher than many Amazonian areas (Peixoto & Gentry, 1990). Plant and animal species that had not been collected for decades, some even considered to be extinct, were recently 'rediscovered', and many species new to science have continuously been described (Lima & Guedes-Bruni, 1994).

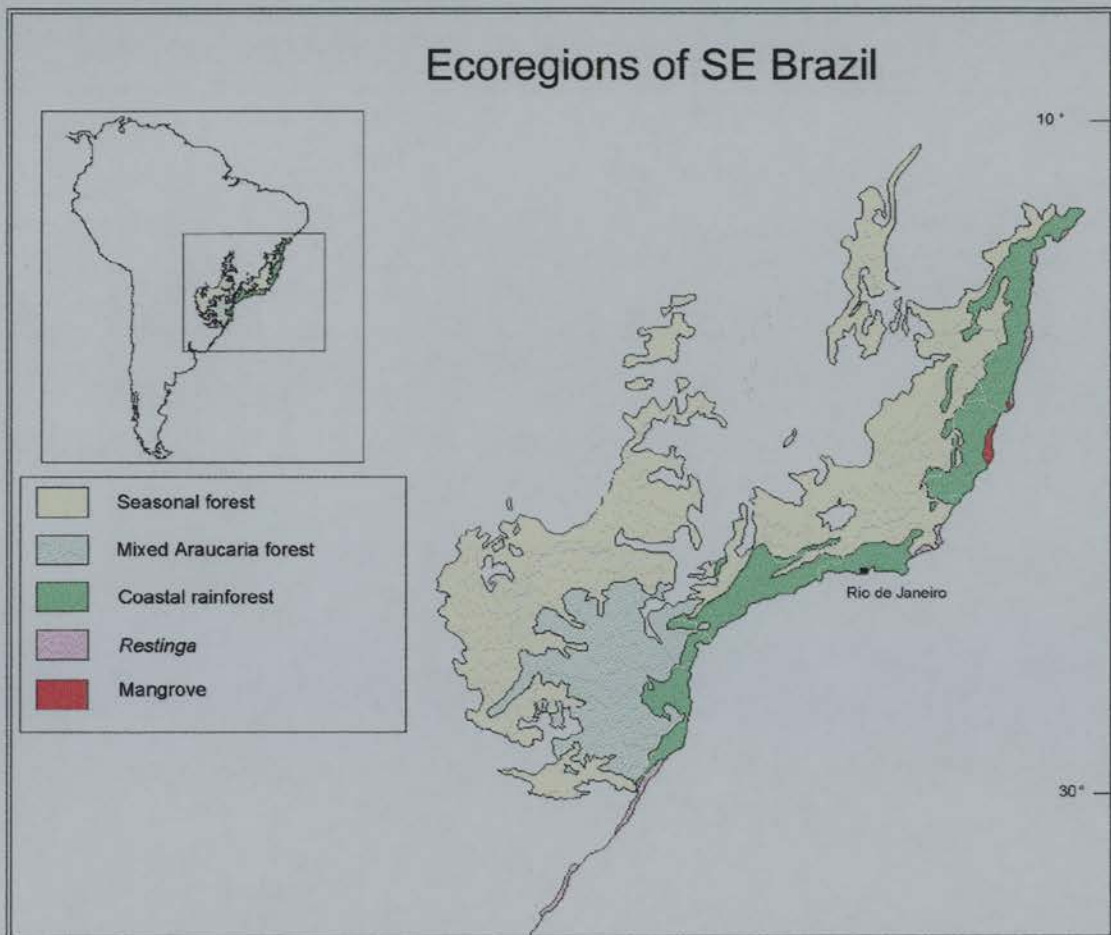
New approaches and re-evaluations of conservation priorities at the international level accompanied all these local developments. The Atlantic forest is now considered as an area of highest priority in terms of both scientific research and establishment of conservation policies (Olson & Dinerstein, 1998). The combination of an integrated effort of intensive studies of its biota with the enforcement of conservation measures could contribute to a more sustainable use of the natural resources of the region, conserving most, if not all, of its highly endemic biota.

3.2. Biogeography

The Atlantic forest covers most of the Brazilian Eastern coastal area (see Fig. 3.1). It is included in the Atlantic-Paranaense biogeographical province, together with the seasonal semideciduous and deciduous forests of the Paraná River Basin and the mixed *Araucaria* forests of the southern Brazilian uplands (Cabrera & Villejak, 1973; Rizzini, 1979). Although some authors include the *Araucaria* and semideciduous forests in a single Atlantic forest domain, based on both floristic and faunal links and similarities (Rizzini, 1963; Por, 1992), others consider only the coastal rainforests as the Atlantic forest *sensu-stricto* (Mantovani, 1993), or as a distinct *phytocoorium* (Prance, 1989). Although the present work concentrates on the coastal rainforest zone, a wider definition of the Atlantic forest was adopted, with boundaries broadly corresponding to the Atlantic morphoclimatic domain (Ab'Sáber, 1973).

The northern limit of the Atlantic forest is located near Cape São Roque at 5° lat. S, while the southern limit is situated along the river Taquari, at 30° lat. S (IBGE,

1993; Por, 1992; Rizzini *et al.*, 1991). The western boundaries are much more difficult to define, due the occurrence of a gradual transition between the formations, combined with the high degree of deforestation and forest fragmentation (see Fig. 3.2). The rainforest has boundaries with different vegetation types, including the dry *caatinga* (steppe-savanna or thorn forest), the cerrado (savanna), the mixed *Araucaria* forests, and the seasonal semideciduous and deciduous forests (IBGE, 1993; Veloso *et al.*, 1991).



Source: IBGE (1993a)

Figure 3.1 Ecoregions of the Atlantic forest domain in SE Brazil.

The original Atlantic forest area covered nearly one million km², but currently only 5-8 % of that area remains forested (Leitão-Filho, 1993; Lino &

Cencig, 1992). The majority of the remaining forests are located in situations with difficult access and steep slopes, in the mountains of the southern part of the region. Most of the lowland areas were converted to agriculture and pastures, with only a few areas of primary or old-secondary forests remaining (Brown & Brown, 1992; Por, 1992). The situation is even more serious in NE Brazil, where only a few small fragments remain (Lino & Cencig, 1992; Mori, 1989).

The Atlantic forest contains more than 100 plant species with endangered status (IUCN, 1986). At least one important tree species, *Caesalpinia echinata*, the Brazilwood, is considered highly endangered, with the remaining natural populations restricted to very few areas (Mori, 1989). Many of the Brazilian animal species considered endangered are endemic or occur preferentially in the Atlantic forest (Bibby *et al.*, 1992; Por, 1992; WCMC, 1992). This situation led recently to the creation of an UNESCO Biosphere Reserve, covering most of the remnant forest areas of the region (IEF, 1994; Lino & Cencig, 1992).

It is difficult to obtain an overall picture of the geographical distribution of the plant and animal species of the Atlantic forest based on the existing data. The information on plant species distribution is based mainly on herbarium data, which have been collected since the early 19th century (Mori *et al.*, 1981). However, the distribution and intensity of such collections are highly skewed. Recent extensive collecting programmes directed to priority regions have improved the situation, but there are still many neglected areas to be covered in all the region, including parts of the Rio de Janeiro state (Mori, 1989; JBRJ, 1993).

The floristic composition of the Atlantic forests is very similar to the Amazonian forests at the family level, although with differences in terms of dominance (Hueck, 1972; Mori *et al.*, 1983; Schnell, 1987). Characteristic families in terms of both dominance and species richness include Leguminosae, Myrtaceae, Meliaceae, Bignoniaceae, Lauraceae, Anacardiaceae, Melastomataceae, Euphorbiaceae, Moraceae, Boraginaceae, Vochysiaceae, Apocynaceae, Lecythidaceae and Palmae. Myrtaceae is often the most important family of the Atlantic forest, in contrast to most Neotropical forests, where the Leguminosae are the dominant family, while in the southern subtropical areas Lauraceae become increasingly important (Hueck, 1972; Mori, 1989; Por, 1992; Schnell, 1987).

Compared to the Amazonian forests, the Atlantic forests are normally richer in epiphytes, especially Orchidaceae, Bromeliaceae, Araceae and Cactaceae. On the other hand, they normally have fewer lianas and palm species. Arborescent and epiphytic ferns are widespread. These patterns might be related to montane and moist environments, as well as to biogeographical events (Gentry, 1982; Rizzini *et al.*, 1991; Por, 1992).

At species level the differences are much more pronounced. The available data show the occurrence of many endemic tree species, some of them with a very limited geographical range. Estimates of the level of endemism vary from 53 % for tree species (Mori *et al.*, 1981) to 73 %, if all plant species are considered (Gentry, 1992). Common tree genera include *Cariniana*, *Lecythis*, *Cedrela*, *Cabralea*, *Dalbergia*, *Enterolobium*, *Melanoxylon*, *Apuleia*, *Piptadenia*, *Hymenaea*, *Parkia*, *Centrolobium*, *Machaerium*, *Myroxylon*, *Myrocarpus*, *Senna*, *Schizolobium*, *Ocotea*, *Nectandra*, *Cryptocarya*, *Psidium*, *Eugenia*, *Myrceugenia*, *Vochysia*, *Aspidospema*, *Tabebuia*, *Jacaranda*, *Tecoma*, *Paratecoma*, *Miconia*, *Tibouchina*, *Tapirira*, *Astronium*, *Schinus*, *Cordia*, *Sloanea*, *Calophyllum*, *Symphonia*, *Clusia*, *Alchornea*, *Croton*, *Ficus*, *Didymopanax (Schefflera)*, *Roupala*, *Weinmannia*, *Talauma*, *Prunus* and *Drimys*. Other tree taxa include palms such as *Euterpe edulis* and *Arecastrum romanzoffianum*, the conifers *Araucaria angustifolia*, *Podocarpus sellowii* and *P. lambertii*, and bambusoids like *Chusquea* and *Glaziophyton*. Arborescent ferns like *Cyathea*, *Dicksonia*, *Alsophila* and others, are also common (Hueck, 1972; Lima & Guedes-Bruni, 1997; Mori *et al.*, 1983; Rizzini *et al.*, 1991; Por, 1992; Schnell, 1987).

The greater availability of data produced by recent floristic studies made it possible to obtain a much more complete picture of the Atlantic forest, and its phytogeographic relationships with the Brazilian southern, central and Amazonian forests (Por, 1992; Prado & Gibbs, 1993; Schnell, 1987; Spichiger, 1992). Oliveira-Filho & Ratter (1995), in an extensive revision of data on central Brazilian forests, suggest the existence of close floristic relationships between the coastal rainforests with those of high altitude plateaus of central Brazil. They also suggest the existence of a greater similarity between the hinterland semideciduous forests and the southeastern coastal rainforests, than between these and the NE rainforests. However,

their research revealed considerable geographical gaps in the spatial distribution of the data. Examination of new data could shed more light on the floristic patterns of the Atlantic forests. It could also perhaps indicate with greater certainty the location of centres of endemism, probably related to Pleistocene forest refuges (Ab'Sáber, 1992a,b; Prance, 1979; WWF & IUCN, 1996; Whitmore & Prance, 1987).

3.3. Forest Ecology

3.3.1. Forest Structure and Composition

Current knowledge of the structure of the different plant communities in the Atlantic forest domain is still limited (Por, 1992). The first studies on the tree community structure were made in Teresópolis-RJ (Davis, 1945; Veloso, 1945) and Ilhéus-BA (Veloso, 1946a,b,c). An extensive study of the southern coastal rainforests was carried out in the 1950s, (Veloso & Klein, 1957, 1963, 1968a,b). Most recent quantitative vegetation research have been concentrated in the semideciduous forests of São Paulo, although a few rainforest areas of S. Paulo and other states, including Rio de Janeiro, have also been covered (Guedes, 1988; Lima & Guedes-Bruni, 1997; Peixoto & Gentry, 1992; Rodrigues *et al.*, 1989; Silva & Leitão-Filho, 1982). The results available so far show that the plant diversity of the Atlantic rainforests is comparable with other species-rich tropical forests of the world, and some areas are particularly rich in plant diversity (Por, 1992; WWF & IUCN, 1997). Recently an area was found in southern Bahia with a very high richness of tree species (>450 sp/ha ≥ 5 cm dbh, or > 270 sp/ha ≥ 10 cm dbh), which makes it one of the richest forests in the world (Thomas & Carvalho, 1993). Several other areas also show a high diversity of plant species (Lima & Guedes-Bruni, 1997; Peixoto & Gentry, 1992; WWF & IUCN, 1997). However, other Atlantic formations such as the seasonal forests, *Araucaria* forests and the *restingas* show a smaller diversity of tree species (Araujo *et al.*, 1998; Giuliatti, 1992; Silva *et al.*, 1997; Oliveira-Filho *et al.*, 1994a).

3.3.2. The Forest and the Physical Environment

The wide latitudinal range of the Atlantic forest, combined with the altitudinal gradient (0-2700 m), and great variation of geology, relief and soil

characteristics, are probably the main causes for the great variation in both its physiognomy and floristic composition (Mori, 1989; Por, 1992; Schnell, 1987; Veloso *et al.*, 1991). Studies made in SE Brazil relate the current forest structure to controlling environmental factors, and show the importance of the local physical environment in the plant community structure, nutrient cycling and phenologic processes (Morellato, 1992b,c; Oliveira-Filho *et al.*, 1994a,c,d,f; Rodrigues & Shepherd, 1992).

Several authors consider altitude, the total annual rainfall and the length of the dry season as the main environmental determinants of the physiognomy of tropical forest communities (Beard, 1955; Veloso *et al.*, 1991). As altitude represents a complex of environmental factors such as temperature, moisture, light and soil types (Austin & Smith, 1989), the resulting interaction between them makes it difficult to identify which factors are the main determinants of each specific situation. Changes in forest composition between the different altitudinal levels are often gradual due to differences in the environmental tolerance amongst the component species (Rodrigues & Shepherd, 1992; Whittaker, 1967).

Most classifications of tropical forest vegetation separate different formations based on altitude (Lamprecht, 1990). The altitudinal levels vary according to each system, and also with the latitude (Frahan & Goldstein, 1991; Küchler & Zonneveld, 1988b). According to the Brazilian vegetation map (IBGE, 1993), the Atlantic dense and mixed *Araucaria* rainforest, and the seasonal semideciduous forest have been classified into four altitudinal levels: lowland, submontane (lower montane), montane and high-montane forests (see Fig. 3.2). A fifth forest type (alluvial forest) is related to terrain conditions, independent of altitude (Veloso *et al.*, 1991). For areas between 16°-24° S, the IBGE classification proposes an altitudinal range from 500-1500 m for the montane formation, and above 1500 m for the high montane formation. Below 24° S, these values change to 400 and 1000 m respectively.

These altitudinal values should only be used only as a general guideline, to be checked and adapted to local conditions (Veloso *et al.*, 1991). A lower limit of 750 m for the montane formation was proposed, based on studies carried out on semideciduous forests in SP (Oliveira Filho & Ratter, 1995; Salis *et al.*, 1995). Whether the same rule could be applied to the coastal moist forest zone is still

uncertain. Some botanists suggest 800 m for the RJ State, based on the distribution of indicator tree species (H.C. de Lima, pers. comm.). There is also uncertainty on the altitudinal boundaries between the montane and high-montane (Falkenberg & Voltolini, 1993; Fontes, 1997).

Both the total annual rainfall and the length of the dry season strongly affect tropical forest structure and composition. The distinctions between categories such as humid, wet, moist forests, rainforests, seasonal evergreen, dry, deciduous or semideciduous forests differ considerably between different classification systems and authors (Beard, 1955; Küchler & Zonneveld, 1988b; Holdridge, 1967; Whittaker, 1978). The IBGE classification system adopts the ombrothermic relationship $P \geq 2T$ (Bagnouls & Gaussen, 1957), which takes into account the interaction between temperature and rainfall (monthly averages), to estimate the number of dry months (Veloso *et al.*, 1991). The system then distinguishes ombrophilous forests (rainforests, with less than three dry months) and seasonal forests (deciduous/semideciduous, with more than three dry months).

Differences in forest structure between river edge areas and those on well-drained soils, without influence of floods or waterlogging, may also occur. Changes in forest structure between riverine and upland forests, related to soil moisture, have been reported for the seasonal semideciduous (mesophilous) forests, where these differences are more likely to be accentuated, due to the occurrence of a strong dry season region (Oliveira Filho *et al.*, 1994a,c,d). Whether this also occurs in the moist coastal forests, with practically no dry season, is less well known.

Apart from forests that occur on seasonally or permanently waterlogged Quaternary coastal lowlands (Scarano *et al.*, 1997; Veloso & Klein, 1961), most coastal forests have been commonly classified as 'slope' forests. However, the existence of at least three different forest zones, according to their position along the slope: bottom valley, mid- and top-slope forests (Mantovani *et al.*, 1990) has been suggested. Bottom valley forests are characterised by a high density of ferns and hygrophilous herbaceous plants such as Marantaceae, Musaceae, Begoniaceae and Araceae. Mid-slope forests have a more developed tree canopy, with higher biomass and occurrence of emergent trees of up to 35-40 m height. Top-slope forests occur on shallow soils, with considerably lower average height and biomass. In montane

areas, due to both high rainfall and high atmospheric humidity throughout the year, there is apparently a high amount of moisture available to most plants even at the top of slopes. Soil characteristics could play an important role in such conditions (Mantovani *et al.*, 1990).

Temperature can have a stronger influence in tropical mountain areas, especially near the Tropic, where lower temperatures and even frost can occur regularly in the winter (Frahan & Goldstein, 1991). In many of those areas, another important factor is the availability of atmospheric humidity, which can affect both the forest evapotranspiration and the nutrient inputs into the forest ecosystem (Bruijnzeel & Proctor, 1993; Nadkarni & Matelson, 1992a,b; Rodrigues & Shepherd, 1992; Stadtmuller, 1987; Weaver, 1995).

The importance of the forests in the local hydrologic cycle is well known. The role of tropical forests in the protection of soils against erosion has long been recognised, especially on wet and steep areas (Hamilton & King, 1983; Lal, 1983, 1987). Few studies have quantified and analysed the specific role of the different components of the forest ecosystem in the process, as well as possible variations due to differences in lithology, soils and landforms (Lugo & Scatena, 1995). Forest components influence hydrological processes through rainfall interception by the forest canopy, moisture storage by the soil litter and decomposed organic matter, water absorption by tree roots and consequent transpiration (Waring & Schlesinger, 1985). They also have an important mechanical role in the maintenance of soil pores and soil structure (Carpenter, 1981; Lal, 1983).

Soil nutrient and moisture content can strongly influence the forest structure (Johnston, 1992; Poorter *et al.*, 1994). Soil moisture is controlled mainly by climate, soil physical properties and relief (Emmerich, 1990). Along a catenary sequence, areas affected by waterlogging, such as those in riverine forests and on depressions, generally show a smaller diversity of tree species than those on higher ground, where the influence of the seasonal variation of the water-table level is less pronounced (Oliveira-Filho *et al.*, 1994c,e). Although a few tree species show great plasticity, occurring in both wet and more dry terrain, most species are less tolerant to extreme moisture conditions (Ashton, 1992b; Scarano *et al.*, 1998).

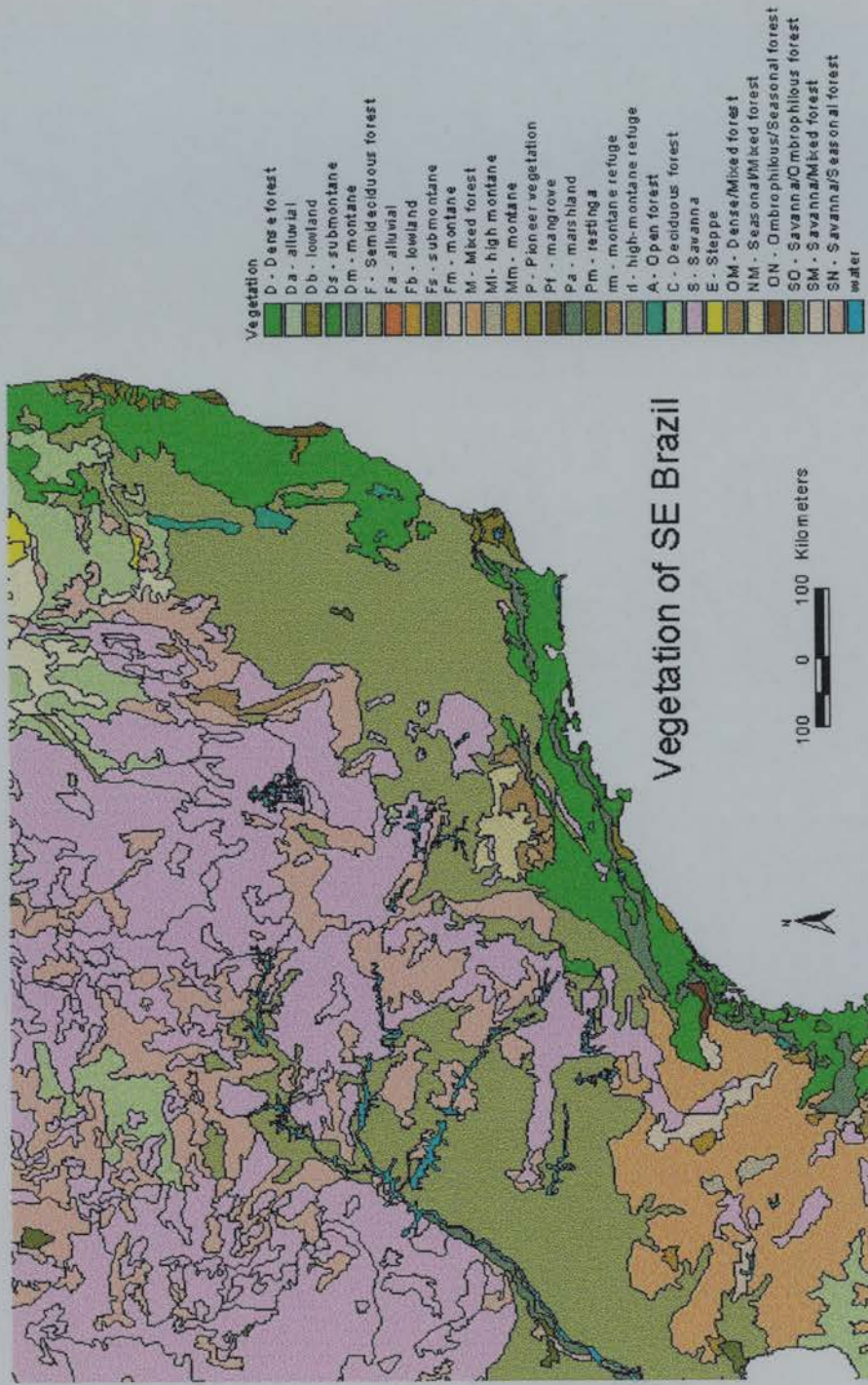


Figure 3.2 Vegetation map of SE Brazil, including the original boundaries of the main forest types (biomes or ecoregions, capital letters), and the few remaining forest areas at formation level (IBGE, 1993a)

Most tropical soils have a low level of nutrients available to plants (Grubb, 1995; Medina & Cuevas, 1994). Despite the importance of nutrient recycling by the forest vegetation (Jordan, 1985), soil fertility is often controlled by the characteristics of the parent material (Emmerich, 1990; Jenny, 1980; Lal, 1983). Most soils in tropical South America have originated from highly weathered old crystalline rocks, which generally result in medium to low levels of nutrients and low organic matter content (Brady, 1990; Sanchez, 1976). However, some areas have more fertile soils, such as on young soils or those derived from basalt or calcareous rocks (Grubb, 1995). The differences in nutrient availability can affect the species composition of the forest significantly, as well as its biomass (Ashton, 1989, 1992; Ratter & Dargie, 1992).

3.3.3. Forest Dynamics and Ecosystem Processes

Studies on the dynamics of the Atlantic forest ecosystem relate the production of organic matter to the local environment and also to the successional stage of the forest (Quintela & Louzada, 1993). Most studies have concentrated on nutrient fluxes throughout the forest litter (Morellato, 1992a,b; Oliveira & Lacerda, 1993; Pagano, 1989; Sampaio *et al.*, 1993; Varjabedian & Pagano, 1988). Some studies are also beginning to show the importance of atmospheric nutrient inputs into the forest ecosystem (Clark *et al.*, 1998a). In the humid mountain areas there is often a great abundance of epiphytes, which could have an important role in the process (Clark *et al.*, 1998b; Fontoura *et al.*, 1993; Nadkarni & Matelson, 1992a). However, the role of the epiphytic vegetation on the capture, conservation and recycling of nutrients, is still poorly understood (Stadtmuller, 1987). Some epiphytic plants, especially Bromeliaceae, constitute an important habitat for several animal species (Por, 1992; Terborgh, 1992), and could also have an important role in the regeneration of tree species on poorly drained soils (Scarano *et al.*, 1997, 1998).

It is important to analyse the forest ecosystem and its processes as a whole for a better understanding of the interrelationships between the vegetation and the physical environment (Jordan, 1985; Likens & Bormann, 1995; Medina, 1995; Waring & Schlesinger, 1985). There have been very few studies made at the ecosystem level in the Atlantic forest (Oliveira & Lacerda, 1993; Sampaio *et al.*,

1993). Data from different but environmentally similar areas could be used to develop a general model of the dynamics of the Atlantic forest ecosystem. Such a model should be calibrated with new data from carefully designed experiments at watershed level in order to be applied into more specific situations. Forest ecosystem models could help to analyse and predict the impacts resulting from climatic changes and also from human intervention in the ecosystem processes (Likens & Bormann, 1995; Waring & Running, 1998).

3.3.4. Disturbance, Forest Structure and Diversity

There is no single or general theory that satisfactorily explains the causes of the greater diversity of the tropical ecosystems in relation to temperate ones, or even the so called latitudinal diversity gradient (Blackburn & Gaston, 1997; Burrows, 1990; Givrish, 1998; Kikkawa, 1990; Runkle, 1989; Terborgh, 1992a). However, there are several theories that could explain, at least in part, why some areas are richer in species than others. The greater diversity of bird species in tropical forests might be explained by the occurrence of a more complex structural habitat, additional guilds, greater plant diversity, availability of larger insects, and close packing of many guilds (Terborgh, 1992a).

Plant diversity based solely on resource competition is more difficult to explain, since all plants basically compete for the same factors: water, light and nutrients (Terborgh, 1992a; Tilman, 1994). In some areas species richness could be related to soil fertility and water availability, with sites of medium fertility and a balanced water budget having the highest diversity. This could be explained by competition for both light and nutrients and consequent specialisation for different soil conditions, *e.g.* in areas with very poor or rich soils, few well-adapted, more competitive species would dominate the forest community (Ashton, 1989). There is also a fairly consistent correlation between species richness in the Neotropics and rainfall patterns, including seasonality (Ashton, 1992a; Gentry, 1992; Givrish, 1998).

The 'intermediate disturbance' hypothesis considers that most tropical forests are maintained in a condition of perpetual disequilibrium, preventing the occurrence of one or few dominant species (Connell, 1978; Givrish, 1998; Terborgh, 1992a). The time factor relates to both seasonal and annual variability, which affect seed

germination responses from different tree species. Species normally show different regeneration strategies (Denslow, 1980,1987; Grubb, 1977b; Hubbel & Foster, 1983). Seed germination physiology and the response of different tree species to disturbance and light availability have an important role on the succession process of tropical forests, as shown by several studies on the gap-phase dynamics (Attiwill, 1994; Denslow, 1987; Hartshorn, 1989; Lieberman *et al.*, 1989,1995; Whitmore, 1989). Past extreme disturbance events, such as fire, hurricanes, floods, pests, droughts, etc., could have a strong influence on the current overall structure of forest communities (Goldammer, 1992; Pickett & White, 1985).

The equilibrium hypothesis considers that species avoid competition through distance-dependent strategies, with more or less regular population fluctuations within a constant long-term population size. This strategy could also help avoid seed predation (Terborgh, 1992a). The spatial heterogeneity in tropical forests could be explained by the variation of recruitment patterns between large and small gaps, between the centre and edges of gaps, between gaps and shaded locations, and between sites near and further from an adult of the same species (Hartshorn, 1989). On the other hand, the vertical structure of the forest could result in adaptations to different levels of light availability, which could also contribute to diversity, especially in the middle layer, which accounts for most of the higher tree diversity of tropical forests (Terborgh, 1992a).

Forest fragmentation is another important factor (Laurance & Bierregaard, 1997; Terborgh, 1992b). Aspects linked to the shape, size, connectivity and edge characteristics of forest fragments could affect forest structure and dynamics. According to the theories of island biogeography and dynamic equilibrium, forest fragments with different sizes should show different diversity levels (Harris, 1984). Different types and intensities of land use could also affect the structure of those fragments. Different species also have different requirements, life history, dispersal strategies, etc (Terborgh, 1992b). Some species could be more easily dispersed than others through a matrix of unsuitable or less suitable habitats. Other aspects such as the distance between fragments or to a possible seed source, the degree of connectivity between fragments, and the role of animal species on pollination, dispersal and predation of tree species could also have an important role (Terborgh,

1992a,b). The complex interactions of all these factors make it very difficult to identify the main causal factors in each specific situation (Burrows, 1990).

The spatial factors linked to tropical forest fragmentation have been receiving an increasingly attention in recent years, in both ecological studies and conservation planning (Harris & Silva-Lopez, 1992; Laurance & Bierregaard, 1997; Rey-Benayas & Pope, 1992; Schelhas & Greenberg, 1996). Results from a large-scale long-term experiment suggest that fragment size and shape can affect considerably the dynamics of Amazonian forests (Laurance *et al.*, 1998). A few studies have begun to address the spatial aspects in the Atlantic forests (Jorge & Garcia, 1997; Ranta *et al.*, 1998; Rodrigues, 1992; Stevens & Husband, 1998; Viana & Tabanez, 1996; Viana *et al.*, 1997).

The interactions of physical and biogeochemical processes could result in relatively stable landforms, where the vegetation is able to accumulate a considerable biomass, even growing on relatively nutrient-poor soils, by developing adaptations to cycle nutrients more effectively (Scatena & Lugo, 1995). The spatial distribution of environmental conditions and the disturbance frequency, associated with the soil catena, play an important role in shaping the forest (Poorter *et al.*, 1994). Drainage conditions and mass movements that link soil-forming processes across the landscape can also influence the distribution of landslides, treefall gaps and the age, structure and composition of the forest. The distribution of soils and vegetation could be thus correlated with landforms, when large time and spatial scales are considered (Scatena & Lugo, 1995).

The role of disturbance events on the diversity of the Atlantic forest has not yet been investigated. The possible causal factors considered so far relate the local biodiversity mainly to the forest refuge theory (climatic oscillations in the Pleistocene) and also to the heterogeneous physical environment (Brown & Ab'Sáber, 1979; Ab'Sáber, 1992a,b). The high degree of endemism and the relative antiquity of the local terrain suggest a long isolation from the other forest areas of the continent (Leitão-Filho, 1994; Prance, 1979; Veloso & Góes-Filho, 1982). Climatic oscillations could have allowed temporary connections with Amazonia through the gallery forests of central Brazil and the *brejos* (moist mountain forest areas) of the northeastern *caatinga* during the Quaternary (Bigarella *et al.*, 1975; Oliveira-Filho &

Ratter, 1995; Prance, 1989). The high diversity of the forest could thus be explained, at least partially, by the contribution of taxa from both the southwestern (Paraná river basin) and northern floras (Mori, 1989; Por, 1992).

Observations of current forest dynamics in the southern uplands (*Araucaria* forests and grasslands) and palaeoecological data suggest a general decrease of temperature and rainfall during Pleistocene glacial maxima (Behlig & Lichte, 1997). A northern and lowland expansion of taxa adapted to colder climates (*Araucaria*, *Podocarpus*), with a consequent retraction of the tropical forest might have occurred (Behlig, 1998; Colinvaux *et al.*, 1996; Klein, 1984; Servant *et al.*, 1993). The existing patches of *Araucaria* forest in high altitude areas surrounded by tropical moist forest could represent contemporary refuges of the flora of a colder past climate (Veloso & Góes-Filho, 1982). However, the data available so far are still not sufficient to allow a clear picture of the effect of late Quaternary climatic events in the Atlantic forest.

Other disturbance factors that must be considered are the role of relief and high rainfall, with consequent landslides, and also breakage of branches due to the abundant epiphytic vegetation (Ashton, 1989; Strong, 1977). A more simplistic explanation is related to both the wide latitudinal and altitudinal gradients and the resulting complex of habitat types (Mantovani & Ybert, 1992). This, combined with both the long term isolation and the climatic fluctuations of the Quaternary could account for the exuberant speciation that occurred in the region, resulting in the high degree of endemism and biological diversity (Mori *et al.*, 1981; Gentry, 1982, 1989, 1992, 1993, Por, 1992; Prance, 1989).

Human influence can mimic to some extent natural disturbance processes. The study of both the gap-phase dynamics and the structure and dynamics of secondary forests are important for forest management (Attiwill, 1994; Brokaw & Sheiner, 1989; Cohet, 1995; Hubbel & Foster, 1983; Jans *et al.*, 1993; Lieberman *et al.*, 1995; Oldeman 1989; Whitmore, 1998). Some studies have already been made on the structure and dynamic processes in secondary forest in the Atlantic region (Klein, 1984, 1990; Mendonça *et al.*, 1992; Quintela & Louzada, 1993; Silva-Jr *et al.*, 1995). However, only the availability of a long temporal series of data could allow a better understanding of the processes involved. Comparisons between forests

of different ages or different successional stages in similar environments could provide a greater insight on both causal factors and forest responses. These studies could be later calibrated through the use of data from long term studies made in permanent forest plots (Alder & Sinnot, 1992; Vanclay, 1995).

Knowledge of secondary forest dynamics can be important in the development of strategies for the management of natural forests and restoration of degraded areas (Aubert & Oliveira-Filho, 1994; Britez *et al.*, 1992; Reis *et al.*, 1993; Rodrigues *et al.*, 1992; Silva-Jr *et al.*, 1995; Tabarelli *et al.*, 1993). Available data suggest that secondary forests could quickly recover some of their structural and functional aspects, such as biomass and the production of organic matter (Silva-Filho & Engel, 1993). However, the process of return to their original community structure appears to be much slower (Attiwill, 1994; Gómez-Pompa *et al.*, 1991; Terborgh, 1992a).

3.4. Land Use and Conservation Planning

3.4.1. Forest Management

Land use planning normally involves several levels of governmental decision. In Brazil, the state governments traditionally have a great influence on agricultural policy, but the federal government controls both forest and conservation policy. With the new Constitution of 1988 both municipal and state governments have a greater influence on and responsibility for environmental policies. The forest policy, traditionally connected with the agricultural sector, is now closely linked to environmental agencies. These changes have allowed a greater integration between forest and conservation policies, with the environmental aspects of forest management being increasingly taken into account. The integration between forest management and conservation and the agricultural policy is more difficult. Although both the government and landowners are increasingly aware of the environmental aspects related to the agricultural use of the land, there is still a long way to go before this awareness becomes widespread (Dean, 1995).

Current forest management in SE Brazil includes selective logging, clear-cutting for firewood harvesting and opening areas for agriculture. Extensive plantations of exotic fast-growth species (*Eucalyptus*, *Pinus*) have been established,

for charcoal, firewood and pulp production (Dean, 1995; Marchak, 1995). Some of the highest forest productivities in tropical forest plantations in the world were obtained in the Atlantic Forest region (Evans, 1992). Although only a few small areas have been planted with native tree species, normally high value hardwoods or *Araucaria angustifolia*, there has been a considerable increase of reforestation with native species for environmental restoration (Rodrigues *et al.*, 1992). Some studies have shown that the native forest structure can be restored, at least partially, through natural regeneration under the canopy of *Eucalyptus* plantations, which suggests that those areas could be converted back to a natural forest cover after logging (Aubert & Oliveira-Filho, 1994; Silva-Jr *et al.*, 1995).

A new legislation (Decree 750/93) established more rigorous norms for forest exploitation, including the need for the establishment of forest management plans on a sustainable basis. The decree also forbids clear-cutting in areas with primary or old-secondary forests. The establishment of the technical criteria for forest management plans, and their evaluation and control is a responsibility of the states environmental agencies.

Ecologically sound forest management needs to be based on the availability of good data on the structure and dynamics of the forest (Gómez-Pompa *et al.*, 1991; Lamprecht, 1990; Rossot *et al.*, 1982; Reis *et al.*, 1993; Whitmore, 1998). Forest inventories provide valuable estimates of the volume and the timber exploitation potential of the forest (FAO, 1977; Heinsdijk, 1975). Most forest inventories in the Atlantic forest region were made at reconnaissance level, providing only a broad view of the forest structure (IBDF, 1984). These inventories include very few, if any, data on species regeneration, growth rates and forest productivity. More recently, detailed inventories have been made as a required step for the preparation of forest management plans (Lobão & Souza, 1993). The availability of a extensive data-set from forest inventories, covering most forest types and periodically updated, could greatly improve the formulation and implementation of adequate forest policies.

A considerable amount of the remaining Atlantic forest is in a greater or smaller degree secondary (Brown & Brown, 1992). Secondary forests could fulfil many production and conservation functions, such as production of timber, firewood and non-timber products, protection of soils and water resources, conservation of

several animal species, and recreational activities (Blockhus *et al.*, 1992; Cohet, 1995; Gómez-Pompa *et al.*, 1991; Sá & Strier, 1992). Many valuable tree species also occur in secondary forests (Lobão & Souza, 1993). Secondary forests could also act as natural corridors between primary forest areas. Well designed silvicultural systems, based on both manipulation of natural regeneration and forest enrichment, could improve the economic value of these forests, while retaining their conservation, protection and aesthetic values (Blockhus *et al.*, 1992; Gómez-Pompa *et al.*, 1991; Lamprecht, 1990; Spelleberg, 1992).

3.4.2. Forest Conservation

The current knowledge of geographical distribution, population size and dynamics of most animal species, including many of those considered endangered, is still limited (Brown & Brown, 1992; Rizzini *et al.*, 1991; WCMC, 1992). Endangered species include primates (*Leontopithecus*, *Brachyteles*, *Callithrix*), sloth (*Bradypus*), jaguar (*Panthera*), puma and small wildcats (*Felis*), giant otter (*Pteromura*), many birds and hummingbirds, and the broad-snouted caiman (*Caiman*) (Ferrari & Diego, 1995; Fonseca, 1985; Mittermeier *et al.*, 1988; SOS Mata Atlântica, 1990; Pinto *et al.*, 1993; Por, 1992). The few available data have been used to guide the selection of areas for conservation. However, conservation strategies and plans should be periodically re-evaluated, refined and updated, as new data become available (Bibby *et al.*, 1992; WCMC, 1992).

The Atlantic forest has been reduced to fragments of variable size in most of its geographical range (Brown & Brown, 1992; Fonseca, 1985; Por, 1992). Most of these fragments are probably not large enough to allow the survival of top predators, but can still support viable populations of many endangered species, especially of birds and small mammals, including primates (Blockhus *et al.*, 1992; Ferrari & Diego, 1995; Sá & Strier, 1992; Strier, 1989; Pinto *et al.*, 1993). The establishment of a network of a number of forest fragments, linked by forest corridors along streams or ridges, would allow the movement of individuals from different populations avoiding isolation and possible in-breeding among these populations (Fiedler & Jain, 1992; WCMC, 1992). This approach can have a lower cost and greater probability of success than the adoption of captive-breeding and

reintroduction programmes (Ferrari & Diego, 1995). A good knowledge of the target species ecological behaviour and of the local environment and land use patterns can help to select adequate areas for the establishment of these corridors.

The oldest National Park of Brazil (P.N. de Itatiaia) was established in an Atlantic forest area in the Rio de Janeiro/Minas Gerais border, in 1939 (Brade, 1956; IBDF, 1982). Several other conservation units were later established in the region, at national, state and municipal levels (IBAMA, 1989; IBDF, 1981; IEF, 1994). However, the establishment of parks and reserves has not avoided the destruction of valuable forest areas. Many conservation units have not yet been totally implemented, or are still subject to human pressure. The units also do not cover all the different types of habitats that occur in the region. Many areas are relatively small, and cannot conserve viable populations of large predators. Only approximately 20,000 km² (2 % of the total area) of the remaining forests are located in conservation units (Por, 1992; SOS Mata Atlântica, 1990).

Traditionally, conservation was not a high priority in governmental policies. Conservation units were regularly established by law, but did not receive adequate financial support. Many lack any infrastructure in terms of personnel, buildings and vehicles, and some never had an appropriate management plan (Oliveira, 1998). This situation has improved recently, but there is still a lot to be done in terms of planning and management. Priorities include a re-evaluation of the present system, with consolidation of the existing units, changes of management categories, better physical infrastructure and increase in the number and qualification of staff. An increase in both the total protected area and the geographical distribution of conservation units, covering habitat types currently poorly or not protected is also needed. Finally, a de-centralisation of decisions, with a better integration with other government areas and the surrounding human communities needs to be implemented, combined with the establishment of long-term ecological research and monitoring programmes (Decanini, 1997; IUCN, 1994; Lino & Cencig, 1992; Oliveira, 1998; SOS Mata Atlântica, 1990).

3.4.3. Integrated Planning for the Atlantic Forest

Clearly, the integration of conservation and forest management policies should be based in a framework where all the ecological and environmental relationships that occur in the forest ecosystem and their interactions with the human activities can be assessed and evaluated (Gómez-Pompa & Brainbridge, 1995). A framework of this nature could combine local, spatial and temporal data, at different scales, taking also into account data obtained from the monitoring of the implementation of the policies, combined with new scientific evidence.

Information systems could allow the storage and retrieval of a great amount of data. Remote sensing technology allows the analysis of both spatial and temporal environmental data at a relatively low cost. These data could be stored and combined with other environmental and socio-economic data through a GIS. Such systems could be used for planning, ecological analysis and environmental modelling purposes (Bridgewater, 1993; Goodchild *et al.*, 1993; Green, 1994; Gregg, 1994; Kessel, 1992; Lankhorst, 1992; McCloy, 1995; Sample, 1994; Stow, 1993).

There are already a few initiatives for the establishment of such information systems at both state and national level (Decanini, 1997; Japiassu. *et al.* 1992; SOS Mata Atlântica, 1990). Most of them cover only a few of the relevant variables involved in conservation planning, and their implementation has been rather slow (Decanini, 1997). Aspects such as the integration of different types of data and the compatibility between the different systems are still far from being resolved. The recent establishment of a network at national level by IBAMA, which combine remote sensing and GIS capabilities, could help to overcome some of these problems.

3.5. The Forests of Rio de Janeiro

The state of Rio de Janeiro covers an area of 43,305 km² (see Fig. 3.3). It has a considerable variety of environmental conditions, due to both its geographical location along the coast near the Tropic of Capricorn (20°45'-23°32' S, 40°57'-44°53' W) and its physiographic characteristics. The altitudinal range varies from the sea level to 2800 m (IBDF, 1984). The main climate types (Köppen system) are Aw, Af, Am, Cw and Cf, with annual average temperatures varying from 14° to 23° C.

Rainfall ranges from 800 mm in the Cabo Frio region to over 2500 mm on the south and eastern slopes of the Serra do Mar mountain ridge (FIDERJ, 1978).

The geology of the state is characterised mainly by Tertiary and Quaternary coastal plains and old Palaeozoic, crystalline rocks, which form the SE fringe of the Brazilian Shield (DRM, 1977). The predominant soil types are Oxisols, Alfisols, Ultisols, Inceptisols, and Spodosols (Radambrasil, 1983; Golfari & Moosmayer, 1980).

The influence of both the physiographic gradients and the geographical situation of Rio de Janeiro have a striking effect on the vegetation diversity. The state can be considered as entirely located within the Atlantic Forest domain. The forest physiognomy varies widely across the state in response to local gradients of soil, climate and relief. Ninety seven per cent of the area of the state was originally covered with semideciduous and evergreen moist forests, which reach the coast in the mountain areas in the SW, with some patches of mixed *Araucaria* forests in southern high altitude areas (IBDF, 1984; Ururahy *et al.*, 1983). Along the central and NE coast there are extensive areas covered by scrub or arboreal sclerophyllous vegetation, known in Brazil as *restinga* (Lacerda *et al.*, 1993). On the central and SW coast, there are several patches of mangrove forest along river estuaries, coastal lagoons, islands and bays (Uruahy *et al.*, 1983).

Most of the forested areas have been converted to coffee and sugar cane plantations and to extensive pastures. Currently only 8,960 km² of primary or old-secondary forests (21% of the original area) remain, 2,450 km² within conservation units. Most of the coastal vegetation areas have also been affected by an increasing urban and industrial expansion (IBDF, 1984; SOS Mata Atlântica, 1990).

3.6. The Study Site – The Macaé de Cima Forest

The central mountain region of Rio de Janeiro State, known as the Serra dos Órgãos, is part of the Serra do Mar, a mountain ridge that represents the SE fringe of the ancient Brazilian Shield, extending from the southern state of Rio Grande do Sul to Rio de Janeiro. During the XIX century, the region was visited and studied by a number of European naturalists such as Saint Hillaire, Darwin, Gardner and Glaziou (Rizzini, 1979; Câmara, 1991). The region provided the toponym *organensis* for the

many plant and animal species described from there (Kunkel, 1990). Glaziou reportedly collected extensively in Macaé de Cima region located in the NE of the Serra dos Órgãos, from where the *alto-macahensis* toponym originated (Kunkel, 1990; Lima & Guedes-Bruni, 1994).

The present research concentrates on the Macaé de Cima Municipal Ecological Reserve (REM). Important factors in the selection of the area were the availability of vegetation and environmental data, including thematic maps, aerial photographs and satellite imagery. Additionally, the region had been studied by the Programa Mata Atlântica (PMA), run by the Botanic Gardens of Rio de Janeiro-JBRJ (Lima & Guedes-Bruni, 1994, 1996). The studies were based on quantitative ecological data collected on two 1 ha square forest plots, complemented by extensive collecting of botanical data (Lima & Guedes-Bruni, 1997). Although they provide valuable information on the composition and overall structure of the forests, they do not allow the analysis of the spatial variability of the forest, especially in an area with such variation of relief. The studies also did not take into account the relationships between the forest structure and the local physical environment.

The Macaé de Cima region is located in the southern portion of the Nova Friburgo municipality, a mountain town with approximately 150,000 inhabitants, between 22°20'-22°28' S and 42°25'-42°35' W (see Figs. 3.3 and 4.2). The name Macaé de Cima (meaning *high Macaé*) refers to the headwaters of the Macaé River, which runs in a E-W direction directly to the Atlantic Ocean. The altitude varies from 800m to 1720m a.s.l.

Climate

Due to its particular geographic location, with a combination of high altitude, proximity to the coast, and its latitude near the Tropic of Capricorn, the climate of the M. de Cima region has been classified either as tropical or subtropical, according to the system adopted. The annual average temperature in Nova Friburgo is 17.8° C (FIDERJ, 1978).

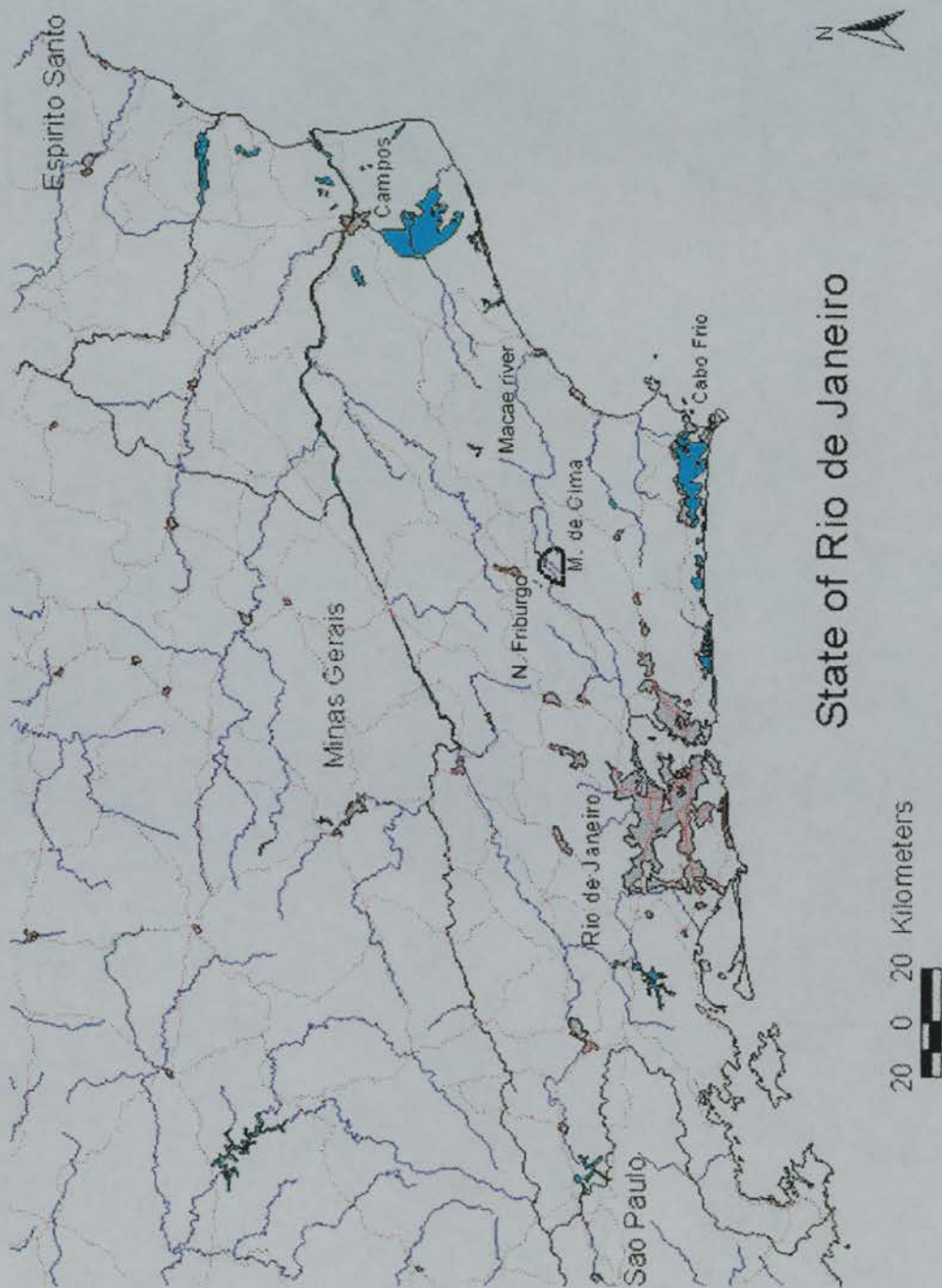


Figure 3.3 Map of the State of Rio de Janeiro, showing the location of the Macaé de Cima Reserve, SE of Nova Friburgo town, and the borders with other SE Brazilian states (São Paulo, Minas Gerais and Espírito Santo).

The rainfall regime shows the occurrence of a short dry season in the winter months (June-Aug). However, the length and the intensity of this dry season vary not only annually, but also spatially. This is due to a combined effect of the local relief and the polar fronts that frequently reach the region, increased by the moisture brought from the Atlantic Ocean by easterly winds. The Serra do Mar mountain ridge acts as a barrier to these winds, which promotes the occurrence of a very wet region on the piedmont and eastern slopes, and an increasingly drier climate as one moves west, due to the 'rain shadow' effect (FIDERJ, 1978; Schnell, 1987).

The local climate can be classified as Cfa (Cf/Cw) in the Köppen system, tropical with summer rains and temperature in the coldest month below 18 C°. According to the ombrothermic relationship $P \leq 2T$ (Walter, 1985), the N. Friburgo station, with 70 dry days, is located on the transition between the ombrophilous (less than 60 dry days) and the seasonal regime. Therefore, the vegetation map of the region shows the boundaries between the ombrophilous (moist) and the seasonal forest right in the N. Friburgo urban area (Uruahy *et al.*, 1993).

The great spatial variation in the local climate suggests the need to apply more sophisticated methods to better represent the variations at local and regional scales. The establishment of a large network of rainfall gauges has increased the amount of climatic data available in the region. This could allow a better spatial resolution for modelling the spatial variation of the climate, taking into account the effect of the local relief on both rainfall and temperature.

The rainfall data (Table 3.1) show a regional range in the average annual rainfall between 1534-2419 mm. The range is considerably greater, if the annual variation (938-3048 mm) is considered. There is an increase as one moves in the SE-NW direction, from the southeastern coast to the Serra dos Órgãos, with a maximum on the piedmont and southeastern slope regions, and a gradual decrease from the mountain ridge to the Paraíba River valley region. The Fazenda São João station is perhaps the most representative of the Reserve's local climate, as it is located just within its northern boundary. However, local observations suggest that the rainfall is considerably higher in the southern boundaries, near the Serra dos Órgãos ridge.

Table 3.1 Average annual rainfall and range (between brackets). Data from six pluviometric stations located in the M. de Cima region

Station Name	Period	Coordinates	Altitude	Average Annual Rainfall
N. Friburgo	1931-75	22° 17' S 42° 32' W	857	1397 mm (938-1882)
Faz. São João	1967-95	22° 23' S 42° 30' W	1010	2193 mm (1518-2699)
Galdinópolis	1950-95	22° 22' S 42° 23' W	740	1983 mm (1274-2778)
Pillar	1950-95	22° 24' S 41° 21' W	670	2419 mm (1515-3943)
Quartéis	1967-95	22° 23' S 42° 18' W	58	2316 mm (1517-3048)
Gaviões	1967-95	22° 24' S 42° 34' W	620	2089 mm (1641-2661)

Source: DNAEE (1995); FIDERJ (1978)

Geology

The Serra dos Órgãos mountain chain is part of the old Palaeozoic Brazilian Shield. The lithology is composed basically of Precambrian intrusive and metamorphic rocks, exposed in most of the area, whose accumulated debris give rise to small surface formations. There is a relative abundance of microcrack dykes, probably of Mesozoic age. The Precambrian rocks are composed of three stratified units, a sirogenetic intrusive body, intensively migmatized rocks, essentially derived from those stratified units, and post-orogenetic granite bodies (Radambrasil, 1983).

There is a general agreement on the mineral composition, structure and texture of the lithologic conjunct known as Serra dos Órgãos, which is constituted of rocks of granite aspect and coarse grain. However, different explanations have been proposed for its genesis, with an hypothesis of migmatogenetic evolution and sintectonic granite intrusion (Radambrasil, 1983; Rosier, 1959, 1965). A geological survey of the region was carried out at 1:50,000 scale (DRM/CPRM, 1980; see Appendix 3).

Geomorphology

The current relief in the Atlantic forest region has its origins in the Gondwana fragmentation (Jurassic). After that event, there was a great amount of Cretaceous Continental deposits inland, with deep sedimentary basins filled with Cretaceous and Cenozoic sediments on the continental margin. An intense reactivation of the former structural lines was accompanied by warping and faulting (Bigarella, 1991).

The Serra do Mar mountain range forms the edge of the Brazilian central plateau. It consists of a set of uplifted, faulted blocks, rising as mountain chains above the plateau edge. Its origins are supposed to be the result of warping and faulting related to the former structural lines of the Precambrian crystalline basement. Aside from the tectonic aspects, erosion had played a considerable role since the Oligocene (Mid-Tertiary). Two alternating groups of process occurred, the extensive erosion of slopes accompanied by lateral terracing of vertical dissection of the land, and an extensive soil formation, accompanied by relative landscape stability (Radambrasil, 1983).

In summary, the factors that contribute to the formation of the current landscape in SE Brazil are: the wet climate, with high summer rainfall and temperatures; the passive continental margin and the dorsal uplift and wiper/faulted continental margin, with a strong tensional fracture pattern; a sheer zone of intersection of dense fractures set; fissile metamorphic or igneous rock with a dense microcrack system; and the occurrence of free-draining sites beneath interfluves and hillslopes protected by duricrust capping (Thomas, 1994). Another important factor is the persistence of the landscape for a period long enough to develop a state of dynamic equilibrium, with lowering of weathering profiles and relief segmentation occurring simultaneously (Thomas, 1994).

Recent reviews of palaeoecological data, correlative deposits of the erosive landforms and current biogeographical patterns point to the existence of a colder and drier climate during Pleistocene glacial events, with consequent changes in the vegetation cover (Ab'Sáber, 1992a,b; Brown Jr & Ab'Sáber, 1979; Bigarella *et al.*, 1975). Humid periods should favour forest expansion, chemical weathering and pedogenesis, besides some vertical dissection, lowering local base level, while colder and drier periods favoured forest retreat, regolith removal, and lateral levelling, with formation of pediplanes or pediments (Bigarella, 1991).

The Radambrasil Project mapped the regional relief based on the interpretation of 1:250,000 SLAR imagery (Radambrasil, 1983). The study area is totally located in the D1/D3 mapping unity (Faixa de Dobramento Remobilizados, Escarpa e Reverso da Serra do Mar/Serra dos Órgãos). The relief is composed of structural valleys or gullies, the dissected front of foliated blocs, the edge of fluvial

terraces, and crest lines. The relief is characterised by differential dissection, signed by structural control (tectonic and lithologic), defined by drainage deepening/lowering. The average drainage incisions measured on transverse profiles in valleys are $D1 = 82-192\text{m}$, and $D3 = 361-446\text{m}$. The structural control is emphasised by extensive sheet lines, dislocated blocs, scarps and the recent relief. Rocks resistance is reflected in dissection forms, highlighting resistant dome outcrops bornhardt/palaeo-inselbergs (*filões* and *pontões*), crests/ridges and gullies on diaclyses and fractured zones relief. The Radambrasil geomorphology report includes a relief evaluation, according to the potential and constraints presented by the relief for land use (see Appendix 3).

Soils

The soils of the Macaé de Cima region result from a combination of powerful influencing factors: the lithology (old Palaeozoic crystalline rocks, gneiss/granite), geomorphology (highly dissected relief), the climate over the Holocene period (tropical/sub-tropical, with wet hot summers and considerable fluctuations over the past 10,000 years) and the dense forest cover (Radambrasil, 1983). Most local soils are in a state of precarious equilibrium, resulting from the complex interactions between several processes that occur simultaneously: erosion, due to rainfall events and the steep relief; the constant weathering due to both high rainfall and temperatures, and processes influenced by the vegetation.

The forest vegetation has a strong role influencing the local properties of soils. It offers protection (rainfall interception) and a mechanical fixing role from its root anchorage and organic matter production. It affects also the chemical nature of the soils, due to the influence on processes such as organic matter decomposition and plant transpiration (water and nutrient recycling). The resulting soils are generally characterised by a low pH and low nutrient content. The slope position affects depth, texture and the amount of carbon, and consequently, the moisture storage capacity. The main soil types of the M. de Cima (Serra dos Órgãos) region (EMBRAPA, 1992; Radambrasil, 1983), are shown on Table 3.3 (see Appendix 3 for soil type description).

Table 3.2. Soil mapping units of the Macaé de Cima region

LVa6	Red-Yellow Latosol, allic A moderate clay texture evergreen tropical forest phase strong hilly relief
LVH1	Humic Red-Yellow Latosol, allic clay texture evergreen tropical forest phase strong hilly relief
PVa3	Red-Yellow Podsol, Tb allic or dystrophic A moderate medium/clay texture evergreen tropical forest phase strong hilly and mountain relief
Ca2 (Ca27)	Cambisol, Tb allic or dystrophic A prominent or moderate clay or medium texture rocky and not-rocky evergreen tropical forest phase strong hilly relief (profile 83)
Ca17 (Ca11)	Cambisol, Tb allic or dystrophic A moderate clay or medium texture rocky evergreen tropical forest phase mountain and scarp relief (profile 82)
CHa1	Humic Cambisol, Tb allic or dystrophic clay or medium texture evergreen tropical forest phase hilly relief
CHa2	Humic Cambisol, Tb allic or dystrophic medium or clay texture evergreen tropical forest phase strong hilly relief
Re1	Lithosol, Tb allic A moderate medium and clay texture rocky and not-rocky phase mountain and scarp relief
AR	Rock outcrop

Sources: Radambrasil (1983); EMBRAPA (1992)

Forest Zoning

A land zoning for forestry was carried out by the state Development Bank (Golfari & Moosmayer, 1980). It produced a bioclimatic map at 1:400,000 scale based on the Thornthwaite method, which takes into account the potential evapotranspiration (Thornthwaite & Mather, 1955). Almost all the study area was included in a single bioclimatic zone (Region 1), which includes almost all areas of the state above 800m, with an average annual temperature < 18° C. The piedmont region, with a super-humid tropical climate, was included in the Region 3 (see Appendix 3).

The work presents also an integrated ecological map at 1:800,000 scale, which divides the state into several ecological (land) systems, established according to an integrated analysis of geology, relief, climate, soil, vegetation and land-use data. The study area was allocated into two different ecological systems, both belonging to the mountain region of Precambrian rocks, Serra do Mar group (see Appendix 3).

The characteristics of the natural vegetation of the Macaé de Cima region and its relationships with the local physical environment will be dealt with more detail in Chapter 5.

Summary

Knowledge of the patterns of variation in the structure and composition of Rio de Janeiro forests in relation to the physical environment is fundamental for a

better understanding of the Atlantic forest biome as a whole. Its physiography and geographical location suggest links with the subtropical coastal moist and upland mixed *Araucaria* forests, with the central semideciduous forests, and possibly also with the lowland moist forest of NE Brazil. The high diversity and level of endemism, as well as the occurrence of endangered animal and plant species are other factors that reinforce the urgent need to increase our knowledge of the ecology of the state's forests.

Rio de Janeiro possesses a considerable area of montane tropical forests, which are relatively less studied than the lowland forests. The study of the relationships between the montane forest and the local physical environment, and of the floristic links with another areas and formations within the Atlantic forest biome fills some of the gaps in current understanding of the Atlantic forest ecosystem. It also provides valuable information for a better management and conservation of the state's montane forests.

CHAPTER 4 - Research Methodology

4.1. Introduction

The research methodology can be divided in three phases (see Fig. 4.1). The first phase (I) relates to the characterisation of the forest community structure and its relationships to the physical environment. It can be subdivided into two parts. The first (Ia) represents a site and local scale analysis. The second part (Ib) investigates which factors affect the distribution of vegetation types at broader scales, through an analysis of floristic and related environmental data from several areas of the Atlantic forest in SE Brazil.

In the second phase (II), the pattern of relationships between the vegetation and the physical environment found earlier will be used in an integrated analysis of remote sensing and aerial photographs together with other spatial environmental data. The aim is to identify and map areas with more or less homogeneous physiognomy and floristic structure that can be related to aspects of the physical environment.

In the third phase (III), the results of the analyses at both local and regional scales will be used in an attempt to build a conceptual model of the spatial relationships between the Atlantic forest vegetation and factors of the physical environment.

4.2. Local scale analysis

The goal of the local scale analysis (forest stand or community level) is to search for possible spatial relationships between important vegetation characteristics and some of the key features of the physical environment. This can be achieved by use of qualitative and quantitative plant and environmental data from field sampling as well as from other studies that have covered the Macaé de Cima region.

The approach adopted in the research is based on the use of vegetation and soils data collected at different locations along known important environmental gradients identified from previous ecological studies, topographical and thematic maps and from aerial photographs and satellite images. The aim is to collect

ecological and environmental data that can be analysed by means of standard methods, as well as to combine and/or compare with data from other sources.

4.2.1. Fieldwork

The main fieldwork was carried out from April to October 1996, which are the driest months (see Table 3.1). Prior to this, a general reconnaissance was made in November of 1995 of the entire Macaé de Cima region. Several aspects were checked, such as the conditions of the roads and trails, the accuracy of the existing maps, and observation of features seen on Landsat TM images and aerial photographs such as landforms, vegetation and land use cover.

The reconnaissance work also provided personal contacts with the local landowners and residents, which helped to give a general overview of the local land and forest management practices. This procedure was important, in view of the recent history of local conflicts with the environmental authorities (IBAMA, IEF, and the Municipal Government). This was especially necessary following the establishment of the Reserve and the introduction of new and more restrictive Federal environmental legislation (Decree N. 750/93). It was considered important to explain clearly the objectives of the research project, in order to get understanding and support from local people.

The field team included a *mateiro* (woodsman), a local ex-hunter and logger with a great experience and knowledge of the local environment. He was skilled at locating trails (and opening up new ones) and identification of tree species by their local names. His knowledge was important also for the safety of all the team, as well as for establishing personal contact with other locals. The team also included a field technician, whose task was to assist in the collection of botanical samples, normally a very difficult task in tropical forest areas, particularly in mountain and wet environments. The team was completed, on most field trips, by one or two graduate students from the Universidade Federal Fluminense (UFF), who helped in the demarcation of the sampling plots, tree measurements, and collecting of botanical and soil samples.

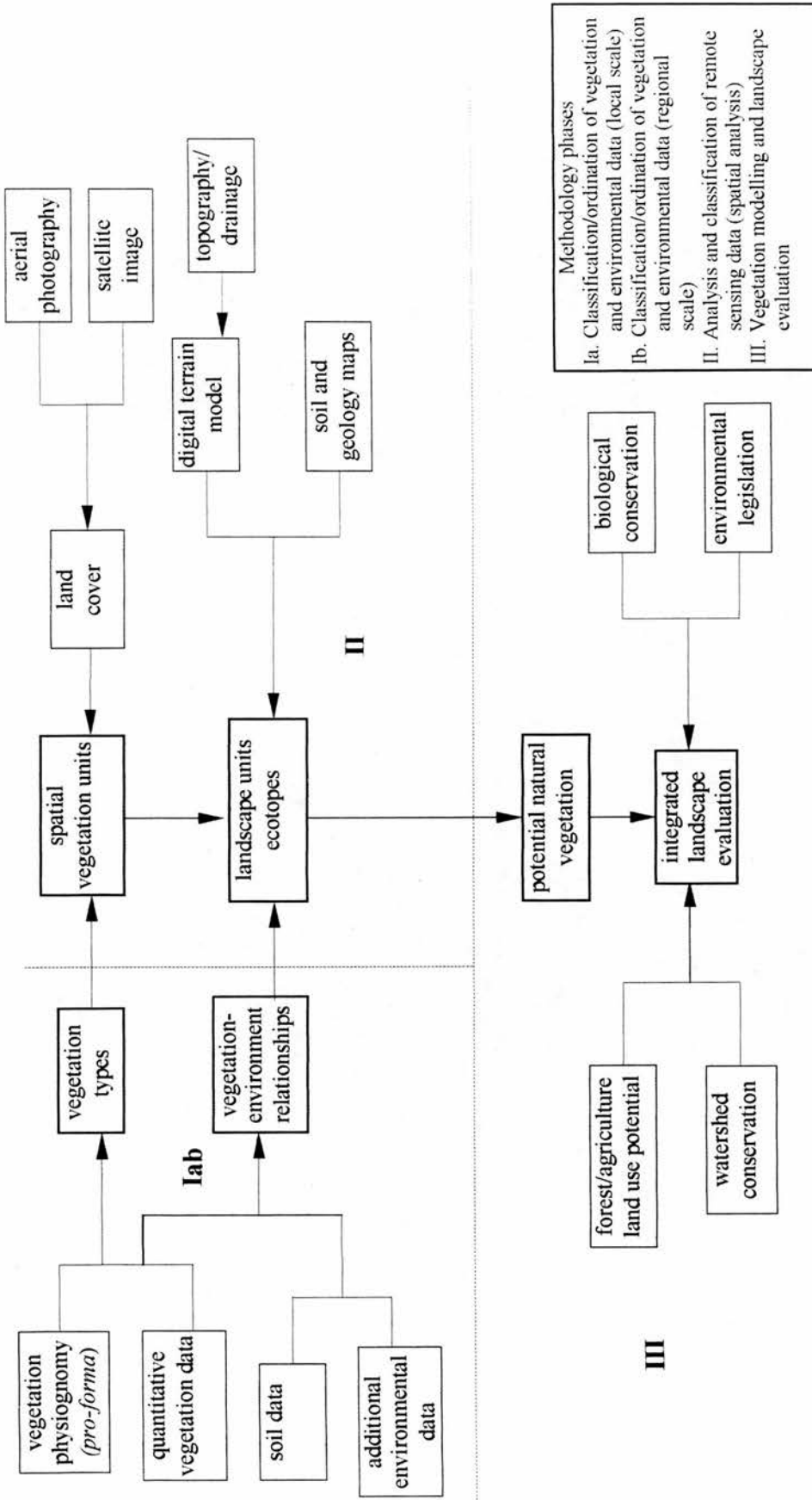


Fig. 4.1 Research methodology outline

Sampling

The sampling strategy was based on a two stage stratified sampling. The first stage was an initial stratification of the area into, as far as possible representative homogeneous units, based mainly on an overall analysis of relief, soil, vegetation cover and physiognomic information obtained from existing maps, aerial photography and Landsat TM imagery, as well as other available environmental information. At a second stage, sampling plots were established within the different forest types or strata. Plot location was based on a subjective choice, aiming to represent the local characteristics of both vegetation and the physical environment within each forest type.

An area based sampling strategy was selected after weighing up the advantages of each of the different approaches to forest sampling (see Chapter 2), as well as an evaluation of the local environmental characteristics and the available resources. Ten (10) 20x20m (400 m²) rectangular plots were established, with four 10x10m (100 m²) subplots in each. All plots were established in primary or old growth secondary forest areas, with varying degrees of slope and altitude. The plots were established in all the three main river basins within the Reserve: Macaé, Flores, and Bonito, to cover as much of the physiognomic, geographic and environmental variation as possible (see Fig. 4.2). Two additional plots of 25x10m (250 m²) were established in an old *Eucalyptus* plantation located on the Reserve border, for comparison with the natural forest biomass, soil properties, and spectral signature from the Landsat TM image.

Data Collection on the Sample Plots

All trees ≥ 10 cm dbh (or 31.4 cm cbh) occurring within the sampling plot boundaries were marked. Measurements included cbh (circumference at breast height, or 1.30 m), canopy (branching) and total height. On inclined trees, which occurred frequently, the cbh was measured along the trunk at 1.30m from the forest floor. When trees bifurcated below 1.30m, both stems were considered as single trees and measured separately. In the case of one stem being less than 31.4cm cbh, the stem was considered as single, but the value of the thinner was summed with it. In

such a case it was also considered as an individual tree in the estimate of species density. The same procedure was adopted for height measurements.

The main difficulty in measuring tree heights was the dense and closed nature of the tropical forest canopy, with many overlapping crowns of different tree species with similar leaf size and shape, combined with the steep relief. For these reasons, the total and canopy (stem) heights were mostly estimated visually, with the aid of a long-arm pruner (sections of 2m) for comparison. Whenever feasible, i.e., in more open or flatter areas, a Blume-Leiss hypsometer was used to improve the accuracy of the height estimate.

The individual plants were identified by their local name, whenever it was known by the *mateiro*. Herbarium specimens were also collected for most plants (with duplicates). Exceptions were made only when there was certainty about the species identification, samples previously collected from the same species, or when it was impossible to collect the samples, as in the case of very tall trees with few or no leaves. This occurred only with two trees. Fertile material was also collected elsewhere in the region, which could help in the identification of the sterile material collected within the sampling plots. The botanical samples were first heat-dried in the field, and later at the Laboratory of Ecology and Biogeography of UFF. The material was sent to the RBGE Herbarium (E), with some duplicates sent also to the JBRJ Herbarium (RB).

Other types of ecological data that might add important information on the characteristics of different forest types were also collected on a systematic basis. Structural/physiognomic data (canopy surface and density special life-forms and ground cover, leaf size, texture and shape, bark and rooting features) were collected by using a *pro-forma* developed for Australian rainforests (Webb *et al.*, 1976), which was adapted to the Atlantic forest conditions. However, it did not prove possible to utilise this information to differentiate between forests, because of the small variation in the structural features amongst the different sampling plots. Further development of the *pro-forma* is necessary for use in the Atlantic forest, with a better characterisation of physiognomic features.

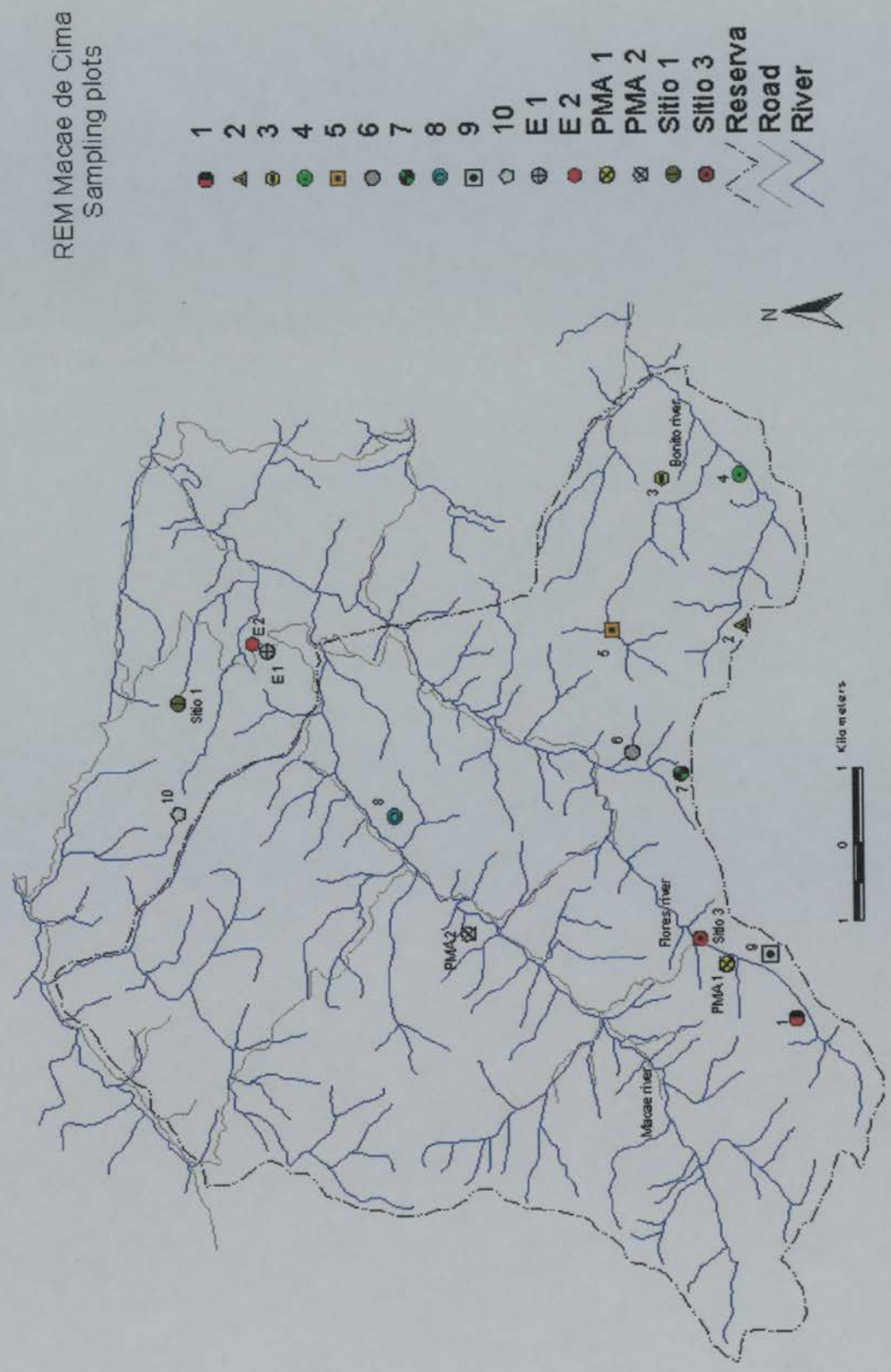


Figure 4.2 Location of the sampling plots in the Macaé de Cima Reserve. Sitio 1 and 3 are the field bases. PMA 1 and 2 are 1 ha plots from previous work (see text).

Environmental data to be used in the analyses included soil properties, relief, altitude, and possible disturbances. Topsoil samples (0-20 cm depth) were collected in all plots for physical and chemical analysis (pH, texture, %C, Al, H+AL, Ca+Mg, Na, P, K, CEC). The analyses were undertaken at the laboratories of the National Centre for Soils Research (CNPS-EMBRAPA), in Rio de Janeiro, according to the standards adopted for the Brazilian soil survey (see Appendix 2).

Other data included approximate plot coordinates, aspect and slope. A Navigator GPS was available on some of the field visits. It proved to be of little value in dense forest cover and mountain conditions, which block the satellite signals. Approximate coordinates were obtained only in more open areas at some reference points, which made it easier to locate the forest sampling plots on the map. However, the use of a differential GPS receiver positioned on the top of the forest canopy could improve the acquisition of more accurate plot coordinates, at least in top-slope and flat sites. Aspect was obtained from compass, while slope was measured through a Haga clinometer.

4.2.2. Additional Environmental Data

During the fieldwork period, several visits were made to Brazilian institutions and university departments, where research has been developed in related fields. In addition to the institutions already mentioned, the visits included the Departments of Geography and Ecology-UFRJ, Dep. of Ecology-UERJ, Inst. of Forestry-UFRRJ, Dep. of Geochemistry-UFF, DRM and CPRM (geological mapping), all in Rio de Janeiro. Field trips were also made to the Poço das Antas Biological Reserve and Búzios/Cabo Frio, areas included in the biogeographical analysis (see 4.4). Other institutions visited include the Cocoa Research Centre-CEPLAC in Ilhéus, Bahia, Dep. of Botany and Ecology-USP, Instituto/Fund. Florestal, and Fund. SOS Mata Atlântica, all in São Paulo, IBAMA and DNAEE in Brasília, DF (see Appendix 1 for acronyms).

These visits also had the objective of collecting additional data. Spatial data collected include topographical and geological maps (1:50,000), vegetation, soil and geomorphology maps (1:250,000), aerial photographs (1:22,000, from 1970), a SLAR image (1:250,000, 1976), Landsat TM imagery (3-band colour composition on

paper, 1989, 6-band image on cartridge, 1987, and a 5-band image on CD-ROM, 1996). Additional data and information on the Atlantic forest environment were also obtained from post-graduate theses, scientific papers, government reports and proceedings of congresses, workshops and seminars. Most floristic and related environmental data obtained were used in the biogeographical analyses (see 4.4).

4.3.3. Identification of tree species

The identification of the plant species vouchers collected in the field was made simultaneously at the Herbaria of the ERBG (E) and Royal Botanical Gardens-Kew (K), in the UK, and at the JBRJ (RB), in Brazil. The recent publication of two volumes on the flora of the region (Lima & Guedes-Bruni, 1994; 1996) greatly helped in the identification.

4.2.4. Classification and Ordination of Vegetation

The classification of plant communities and analysis of the relationships between plant communities and the physical environment were made by use of quantitative floristic data (species abundance), organised in a matrix (species-abundance x plot). The first stage was to organise the quantitative data in tables (spreadsheets) using the program EXCEL 5.0. The software FITOPAC (Shepherd, 1995) was used to summarise the structural data for all sampling plots, to estimate the main forest structural criteria (density, cover, frequency and IVI), both by plot and for all the dataset. FITOPAC was used also to transform the structural data into Cornell file format, in order to be used in the TWINSpan (classification), DECORANA and CANOCO (ordination) softwares (see 2.3). The software PC-ORD 3.0 (McCune & Mefford, 1997), which performs TWINSpan, UPGMA, PCA, DCA and CCA, was also used in both local and regional scale (see section 4.3) analyses.

The forest plots were classified by use of the Two-Way INDividual SPecies ANalysis-TWINSpan (Hill, 1979b). The ordination of vegetation data was initially made by the Indirect Gradient analysis technique Detrended Correspondence Analysis-DCA, through the software DECORANA (Hill, 1979a). DCA explores unidentified or non-explicit environmental gradients (Kent & Coker, 1992). The

results of the structural analysis, classification and indirect ordination of the Macaé de Cima vegetation are presented and discussed in Chapter Five.

Both soil and additional environmental data from the sampling plots were analysed by use of Principal Components Analysis-PCA, in order to analyse the environmental variation within the study area. PCA analysis explores possible auto-correlations between the variables. It is also useful in selecting from all the variables, those responsible for a greater part of the local environmental variation, reducing information redundancy (Ter Braak 1995; Kent & Coker, 1992). Direct gradient analysis was carried out via Canonical Correspondence Analysis, through the software CANOCO (Ter Braak, 1988). CCA allows identification of relationships between variations in the vegetation and known environmental gradients such as soils and altitude. It also provides correlation coefficients between the vegetation and the environmental variables (Ter Braak, 1995). The results of the direct ordination and discussions of the role of the environmental factors in the variation of the Macaé de Cima vegetation are presented in Chapter Six.

4.3. Analysis of Biogeographical Patterns

The results of the local scale study of the Macaé de Cima vegetation were further compared with other studies in the Atlantic forest region by analysis of both floristic and environmental similarities. The objective was to investigate the biogeographical links between the study area and other areas of the Atlantic forest, and whether these links can be related also to environmental and/or geographical variables.

Floristic checklists and quantitative ecological surveys, together with complementary environmental data were obtained from both published (books, journals and proceedings of congresses and seminars) and unpublished (theses, internal reports) sources. There were extensive checks on the possible occurrence of synonyms and elimination of doubtful taxa. This work was greatly supported by use of a database on the woody flora of Brazil developed by Oliveira-Filho & Ratter (1994). This database, available at the RBGE library, provided floristic data, complemented by recent publications, for 26 of the 51 forest areas used in the analysis. Species that occurred in only one area (unicates) were eliminated from the

final matrix of species *per* area (presence/absence), as they do not increase the information necessary to differentiate floristically the forest areas (Gauch, 1982; Oliveira-Filho & Ratter, 1995). The matrix was used in both classification (TWINSpan, UPGMA) and ordination (DCA, CCA) analyses. The results and discussion are presented in Chapter Seven.

4.4 Spatial Analysis

The spatial analysis procedures aim to identify spatial patterns of relationships between the vegetation and both local environmental factors and man-made disturbance, and to evaluate possible alternative scenarios of landscape evolution. Spatial data on plant community distribution were analysed in combination with other thematic data such as relief and soils. The objective was to obtain a clear picture of the vertical (topological) and horizontal (chorological) relationships between the vegetation and the physical environment.

The landscape of the Macaé de Cima region was analysed by use of aerial photographs, thematic maps and fieldwork data and observations. The vegetation cover was analysed by the interpretation of aerial photographs and digital processing of a Landsat TM image. Spatial ecological and environmental data were stored in a GIS for further analyses. The final objective was the production of a landscape ecological map, with the landscape classes established according to the spatial patterns of relationships between vegetation and environmental variables, and the correlation between image and ground vegetation and environmental data (Jongman *et al.*, 1995; Zonneveld, 1995).

4.4.1 Data Input and Image Processing

Interpretation of Aerial Photographs

Visual interpretation was carried out using stereo pairs of aerial photographs at 1:22,000 scale, analysed through a mirror stereoscope. The different types of vegetation cover and the associated landscape patterns were used as the main mapping criteria. The three-dimensional effect provided by the stereoscope also helped to identify relationships between landforms and the vegetation structure. The vegetation cover map (1970) produced was adopted as the main baseline information

on the spatial distribution of different vegetation and land-use types (or landscape elements), and for the identification of changes in the local landscape.

Digital Image Processing-DIP

A CD-ROM containing a 5-band (2, 3, 4, 5 and 7) Landsat TM image (scene 216/76A, from 27/07/1996) was obtained from the National Institute for Space Research (INPE). The image was processed and analysed using Alpha DEC UNIX workstations of the Department of Geography network, by use of the image processing software ERDAS IMAGINE 8.03. The objective was to investigate possible correlations between the vegetation types and the image spectral signatures, to identify landscape changes through comparison with the land cover map generated from the interpretation of aerial photographs, and to produce a map of the current land cover. The main steps of the approach adopted were:

- Pre-processing - a sub-image including only the Area of Interest (AOI) was selected. Image rectification or geometrical correction was performed, to correct spatial errors due to platform altitude and orientation, and also for the effects of the topographic relief, by linking visible features on the image (Ground Control Points-GCP) to their known coordinates extracted from the 1:50,000 topographic maps. A total of 35 GCPs were used, with a second order polynomial transformation, cubic convolution resampling and a total of six iterations. The same procedure was adopted for the full image, with the GCPs selected from topographic maps at 1:250,000 scale.
- Unsupervised classification (ISODATA) - the objective was to partition the continuous spectral range of the image (bands 452) into discrete classes or areas (groups of pixels) with similar spectral signatures. The number of spectral classes adopted was six for the Macaé de Cima sub-image and ten for the full scene.
- Supervised classification (Maximum Likelihood) - this classification is based on the average spectral signatures of known cover types such as water bodies, bare soil, urban areas, dense primary forest, secondary forest, pastures and crop land, used as a training dataset, which was then applied to the Macaé de Cima sub-image.

Input of Additional Environmental Data

This step covers the input of spatial environmental and cartographic data into the GIS ARC/INFO 7.0. Data from existing maps at 1:50,000 and 1:250,000 scales, including the Macaé de Cima vegetation cover maps (see previous sections) were used, forming two separated databases with a common geographic reference and projection system (UTM). The paper maps were digitised and edited by use of the module ARCEDIT, while the classified image was exported as a raster file. The spatial data were stored as separate layers or coverages, according to their spatial and topological characteristics. Digital files containing the vegetation (IBGE, 1993a) and soil (EMBRAPA, 1981) maps of Brazil (1:5,000,000 scale) were obtained from the USGS/IUCN via internet and incorporated into the spatial database. The spatial data input sequence is summarised below.

- Digitising of vegetation, soil and geological/geomorphological maps (polygons).
- Digitising of the drainage and roads network, and the Reserve's boundaries (lines).
- Digitising of sampling plots and field stations (points). The forest areas used in the biogeographical analysis (see item 4.3) were also digitised as points, using the IBGE vegetation map layer as a background cover.
- Digitising of contour lines (40m intervals) and ridge tops (points).
- Corrections, construction and editing of topology.
- Input of associated attribute data, related to the point, line and point identifiers into the database (INFO).
- Projection transformation into UTM coordinates.

4.4.2 Spatial and landscape analysis

The goal of landscape analysis is to combine both local and spatial data and information gathered for the analysis of the spatial relationships between the vegetation and the physical environment. The results ultimately lead to the design of a Landscape Ecological map of the Reserve, combining in a single document (or GIS layer) the most important characteristics of both physical and biotic environment, including also human aspects.

Digital Terrain Model (DTM)

A DTM of the Macaé de Cima Reserve at the scale 1:50,000 was constructed, by use of the contour line, ridge top and drainage layers through the ARC/INFO commands TIN and TOPOGRID (LATTICE). The DTM was used primarily to estimate and map different slope classes within the Reserve. It also provides a visual three-dimensional representation of the local relief and of the hypsometric classes.

Integrated Analysis of Plot and Spatial Environmental Data

The spatial patterns of relationships between vegetation and the environmental variables were investigated through an overlay analysis of spatial vegetation (vegetation cover map, classified image), terrain (DTM) and environmental (climate, soils, geology) data. The resulting Landscape Ecological map shows the spatial distribution of the different landscape units, e.g., areas with common characteristics relating to geology, relief, soils and vegetation cover. The results of the spatial analysis are presented in Chapter Eight.

4.5. Vegetation Modelling

The results of the analysis at both local and regional scale were used as a basis for the development of a 'conceptual model' of the Atlantic forest landscape, translated into a cartographic model (GIS). The model is based on the forest-physical environment relationships that were found through the multivariate and spatial analysis. Therefore, it includes those environmental factors that showed a stronger correlation with the distribution of vegetation or community types. To illustrate the model output, the spatial dataset at 1:250,000 scale (digitised thematic maps and Landsat TM image) was used to produce a 'potential natural vegetation' map of the eastern region of the Rio de Janeiro State. The reasoning behind the conceptual model is presented in Chapter Nine.

CHAPTER 5. The Vegetation of Macaé de Cima

5.1. Vegetation and Land Use

Most of the Macaé de Cima region is covered by dense primary or old growth secondary tropical forest. Despite all the pressures and impacts due to human occupation of the area, there has been apparently an increase in the area covered by forest vegetation over the last decades (see Chapter 8). This process can be explained partially from both socio-economic and political reasons. Crop growing and cattle raising have been abandoned in many areas, mainly due to increasing costs of labour and low fertility of soils. As in many rural areas of Brazil, the local population has been decreasing as a result of emigration towards urban areas. Recent changes in both farmers' and government's attitude towards the environment has also contributed to a decrease in timber exploitation and land clearing.

Features such as access and slope appear to have an important role on agricultural land use. Flat and low slope terrain areas are more likely to be cleared or disturbed. As a consequence, early secondary forests occur mainly along roads and rivers to the foothills. Climate also may have a role, since there is an increase in the area of disturbed or cleared land in a SW-NE direction. This can be related to a gradual decrease in rainfall, and consequently longer dry winter seasons towards the NE. Exposure may also be important, as the slopes facing south are more exposed to cold winds originating from the sea and from polar fronts. North-facing slopes are warmer and also receive more light during the winter. Therefore, as a general rule, the areas more likely to be in a better state of conservation are located on the southern slopes of the ridge of the Serra dos Órgãos and on the higher altitude areas of the Macaé River headwaters.

5.2. Forest Physiognomy

According to the IBGE vegetation classification system, the vegetation of Macaé de Cima falls entirely within the ombrophilous dense forest region (Veloso *et al.*, 1991). At the formation level, the local vegetation corresponds to the montane and high-montane forest formations (see Figs. 3.2 and 8.1).

Montane Forest

The montane forest formation is the dominant vegetation type within the reserve. It covers slopes up to 1400-1500m asl in altitude, especially in areas of more difficult access in the headwaters of the Macaé, Flores and Bonito rivers. The forest is characterised by an evergreen dense, closed canopy, with an average height of 25 to 35m. Some large emergent trees reach 40m, especially on mid-slope areas with deeper and well-drained soils. Although very large trees are rather rare, the forest has a considerable biomass, with a high density of small and medium-sized trees. The sub-canopy is also dense, with an abundance of saplings. Natural regeneration is intense, with a high density of seedlings and poles of both smaller (lower canopy) and climax (canopy) tree species.



Plate 5.1 Overall view of the Macaé de Cima forest from the field station Sitio 3 (1050 m asl., see location on Fig. 4.2), showing the steep relief and the closed canopy of the montane forest formation. The rock outcrop (gneiss) on the background is Pedra Bicuda (Peaked rock), a well-known local landmark.



Plate 5.2 Aspect of a small gap on the montane forest formation. Characteristic features include the relatively high canopy, abundance of palms (*Euterpe edulis* Mart.), ground layer with herbs and poles (natural regeneration) of trees, and a large Bromeliaceae on tree crown.

The montane forest has a considerable density and diversity of epiphytes, with many species of Orchidaceae, Bromeliaceae, Cactaceae, and Araceae. Lichens and Bryophytes are also abundant on tree trunks. The palm *Euterpe edulis* is particularly abundant, especially in more humid areas along the drainage and streams, and reaches up to the middle slopes. Another large palm, *Attalea dubia*, also

occurs, especially at lower altitudes, being frequent in secondary forest areas. In valley bottom and riverine forest areas, the lower availability of light, the frequent occurrence of mist, and the high availability of soil moisture favour a great density of Marantaceae, Musaceae, Begoniaceae, Araceae, Cyatheaceae and other ferns.

Although predominantly dense, the canopy surface is irregular, with frequent occurrence of small gaps, probably related to the natural dynamic process of death of large trees, or local soil conditions (e.g., presence of stone outcrops). The steep relief and shallow soils also produce landslides during extreme rainfall events, causing larger gaps to occur. As the landslides cause changes in soil characteristics, with loss of the topsoil horizon and debris (branches and dead trees), the process of recolonisation of these gaps can be very slow in comparison to gaps originating from the death of trees. The forest also has irregularly occurring, large dense patches of the bamboo *Guadua tagoara*, probably related to disturbance. Observations made by locals also suggest that the presence of bamboo may considerably delay the regeneration of other tree species. A study of the environmental factors relating to these bamboo patches would undoubtedly give a better understanding of the dynamics of the mountain forest ecosystem.

High Montane Forest

The high montane forest occurs on the top portion of the mountain slopes above 1400m asl, along the south and west borders of the reserve. This forest has a considerably lower stature, with the average height varying from 10-20m. It is characterised by small trees, often with twisted trunks, almost totally covered by mosses (see Plate. 5.3). Tree stature and life sizes are generally smaller than in the montane forests. There is a high abundance of Bromeliaceae and other epiphytes. Palms (*Geonoma pohliana* and *G. wittigiana*) and small bamboos (*Chusquea*, *Merostachys*) are also conspicuous. The high montane forest physiognomy corresponds closely to the tropical cloud and elfin forests that occur in several areas in the Andes, Central America and Caribbean (Churchill *et al.*, 1995).

The transition from the montane to the high montane forest can be either gradual or abrupt, according to local environmental conditions. Although probably the main controlling factor is altitude, in Macaé de Cima the position on the slope

and the consequent pattern of soil characteristics also appear to have important roles. Most high montane forests that were identified in the field and in aerial photographs (see Chapter 8) were restricted to the mountain ridge areas. As one goes up the slope, changes in the physiognomy appear to correspond to an increase in the organic matter content of the soils, and there is also a decrease in soil depth. In many areas the soils are covered by a thick layer that resembles peat, composed of large and fine roots, leaves and humus. Therefore, the local environmental conditions, although apparently totally different, show some similarities with those of alluvial flooded forest areas. In both environments, high moisture and soils with high organic matter content are important controlling factors. However, the ecophysiological effects of lower temperatures, wind exposure and the occurrence of clouds, are also important additional factors in the high montane forests.



Plate 5.3 Aspect of the high montane forest near plot 10, at 1550m asl. (see location on Fig. 4.2). Characteristic features include the reduced stature of trees with twisted trunks, and the abundance of Bryophytes and Bromeliaceae.

Secondary Forests

Secondary forests occur mainly on medium and lower northward facing slopes, in the central and northeastern parts of the reserve (see Fig. 8.1). The secondary forests show a continuous physiognomic gradient, from the early successional stages to old-growth forests exhibiting most of the characteristics of primary forests. The abundance of pioneer species depends on the time period since initial regeneration, as well as the occurrence of new disturbances, such as fire and firewood extraction (Lima & Bruni-Guedes, 1997). Among the characteristic pioneer taxa are *Cecropia*, *Miconia* and *Tibouchina*, Solanaceae, Euphorbiaceae and Compositae. Although less disturbed and older secondary forests show many species in common with the primary forests, they can be characterised by the absence of large emergent trees, as well as absence or lower density of epiphytes.

5.3. Forest Structure

The results of the surveys at Macaé de Cima are summarised in Table 5.1. A total of 445 trees with $\text{dbh} \geq 10\text{cm}$ were measured in the 10 sampling plots established in natural forest, representing a total of 164 (morpho) species. From this total, 117 were identified to species level, 17 to genus and 12 to family. Eighteen individuals are still not identified. In one case it was not possible to collect a specimen, and in another the wrong species was collected (a parasite, belonging to the Loranthaceae). Fourteen dead standing trees were also measured. Adding the six species collected elsewhere in the area, a total of 170 species were recorded in the fieldwork.

The number of individuals within each plot varied from 27 to 61, which is equivalent to 700-1525 trees/ha. The average figure of 44.5 individuals per plot is equivalent to an average density of 1112 trees/ha. The average dbh was 19.9 cm, with a range varying from 17 to 25 cm. The largest tree (a specimen of *Ocotea indecora*) reached a dbh of 92.3 cm. If trees with more than one trunk are taken into account, the largest tree was a *Calycorectes* sp., with a summed total dbh of 106.7 cm from five trunks.

The average basal area reached the high value of 43 m^2/ha , with the average range varying from 33.6 to 57.2 m^2/ha . The average total height was 14m, with the tallest tree reaching 35m. Among the plots, the average height varied from 12 to

15.5m. Average bole height varied from 9.1 to 10.4m, with an overall average of 9.7m. Average canopy depth (total height less bole height) was 4.3m, with an average range of 2.8-5.3m.

Table 5.1. Quantitative summary of forest plot measurements.

Plot	Density	dbh	Hmax	Hbol	CaDep	BA	BA/ha	Vol 1	Vol 1/ha	Vol 2/ha
1	45	21.26	14.60	10.40	4.11	1.942	48.55	13.519	337.98	178.10
2	28	25.06	13.73	9.44	3.88	2.031	50.78	14.113	352.83	123.95
3	43	17.34	12.05	9.25	2.81	1.661	41.53	11.140	278.50	168.58
4	41	19.64	13.74	9.45	4.19	1.598	39.95	10.701	267.53	161.25
5	49	15.60	13.14	9.24	3.66	1.562	39.05	9.479	236.98	179.68
6	41	13.05	13.98	9.94	4.04	1.343	33.58	9.149	228.73	150.93
7	51	16.23	15.34	9.78	5.11	2.288	57.20	12.408	310.20	197.18
8	62	19.42	13.64	9.69	3.89	1.764	44.10	10.542	263.55	222.68
9	54	17.19	14.88	9.75	5.13	1.468	36.70	8.947	223.68	196.73
10	30	21.61	15.47	10.44	5.03	1.537	38.43	9.863	246.58	134.28
Total:	445					17.194		109.86		
Average	44.5	19.87	14.06	9.74	4.19	1.719	42.99	10.986	274.65	171.33
Std Dev	10.19	2.624	1.047	0.426	0.733	0.289	7.23	1.813	45.32	30.20
Variance	103.79	6.887	1.097	0.182	0.537	0.084	52.20	3.287	2054.35	912.02

Key: plot average values of diameter (dbh, cm); maximum (Hmax) and bole (Hbol) heights (m); canopy depth (CaDep, m); basal area (BA, m²); volume (Vol, m³) per plot and per ha, Vol 1 = Hmax*BA*F, and Vol 2 = EXP {-11.4932 + 0.9317351 Ln (cbh2*Hmax)} (r² = 0.98), where cbh is circumference at breast height.

The average timber (stem) volume showed great variation, according to the model adopted. Forest volume estimates are very sensitive to the criteria adopted on height measurement, measurement errors, and also on the volume equation adopted. The estimate based on the general model $V = H_{max} * BA * F$ resulted in an average volume of 109.9 m³, equivalent to 274.63 m³/ha, a result that is highly dependent on the form factor value (F = 0.65) adopted. Several different models were tested during a forest inventory carried out at state level (IBDF, 1984). The volumetric model that best fitted the forests of the region (see key on Table 5.1) resulted in an average volume equivalent to 171.3 m³/ha, which is within the range of values found in similar types of forests (IBDF, 1984).

Size Distribution

The forest structure size distribution was estimated according to the diameter distribution (number of trees for each dbh class). The result for the Macaé de Cima forest as a whole is shown in the Fig. 5.1, while Fig. 5.2 shows the size distribution classes for each forest plot. The histogram (Fig. 5.1) suggests a well-balanced forest

structure in a state of dynamic equilibrium, with an elevated degree of natural regeneration, characterised by the high number of trees belonging to the first diameter class (10-20cm). The size distribution at plot level shows a similar pattern to that of the whole forest. However, in plots 3, 5, 9 and especially 8, the first diameter class has a much higher proportion of the trees than the average, which may suggest some degree of disturbance.

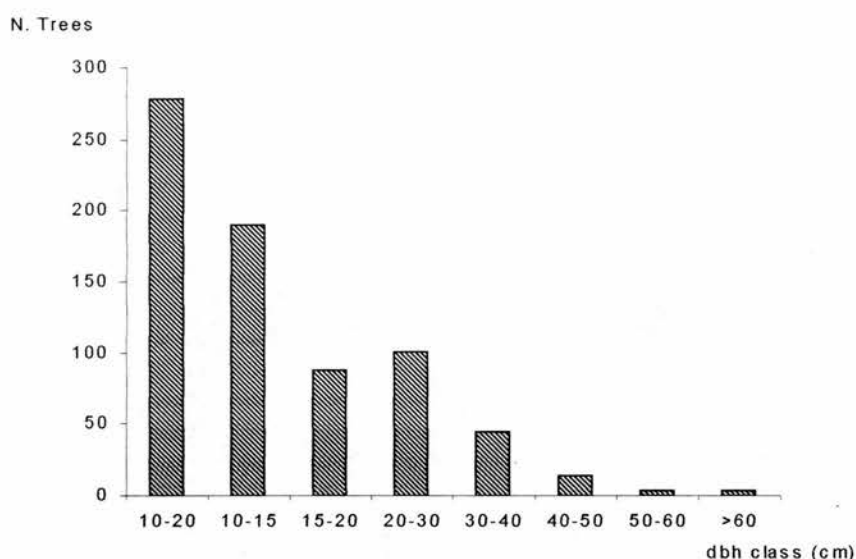


Figure 5.1 Diameter distribution (all plots). The first diameter class (10-20 cm) is sub-divided into two classes (10-15, 15-20 cm) to illustrate the dominance of small size trees in the overall structure of the forest

5.4. Floristic Composition

The total list of species recorded on the forest plots established in Macaé de Cima Reserve is shown in Table 5.2. With the exception of *Euterpe edulis* Mart., all the identifications were based on collected vouchers. The list also includes a few tree species collected outside the forest plots. The main reason for the relatively high number of trees being unidentified or identified only to family or generic level was the high proportion of infertile material. This made the identification to species level particularly difficult, especially in the families Myrtaceae and Lauraceae.

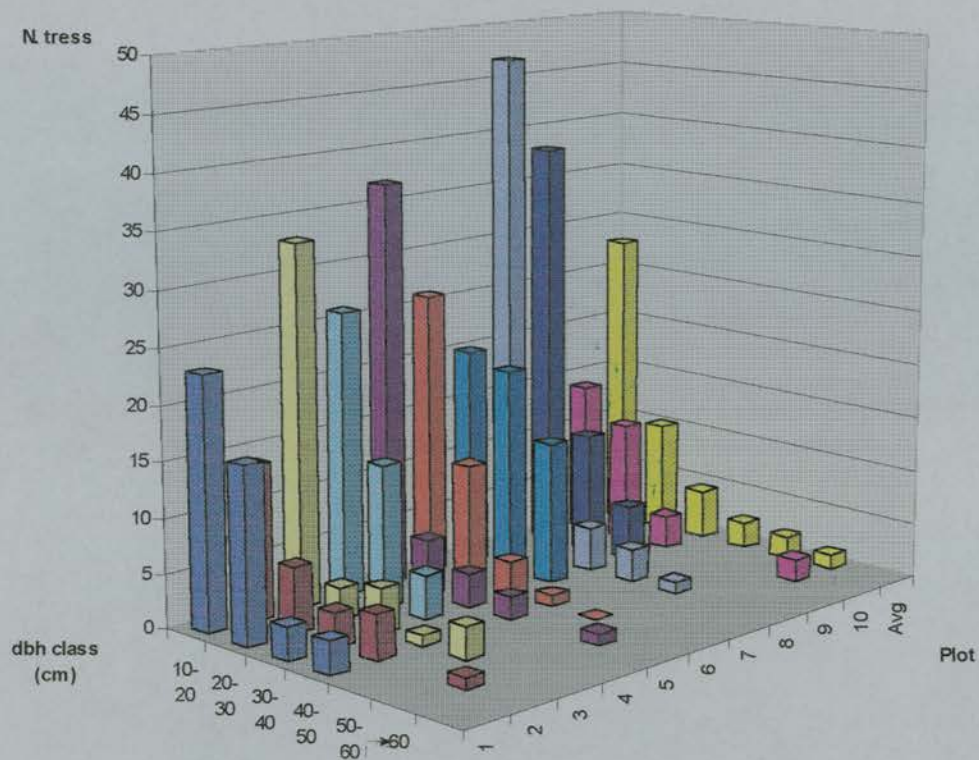


Fig. 5.2 Diameter distribution by plot

Figure 5.2 Diameter distribution (by plot), showing that most trees fall within the smaller classes (10-20, 20-30 cm dbh) in all plots.

At the floristic level, the Macaé de Cima forest has shown a high diversity in terms of both species (164) and families (42), especially considering the relatively small total sampling area (0.4 ha), and the inclusion criteria ($\text{dbh} \geq 10$ cm). As in many other Atlantic forest areas, Myrtaceae have the greatest number of species (36), followed by Lauraceae (14), Leguminosae (12), Melastomataceae, Monimiaceae and Rubiaceae (7 each), Clusiaceae (6), Moraceae and Sapindaceae (4 each), and Annonaceae, Araliaceae, Malpighiaceae, Meliaceae, Sapotaceae and Vochysiaceae, with three species each.

Table 5.2 Total list of tree species registered at the Macaé de Cima forest

Aegiphila fluminensis Vell. (Verbenaceae)
Alchornea triplinervia Muell. Arg. (Euphorbiaceae)
Alibertia sp.1 (Rubiaceae)
Amaioua intermedia Mart. (Rubiaceae)
Aspidosperma olivaceum Muell. Arg. (Apocynaceae)
Bathysa mendoncae Schum. (Rubiaceae)
Beilschmiedia rigida (Mez) Kosterm. (Lauraceae)
Brosimum sp.1
Brosimum sp.2
Byrsonima laevigata DC. (Malpighiaceae)
Byrsonima laxiflora Griseb. (Malpighiaceae)
Byrsonima myricifolia Griseb. (Malpighiaceae)
Cabralea cangerana (Vell.) Mart. (Meliaceae)
Calycorectes sp.1 (Myrtaceae)
Calyptranthes lucida Mart. ex DC. (Myrtaceae)
Calyptranthes concinna DC. (Myrtaceae)
Calyptranthes glazioviana Kiaersk. (Myrtaceae)
Cecropia hololeuca Miq. (Moraceae)
Cedrela odorata L. (Meliaceae)
Cinnamomum glaziovii Mez (Lauraceae)
Clethra scabra Pers. (Clethraceae)
Clusia lanceolata Cambess. (Clusiaceae)
Clusia sturdiana C. Vieira & Gomes da Silva (Clusiaceae)
Coccoloba sp.1 (Polygonaceae)
Couepia venosa Prance (Chrysobalanaceae)
Coussapoa microcarpa (Schott.) Rizzini (Moraceae)*
Croton sp.1 (Euphorbiaceae)
Cryptocarya moschata Nees & Mart. (Lauraceae)
Cupania emarginata Cambess. (Sapindaceae)
Cupania sp.1 (Sapindaceae)
Dalbergia aff. *foliolosa* Benth. (Leg. Pap.)
Dendropanax trilobium Seem. (Araliaceae)
Didymopanax (Shefflera) angustissimum March. (Araliaceae)
Didymopanax (Shefflera) anomalum Taub. (Araliaceae)
Drimys brasiliensis Miers (Winteraceae)
Duguetia salicifolia R.E. Fries (Annonaceae)
Endlicheria paniculata Mack. (Lauraceae)
Eugenia cuprea (Berg) Ndz. (Myrtaceae)
Eugenia curvatopeciolata Kiaersk. (Myrtaceae)
Eugenia stictosepala Kiaersk. (Myrtaceae)
Eugenia subavenia Berg (Myrtaceae)
Eugenia sp.1 (Myrtaceae)
Eugenia sp.2 (Myrtaceae)
Euplassa hoehnei Sleumer (Proteaceae)
Euterpe edulis Mart. (Palmae)
Ficus sp.1 (Moraceae)
Gomidesia spectabilis (DC.) Berg (Myrtaceae)*
Guapira opposita (Vell.) Reitz (Nyctaginaceae)
Gutteria pubens (Mart.) R.E. Fries (Annonaceae)
Huberia glazioviana Cogn. (Rubiaceae)
Ilex paraguariensis A. St. Hil. (Aquifoliaceae)
Ilex theezans Mart. ex Reiss. (Aquifoliaceae)
Inga barbata Benth. (Leg. Mim.)
Inga cylindrica Mart. (Leg. Mim.)
Inga lancaefolia Benth. (Leg. Mim.)
Inga sp.1
Kielmeyera insignis N. Saddy (Clusiaceae)
Lacistema pubescens Mart. (Lacistemaceae)
Lamanonia ternata Vell. (Cunoniaceae)
Lauraceae sp.1
Licania kunthiana Hook. f. (Chrysobalanaceae)
Macropeplus ligustrinus (Tul.) Perk. var. *friburguensis* Perk. (Monimiaceae)

Marlierea regeliana Berg (Myrtaceae)
Marlierea silvatica Kiaersk. (Myrtaceae)
Marlieria suaveolens Cambess (Myrtaceae)
Matayba guianensis Aubl. (Sapindaceae)
Maytenus alaternoides Reiss. (Celastraceae)
Maytenus sp.1 (Celastraceae)
Meriania daussenii Triana (Rubiaceae) *
Meriania robusta Cogn. (Rubiaceae)
Miconia altissima Cogn. (Melastomataceae)
Miconia buddlejoides Triana (Melastomataceae)
Miconia jucunda Triana (Melastomataceae)
Micropholis crassipedicellata Pierre (Sapotaceae)
Mollinedia gilgiana Perk. (Monimiaceae)
Mollinedia glaziovii Perk. (Monimiaceae)
Mollinedia heteranthera Perk. (Monimiaceae)
Mollinedia myriantha Perk. (Monimiaceae)
Mollinedia salicifolia Perk. (Monimiaceae)
Mollinedia schottiana (Spreng.) Perk. (Monimiaceae)
Mouriri arborea Gardner (Melastomataceae)
Myrceugenia kleinii Legrand & Krause (Myrtaceae)
Myrceugenia pilotantha Ledrun (Myrtaceae)
Myrceugenia sp.1 (Myrtaceae)
Myrcia fallax (Rich.) DC. (Myrtaceae)
Myrcia rhabdoides Kiaersk. (Myrtaceae)
Myrciaria floribunda (West.ex Willd.) Berg (Myrtaceae)
Myrocarpus frondosus Allem. (Leg. Pap.)
Myrsine umbellata Mart. (Myrsinaceae)
 Myrtaceae sp.1
 Myrtaceae sp.2
 Myrtaceae sp.3
 Myrtaceae sp.4
 Myrtaceae sp.5
 Myrtaceae sp.6
 Myrtaceae sp.7
 Myrtaceae sp.8
 Myrtaceae sp.9
 Myrtaceae sp.10
 Myrtaceae sp.11
Ocotea aciphila (Nees) Mez (Lauraceae)
Ocotea divaricata Mez (Lauraceae)
Ocotea glaziovii Mez (Lauraceae)
Ocotea indecora (Schott) Mez (Lauraceae)
Ocotea notata (Nees) Mez (Lauraceae)*
Ocotea pretiosa Nees (Lauraceae)
Ocotea silvestris Vatt. (Lauraceae)
Ocotea sp.1 (Lauraceae)
Ocotea sp.2 (Lauraceae)
Ormosia sp. nov. (Leg. Pap.)
Ouratea vaccinioides (St. Hil. & Pohl) Engl. (Ochnaceae) *
Persea cordata Mez (Lauraceae)
Pimenta pseudocaryophyllus (Gomes) Landrum (Myrtaceae)
Piptocarpha macropoda Baker (Compositae)
Plinia trunciflora (Berg) Rotman (Myrtaceae)
Posoqueria acutifolia Mart. (Rubiaceae)
Pouteria caimito Radlk. (Sapotaceae)
Pouteria durlandii (Standley) Baehni (Sapotaceae)
Prunus myrtifolia (L.) Urban var. *brasiliensis* Steyerl. (Rosaceae)
Pseudopiptadenia schumanniana (Taub.) Lew. & Lima
Psychotria pubigera Schlecht. (Rubiaceae)
Psychotria sessilis (Vell.) Muell. Arg. (Rubiaceae)
Quina glaziovii Engl. (Quinaceae)
Rhedia gardneriana Planch. & Triana (Clusiaceae)
Rollinia laurifolia Schlecht. (Annonaceae)
Roupala rhombifolia Mart. (Proteaceae)*

Roupala scultpa Sleumer (Proteaceae)
Rudgea corniculata Benth. (Rubiaceae)
Salacia grandifolia (Mart.) Peyr. (Hippocrateaceae)
Salacia sp.1 (Hippocrateaceae)
Sclerolobium rugosum Mart. (Leg. Caes.)
Simarouba amara Aubl. (Simaroubaceae)
Siphoneugena kiaerskoviana Kausel (Myrtaceae)
Siphoneugena sp.1 (Myrtaceae)
Sloanea lasiocoma K. Schum. (Elaeocarpaceae)
Sorocea bonplandii (Baillon) Burger (Moraceae)
Stephanopodium organense (Engl.) Prance (Dichapetalaceae)
Swartzia acutifolia Vog. (Leg. Pap.)
Symplocos corymboclados Brand. (Symplocaceae)
Symplocos nitidifolia Brand. (Symplocaceae)
Symplocos variabilis Mart. (Symplocaceae)*
Tabebuia heptaphylla (Vell.) Toledo (Bignoniaceae)
Tapirira guianensis Aubl. (Anacardiaceae)
Terminalia januariensis DC. (Combretaceae)
Tibouchina canescens (D. Don) Cogn. (Melastomataceae)
Tovomita glazioviana Engler (Clusiaceae)
Tovomitopsis saldanhae Engler (Clusiaceae)
Trichilia lepidota Mart. var. *schrawaniana* Penn. (Meliaceae)
Vernonia discolor Less. (Compositae)
Vochysia glazioviana Warm. (Vochysiaceae)
Vochysia saldanhae Warm. (Vochysiaceae)
Vochysia sp.1 (Vochysiaceae)
Weinmannia pauliniifolia Pohl (Cunoniaceae)
Zanthoxylum (Fagara) rhoifolium (Lam.) Engl. (Rutaceae)

* Collected outside the forest plots

The Macaé de Cima forest shows similarities at the generic level with both Neotropical cloud forests and the Southern Brazil subtropical forests, e.g. in the presence of genera such as *Clethra*, *Clusia*, *Dendropananx*, *Schefflera* (*Didymopanax*), *Drimys*, *Eugenia*, *Ficus*, *Ilex*, *Inga*, *Miconia*, *Micropholis*, *Ocotea*, *Quiina*, *Persea*, *Prunus*, *Rapanea*, *Myrsine* (*Roupala*), *Sloanea*, *Stephanopodium*, *Symplocos*, *Tibouchina*, *Weinmannia*, and *Zanthoxylum* (Klein, 1984; Webster, 1995).

Species/Area Curve

The collector's curve, based on the relationship new species occurrence x area sampled (Cain & Castro, 1959), is shown in Fig. 5.3. The relationship species/area has been traditionally adopted in quantitative studies as the main test to estimate the minimum sampling area necessary to represent the variability of the vegetation within one area (Greig-Smith, 1983). However, the minimum sampling area should also be estimated on the basis of other criteria, as the shape of the curve

can be influenced by the order of the samples, e.g., different results can be obtained when one changes the order of the samples. In the present study, the area was estimated on the basis of sub-plot size (100m^2), put in the same order as the field sampling.

The curve shows an almost constant increase in the number of new species, as new samples were taken. Small variations in the curve can be related to new plots, i.e., new species are more likely to appear in the first subplot of the next sample plot than in the last. Another factor is the predominance of a clustered spatial distribution among many tropical tree species. It can be expected that trees from such species should be recorded in a single or a few sample plots.

A relatively high proportion (50%) of the total number of tree species found in a previous extensive botanical survey (Lima & Guedes-Bruni, 1994) was recorded in the forest samples. The number can also be compared with the two other phytosociological surveys carried out in the reserve (Guedes-Bruni *et al.*, 1997; Pessoa *et al.*, 1997). The surveys reported a total of 189 and 157 species, in a primary and a secondary forest respectively (see Fig. 4.3), which is remarkable, considering that both of the plots have a larger sampling area (1 ha) and included trees down to 5cm dbh.

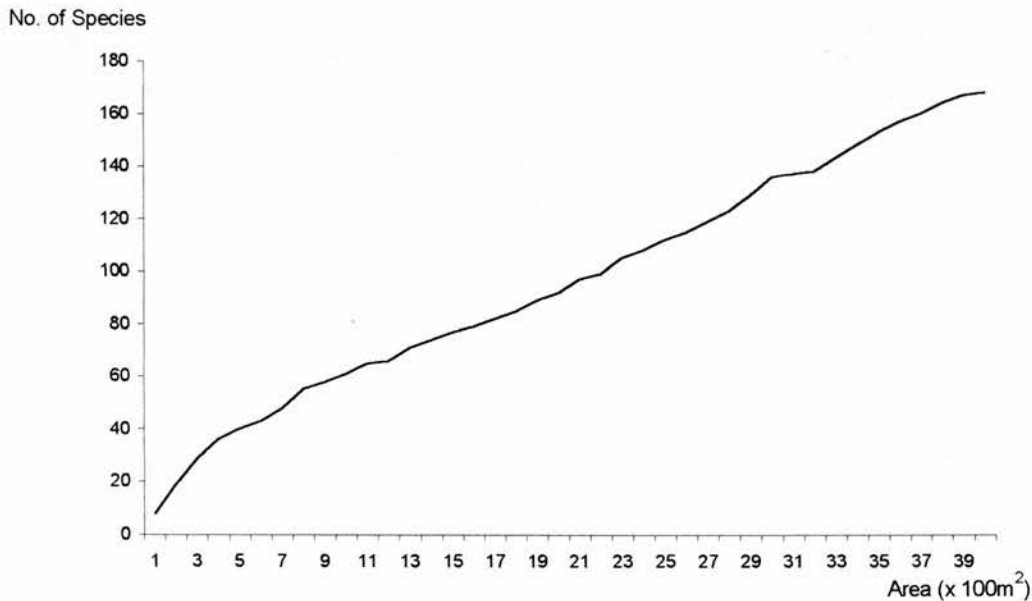


Figure 5.3 Species x area curve, showing a relatively continuous increase in the number of species with the sampled area.

It can be argued that the approach of sampling smaller plots more distant from each other may reflect the heterogeneity of the local vegetation better than using a few large plots. However, to test this it would be necessary to establish more plots, in a sampling design that considers both plot size and the distance between. Such design must also take into account the great variability of the local relief. But with regard to the aims of this study, the sample size and intensity were sufficient to characterise the Reserve's forest vegetation as a whole, and to distinguish between different forest communities (see 5.6 and 5.7).

5.5. Phytosociology

The phytosociological indices resulting from the quantitative analysis of the data for all plots are shown on Table 5.3. The ten most important elements were, in decreasing order, *Euterpe edulis*, dead trees, *Licania kunthiana*, *Vochysia saldanhae*, *Ocotea indecora*, *Calycorectes* sp.1, *Dendropanax trilobium*, *Kielmeyera insignis*, *Cryptocarya moschata*, and *Meriania robusta*. The 30 most important species (ignoring dead trees) belong to the families Myrtaceae (6), Clusiaceae, Leguminosae, and Sapindaceae (3 each), Lauraceae (2), and Annonaceae, Araliaceae, Chrysobalanaceae, Clethraceae, Euphorbiaceae, Monimiaceae, Melastomataceae, Meliaceae, Nyctaginaceae, Palmae, Rubiaceae, Sapotaceae, and Vochysiaceae with one species each. The results confirm the importance of the palm *E. edulis* in the overall structure of the Atlantic forest. The importance of dead trees suggests some degree of disturbance, and perhaps a high species turnover, which may be due to either human or natural causes.

In relation to density, most species are represented by a single individual, a characteristic that is common to most such analyses of tropical forests (Richards, 1996). The species with highest density was *E. edulis*, with a total of 72 individuals recorded, equivalent to an absolute density (AbDen) of 180 trees/ha, or 16.2% of the trees (ReDen). It was followed by dead trees (35), *Licania kunthiana* and *Calycorectes* sp.1. (27.5), *Dendropanax trilobium* and *Meriania robusta* (22.5), *Vochysia saldanhae* (20) and *Clethra scabra* (17.5). These results again show *E. edulis* as the most characteristic species in the forest.

Table 5.3 Phytosociology of the Macaé de Cima forest (frequency by subplot)

	Species	N.trees	N.subplot	AbDen	ReDen	AbFreq	ReFreq	AbCov	ReCov	AvgCov	IVI	IVC
1	<i>Euterpe edulis</i>	72	21	180.0	16.18	52.5	6.12	1.876	4.33	0.010	26.63	20.51
2	Dead spp.	14	11	35.0	3.15	27.5	3.21	1.735	4.00	0.050	10.35	7.15
3	<i>Licania kunthiana</i>	11	8	27.5	2.47	20.0	2.33	1.168	2.69	0.043	7.50	5.17
4	<i>Ocotea indecora</i>	5	5	12.5	1.12	12.5	1.46	2.015	4.65	0.161	7.23	5.77
5	<i>Vochysia saldanhae</i>	8	6	20.0	1.80	15.0	1.75	1.495	3.45	0.075	6.99	5.25
6	<i>Calycorectes sp.1</i>	11	9	27.5	2.47	22.5	2.62	0.623	1.44	0.023	6.53	3.91
7	<i>Dendropanax trilobium</i>	9	8	22.5	2.02	20.0	2.33	0.916	2.11	0.041	6.47	4.13
8	<i>Kielmeyera insignis</i>	5	4	12.5	1.12	10.0	1.17	1.666	3.84	0.133	6.13	4.97
9	<i>Cryptocaria moschata</i>	6	5	15.0	1.35	12.5	1.46	1.333	3.07	0.089	5.88	4.42
10	<i>Meriania robusta</i>	9	8	22.5	2.02	20.0	2.33	0.430	0.99	0.019	5.35	3.01
11	<i>Clethra scabra</i>	7	5	17.5	1.57	12.5	1.46	0.900	2.07	0.051	5.11	3.65
12	<i>Matayba guianensis</i>	6	5	15.0	1.35	12.5	1.46	0.891	2.05	0.059	4.86	3.40
13	<i>Ocotea divaricata</i>	5	5	12.5	1.12	12.5	1.46	0.827	1.91	0.066	4.49	3.03
14	<i>Cupania sp.1</i>	6	5	15.0	1.35	12.5	1.46	0.653	1.50	0.044	4.31	2.85
15	<i>Sclerolobium rugosum</i>	5	4	12.5	1.12	10.0	1.17	0.869	2.00	0.070	4.29	3.13
16	<i>Marlierea suaveolens</i>	6	5	15.0	1.35	12.5	1.46	0.504	1.16	0.034	3.97	2.51
17	<i>Mollinedia gilgiana</i>	6	4	15.0	1.35	10.0	1.17	0.538	1.24	0.036	3.76	2.59
18	<i>Eugenia stictosepala</i>	6	6	15.0	1.35	15.0	1.75	0.242	0.56	0.016	3.66	1.91
19	<i>Ormosia sp.new</i>	4	4	10.0	0.90	10.0	1.17	0.685	1.58	0.069	3.65	2.48
20	<i>Cupania emarginata</i>	5	3	12.5	1.12	7.5	0.87	0.491	1.13	0.039	3.13	2.26
21	<i>Amaloua intermedia</i>	4	3	10.0	0.90	7.5	0.87	0.568	1.31	0.057	3.08	2.21
22	<i>Myrcia fallax</i>	4	4	10.0	0.90	10.0	1.17	0.436	1.01	0.044	3.07	1.90
23	<i>Ocotea aciphila</i>	6	4	15.0	1.35	10.0	1.17	0.228	0.53	0.015	3.04	1.87
24	<i>Myrcuegenia kleinii</i>	4	3	10.0	0.90	7.5	0.87	0.525	1.21	0.053	2.98	2.11
25	<i>Marlierea silvatica</i>	3	3	7.5	0.67	7.5	0.87	0.601	1.39	0.080	2.93	2.06
26	<i>Clusia sturdiana</i>	4	3	10.0	0.90	7.5	0.87	0.495	1.14	0.050	2.91	2.04
27	<i>Pseudopiptadenia schumaniana</i>	3	3	7.5	0.67	7.5	0.87	0.568	1.31	0.076	2.86	1.98
28	<i>Coccoloba sp.1</i>	3	2	7.5	0.67	5.0	0.58	0.652	1.50	0.087	2.76	2.18
29	<i>Guapira opposita</i>	1	1	2.5	0.22	2.5	0.29	0.963	2.22	0.385	2.74	2.45
30	<i>Alchornea triplinervia</i>	4	3	10.0	0.90	7.5	0.87	0.421	0.97	0.042	2.74	1.87
31	<i>Trichilia lepidota</i>	6	2	15.0	1.35	5.0	0.58	0.334	0.77	0.022	2.70	2.12
32	<i>Pouteria caimito</i>	2	2	5.0	0.45	5.0	0.58	0.721	1.66	0.144	2.70	2.11
33	<i>Brosimum sp.2</i>	3	3	7.5	0.67	7.5	0.87	0.433	1.00	0.058	2.55	1.67
34	<i>Eugenia sp.1</i>	4	4	10.0	0.90	10.0	1.17	0.205	0.47	0.021	2.54	1.37
35	<i>Clusia lanceolata</i>	3	2	7.5	0.67	5.0	0.58	0.554	1.28	0.074	2.53	1.95
36	<i>Cabralea cangerana</i>	4	4	10.0	0.90	10.0	1.17	0.186	0.43	0.019	2.49	1.33
37	<i>Calyptanthes lucida</i>	3	3	7.5	0.67	7.5	0.87	0.386	0.89	0.052	2.44	1.56
38	<i>Pimenta pseudocaryophyllus</i>	3	3	7.5	0.67	7.5	0.87	0.346	0.80	0.046	2.35	1.47
39	<i>Ocotea silvestris</i>	3	2	7.5	0.67	5.0	0.58	0.445	1.03	0.059	2.28	1.70
40	<i>Psychotria pubigera</i>	2	2	5.0	0.45	5.0	0.58	0.533	1.23	0.107	2.26	1.68
41	<i>Mollinedia salicifolia</i>	3	3	7.5	0.67	7.5	0.87	0.276	0.64	0.037	2.18	1.31
42	<i>Posoqueria acutifolia</i>	3	3	7.5	0.67	7.5	0.87	0.254	0.58	0.034	2.13	1.26
43	<i>Myrcuegenia sp.1</i>	3	3	7.5	0.67	7.5	0.87	0.248	0.57	0.033	2.12	1.25
44	<i>Duguetia salicifolia</i>	3	2	7.5	0.67	5.0	0.58	0.363	0.84	0.048	2.10	1.51
45	<i>Ilex paraguariensis</i>	3	3	7.5	0.67	7.5	0.87	0.181	0.42	0.024	1.97	1.09
46	<i>Vochysia sp.1</i>	2	2	5.0	0.45	5.0	0.58	0.399	0.92	0.080	1.95	1.37
47	<i>Prunus myrtilifolia</i>	3	3	7.5	0.67	7.5	0.87	0.154	0.35	0.021	1.90	1.03
48	<i>Eugenia curvatopetiolata</i>	3	3	7.5	0.67	7.5	0.87	0.123	0.28	0.016	1.83	0.96
49	<i>Myrocarpus frondosus</i>	2	2	5.0	0.45	5.0	0.58	0.316	0.73	0.063	1.76	1.18
50	<i>Myrciaria floribunda</i>	3	3	7.5	0.67	7.5	0.87	0.091	0.21	0.012	1.76	0.88
51	<i>Bathysa mendoncaei</i>	3	2	7.5	0.67	5.0	0.58	0.171	0.39	0.023	1.65	1.07
52	<i>Ficus sp.1</i>	2	2	5.0	0.45	5.0	0.58	0.252	0.58	0.050	1.61	1.03
53	<i>Eugenia sp.2</i>	1	1	2.5	0.22	2.5	0.29	0.468	1.08	0.187	1.60	1.30
54	<i>Maytenus alaternoides</i>	3	2	7.5	0.67	5.0	0.58	0.144	0.33	0.019	1.59	1.01
55	<i>Simarouba amara</i>	1	1	2.5	0.22	2.5	0.29	0.448	1.03	0.179	1.55	1.26
56	<i>Byrsonima myricifolia</i>	2	2	5.0	0.45	5.0	0.58	0.224	0.52	0.045	1.55	0.97
57	<i>Mouriri arborea</i>	2	2	5.0	0.45	5.0	0.58	0.215	0.50	0.043	1.53	0.95
58	<i>Lacistema pubescens</i>	4	1	10.0	0.90	2.5	0.29	0.129	0.30	0.013	1.49	1.20
59	<i>Miconia altissima</i>	2	2	5.0	0.45	5.0	0.58	0.181	0.42	0.036	1.45	0.87
60	<i>Syphoneugena glazioviana</i>	2	1	5.0	0.45	2.5	0.29	0.302	0.70	0.060	1.44	1.15
61	<i>Mollinedia glaziovii</i>	2	2	5.0	0.45	5.0	0.58	0.163	0.38	0.033	1.41	0.82
62	<i>Cecropia hololeuca</i>	2	2	5.0	0.45	5.0	0.58	0.159	0.37	0.032	1.40	0.82
63	<i>Vernonia discolor</i>	2	2	5.0	0.45	5.0	0.58	0.156	0.36	0.031	1.39	0.81

Table 5.3 Cont.

Species	N.trees	N.subplot	AbDen	ReDen	AbFreq	ReFreq	AbCov	ReCov	AvgCov	IVI	IVC
64 Aegiphila fluminensis	2	2	5.0	0.45	5.0	0.58	0.138	0.32	0.028	1.35	0.77
65 Drimys brasiliensis	2	2	5.0	0.45	5.0	0.58	0.138	0.32	0.028	1.35	0.77
66 Rollinia laurifolia	2	2	5.0	0.45	5.0	0.58	0.100	0.23	0.020	1.26	0.68
67 Cedrela odorata	2	2	5.0	0.45	5.0	0.58	0.074	0.17	0.015	1.20	0.62
68 Calyptranthes concina	1	1	2.5	0.22	2.5	0.29	0.291	0.67	0.117	1.19	0.90
69 Brosimum sp.1	2	2	5.0	0.45	5.0	0.58	0.062	0.14	0.012	1.18	0.59
70 Myrsine umbellata	2	1	5.0	0.45	2.5	0.29	0.184	0.43	0.037	1.17	0.87
71 Indet sp.1	1	1	2.5	0.22	2.5	0.29	0.254	0.59	0.102	1.10	0.81
72 Inga cylindrica	2	1	5.0	0.45	2.5	0.29	0.144	0.33	0.029	1.07	0.78
73 Pouteria durlandii	1	1	2.5	0.22	2.5	0.29	0.241	0.56	0.096	1.07	0.78
74 Euplassa hoehnei	1	1	2.5	0.22	2.5	0.29	0.236	0.55	0.095	1.06	0.77
75 Myrtaceae sp.5	2	1	5.0	0.45	2.5	0.29	0.117	0.27	0.023	1.01	0.72
76 Roupala sculpta	1	1	2.5	0.22	2.5	0.29	0.215	0.50	0.086	1.01	0.72
77 Croton sp.1	1	1	2.5	0.22	2.5	0.29	0.203	0.47	0.081	0.98	0.69
78 Weinmannia pauliniifolia	1	1	2.5	0.22	2.5	0.29	0.195	0.45	0.078	0.97	0.67
79 Micropholis crassipedicellata	2	1	5.0	0.45	2.5	0.29	0.090	0.21	0.018	0.95	0.66
80 Tovomita glazioviana	2	1	5.0	0.45	2.5	0.29	0.084	0.19	0.017	0.93	0.64
81 Huberia glazioviana	1	1	2.5	0.22	2.5	0.29	0.171	0.39	0.068	0.91	0.62
82 Tibouchina canescens	1	1	2.5	0.22	2.5	0.29	0.172	0.40	0.069	0.91	0.62
83 Mollinedia myriantha	1	1	2.5	0.22	2.5	0.29	0.165	0.38	0.066	0.90	0.60
84 Mollinedia heteranthera	2	1	5.0	0.45	2.5	0.29	0.066	0.15	0.013	0.89	0.60
85 Guateria pubens	2	1	5.0	0.45	2.5	0.29	0.054	0.12	0.011	0.87	0.57
86 Inga lancaefolia	1	1	2.5	0.22	2.5	0.29	0.144	0.33	0.058	0.85	0.56
87 Myrtaceae sp.12	1	1	2.5	0.22	2.5	0.29	0.140	0.32	0.056	0.84	0.55
88 Myrtaceae sp.9	1	1	2.5	0.22	2.5	0.29	0.137	0.32	0.055	0.83	0.54
89 Tapirira guianensis	1	1	2.5	0.22	2.5	0.29	0.131	0.30	0.052	0.82	0.53
90 Mollinedia schottiana	1	1	2.5	0.22	2.5	0.29	0.134	0.31	0.054	0.82	0.53
91 Indet sp.12	1	1	2.5	0.22	2.5	0.29	0.134	0.31	0.054	0.82	0.53
92 Indet sp.9	1	1	2.5	0.22	2.5	0.29	0.127	0.29	0.051	0.81	0.52
93 Lamanonia ternata	1	1	2.5	0.22	2.5	0.29	0.124	0.29	0.050	0.80	0.51
94 Zanthoxylom rhoifolium	1	1	2.5	0.22	2.5	0.29	0.121	0.28	0.048	0.80	0.50
95 Myrtaceae sp.10	1	1	2.5	0.22	2.5	0.29	0.121	0.28	0.048	0.80	0.50
96 Vochysia glazioviana	1	1	2.5	0.22	2.5	0.29	0.118	0.27	0.047	0.79	0.50
97 Inga sp.1	1	1	2.5	0.22	2.5	0.29	0.115	0.27	0.046	0.78	0.49
98 Tabebuia heptaphyla	1	1	2.5	0.22	2.5	0.29	0.112	0.26	0.045	0.77	0.48
99 Lauraceae sp.1	1	1	2.5	0.22	2.5	0.29	0.103	0.24	0.041	0.75	0.46
100 Dalbergia foliolosa	1	1	2.5	0.22	2.5	0.29	0.103	0.24	0.041	0.75	0.46
101 Siphoneugena sp.1	1	1	2.5	0.22	2.5	0.29	0.098	0.22	0.039	0.74	0.45
102 Couepia venosa	1	1	2.5	0.22	2.5	0.29	0.092	0.21	0.037	0.73	0.44
103 Cinnamomum glaziovii	1	1	2.5	0.22	2.5	0.29	0.095	0.22	0.038	0.73	0.44
104 Myrceugenia pilotantha	1	1	2.5	0.22	2.5	0.29	0.092	0.21	0.037	0.73	0.44
105 Indet sp.5	1	1	2.5	0.22	2.5	0.29	0.092	0.21	0.037	0.73	0.44
106 Ocotea sp.1	1	1	2.5	0.22	2.5	0.29	0.089	0.21	0.036	0.72	0.43
107 Myrcia rhabdoides	1	1	2.5	0.22	2.5	0.29	0.087	0.20	0.035	0.72	0.42
108 Symplocos corymboclados	1	1	2.5	0.22	2.5	0.29	0.087	0.20	0.035	0.72	0.42
109 Ocotea sp.2	1	1	2.5	0.22	2.5	0.29	0.082	0.19	0.033	0.70	0.41
110 Myrtaceae sp.1	1	1	2.5	0.22	2.5	0.29	0.079	0.18	0.032	0.70	0.41
111 Indet sp.11	1	1	2.5	0.22	2.5	0.29	0.082	0.19	0.033	0.70	0.41
112 Swartzia acutifolia	1	1	2.5	0.22	2.5	0.29	0.074	0.17	0.030	0.69	0.40
113 Myrtaceae sp.11	1	1	2.5	0.22	2.5	0.29	0.074	0.17	0.030	0.69	0.40
114 Myrtaceae sp.7	1	1	2.5	0.22	2.5	0.29	0.072	0.17	0.029	0.68	0.39
115 Sloanea lasiocoma	1	1	2.5	0.22	2.5	0.29	0.067	0.15	0.027	0.67	0.38
116 Macropeplus ligustrinus	1	1	2.5	0.22	2.5	0.29	0.065	0.15	0.026	0.67	0.38
117 Indet sp.6	1	1	2.5	0.22	2.5	0.29	0.065	0.15	0.026	0.67	0.37
118 Stephanopodium organense	1	1	2.5	0.22	2.5	0.29	0.062	0.14	0.025	0.66	0.37
119 Aspidosperma olivaceum	1	1	2.5	0.22	2.5	0.29	0.060	0.14	0.024	0.66	0.36
120 Ocotea pretiosa	1	1	2.5	0.22	2.5	0.29	0.058	0.13	0.023	0.65	0.36
121 Plinia trunciflora	1	1	2.5	0.22	2.5	0.29	0.058	0.13	0.023	0.65	0.36
122 Myrtaceae sp.3	1	1	2.5	0.22	2.5	0.29	0.058	0.13	0.023	0.65	0.36
123 Myrtaceae sp.6	1	1	2.5	0.22	2.5	0.29	0.058	0.13	0.023	0.65	0.36
124 Piptocarpha macropoda	1	1	2.5	0.22	2.5	0.29	0.056	0.13	0.022	0.65	0.35
125 Symplocos nitidifolia	1	1	2.5	0.22	2.5	0.29	0.056	0.13	0.022	0.65	0.35
126 Rheedea gardneriana	1	1	2.5	0.22	2.5	0.29	0.054	0.12	0.022	0.64	0.35

Table 5.3 Cont.

Species	N.trees	N.subplot	AbDen	ReDen	AbFreq	ReFreq	AbCov	ReCov	AvgCov	IVI	IVC
127 <i>Tovomitopsis saldanhae</i>	1	1	2.5	0.22	2.5	0.29	0.054	0.12	0.022	0.64	0.35
128 <i>Byrsonima laxiflora</i>	1	1	2.5	0.22	2.5	0.29	0.054	0.12	0.022	0.64	0.35
129 <i>Didimopanax anomalum</i>	1	1	2.5	0.22	2.5	0.29	0.052	0.12	0.021	0.64	0.34
130 Indet sp.10	1	1	2.5	0.22	2.5	0.29	0.052	0.12	0.021	0.64	0.34
131 Indet sp.14	1	1	2.5	0.22	2.5	0.29	0.052	0.12	0.021	0.64	0.34
132 <i>Ocotea glaziovii</i>	1	1	2.5	0.22	2.5	0.29	0.050	0.11	0.020	0.63	0.34
133 <i>Quiina glaziovii</i>	1	1	2.5	0.22	2.5	0.29	0.050	0.11	0.020	0.63	0.34
134 <i>Endlicheria paniculata</i>	1	1	2.5	0.22	2.5	0.29	0.046	0.11	0.018	0.62	0.33
135 <i>Inga barbata</i>	1	1	2.5	0.22	2.5	0.29	0.044	0.10	0.018	0.62	0.33
136 Indet sp.8	1	1	2.5	0.22	2.5	0.29	0.040	0.09	0.016	0.61	0.32
137 <i>Didimopanax angustissimum</i>	1	1	2.5	0.22	2.5	0.29	0.039	0.09	0.015	0.61	0.31
138 <i>Maytenus</i> sp.1	1	1	2.5	0.22	2.5	0.29	0.037	0.08	0.015	0.60	0.31
139 <i>Sorocea bonplandii</i>	1	1	2.5	0.22	2.5	0.29	0.037	0.08	0.015	0.60	0.31
140 Indet sp.17	1	1	2.5	0.22	2.5	0.29	0.035	0.08	0.014	0.60	0.31
141 <i>Ilex theezans</i>	1	1	2.5	0.22	2.5	0.29	0.033	0.08	0.013	0.59	0.30
142 <i>Byrsonima laevigata</i>	1	1	2.5	0.22	2.5	0.29	0.033	0.08	0.013	0.59	0.30
143 <i>Calyptanthes glazioviana</i>	1	1	2.5	0.22	2.5	0.29	0.032	0.07	0.013	0.59	0.30
144 <i>Psychotria sessilis</i>	1	1	2.5	0.22	2.5	0.29	0.032	0.07	0.013	0.59	0.30
145 Indet sp.20	1	1	2.5	0.22	2.5	0.29	0.033	0.08	0.013	0.59	0.30
146 <i>Terminalia januariensis</i>	1	1	2.5	0.22	2.5	0.29	0.030	0.07	0.012	0.59	0.29
147 <i>Beilschmiedia rigida</i>	1	1	2.5	0.22	2.5	0.29	0.030	0.07	0.012	0.59	0.29
148 <i>Eugenia cuprea</i>	1	1	2.5	0.22	2.5	0.29	0.030	0.07	0.012	0.59	0.29
149 <i>Persea cordata</i>	1	1	2.5	0.22	2.5	0.29	0.027	0.06	0.011	0.58	0.29
150 <i>Eugenia subavenia</i>	1	1	2.5	0.22	2.5	0.29	0.029	0.07	0.012	0.58	0.29
151 <i>Marlierea regeliana</i>	1	1	2.5	0.22	2.5	0.29	0.027	0.06	0.011	0.58	0.29
152 Myrtaceae sp.2	1	1	2.5	0.22	2.5	0.29	0.029	0.07	0.012	0.58	0.29
153 <i>Alibertia</i> sp.1	1	1	2.5	0.22	2.5	0.29	0.027	0.06	0.011	0.58	0.29
154 Indet sp.3	1	1	2.5	0.22	2.5	0.29	0.029	0.07	0.012	0.58	0.29
155 Indet sp.18	1	1	2.5	0.22	2.5	0.29	0.027	0.06	0.011	0.58	0.29
156 <i>Salacia grandifolia</i>	1	1	2.5	0.22	2.5	0.29	0.026	0.06	0.010	0.58	0.28
157 <i>Rudgea comiculata</i>	1	1	2.5	0.22	2.5	0.29	0.026	0.06	0.010	0.58	0.28
158 Indet sp.2	1	1	2.5	0.22	2.5	0.29	0.026	0.06	0.010	0.58	0.28
159 <i>Miconia jucunda</i>	1	1	2.5	0.22	2.5	0.29	0.024	0.06	0.010	0.57	0.28
160 Indet sp.7	1	1	2.5	0.22	2.5	0.29	0.023	0.05	0.009	0.57	0.28
161 Myrtaceae sp.13	1	1	2.5	0.22	2.5	0.29	0.024	0.06	0.010	0.57	0.28
162 <i>Miconia budlejoides</i>	1	1	2.5	0.22	2.5	0.29	0.020	0.05	0.008	0.56	0.27
163 Indet sp.4	1	1	2.5	0.22	2.5	0.29	0.020	0.05	0.008	0.56	0.27
164 Indet sp.13	1	1	2.5	0.22	2.5	0.29	0.020	0.05	0.008	0.56	0.27
165 Indet sp.13	1	1	2.5	0.22	2.5	0.29	0.020	0.05	0.008	0.56	0.27
Total	445	2.08	6.7	99.5	5.2	99.7	0.263	99.99	0.042	300	200

Cover values are especially influenced by the size a species can reach. Therefore, a different sequence of relative cover (ReCov) values was expected. Again *E. edulis* appears in first place, followed by *O. indecora*, dead trees, *K. insignis*, *V. saldanhae*, *C. moschata*, *L. kunthiana*, *Guapira opposita*, *D. trilobium* and *C. scabra*. The inclusion among the ten highest cover values of *G. opposita*, with only one tree, highlights the importance of plant size in this estimate. High cover and low density values suggest the use by the species of a niche occupation strategy that emphasises a few large individuals spread over the landscape, instead of a high

number of individuals with small size, or evenly distributed among several size classes.

Relative frequency (ReFreq) values, one of the components of IVI, are highly influenced by both plot size and location (Greig-Smith, 1983). In order to investigate the influence of plot size, frequency was also estimated at plot level (Table 5.4). The result suggests different spatial patterns, according to the use of either 100 m² or 400 m² plots. The ten elements with highest IVI were, in a decreasing order, *E. edulis*, *L. kunthiana*, dead trees, *D. trilobium*, *V. saldanhae*, *C. moschata*, *K. insignis*, *Calycorectes* sp.1, *M.robusta* and *C. scabra*. Elements with the highest relative frequency at plot level are *Euterpe edulis* and dead trees, followed by *Licania kunthiana*, *Calycorectes* sp.1, *Ocotea divaricata*, *Meriania robusta*, *Cryptocarya moschata*, *Eugenia stictosepala*, *Myrciaria floribunda*, *Ocotea indecora*, *Cabralea cangerana*, and *Vochysia saldanhae*. The sequence of decreasing relative frequency values at sub-plot level is *E. edulis*, *D. trilobium*, *L. kunthiana*, *Calycorectes* sp.1, *Meriania robusta*, dead trees, *E. stictosepala*, *C. moschata*, *V. saldanhae*, *Clethra scabra*, *Matayba guianensis*, *Cupania emarginata*, *Cupania* sp.1 and *Marlierea suaveolens*. The occurrence of species with a higher IVI in Table 5.3, compared to Table 5.4, suggest a tendency towards a more clustered spatial distribution (Greig-Smith, 1983).

In order to minimise or simply avoid the effect of plot size and location on frequency, and therefore IVI values, the Importance Cover Value (IVC) could be adopted, instead of IVI, as an index of the species importance within the forest community structure. The ten species with highest IVC were, in decreasing order, *E. edulis*, dead trees, *L. kunthiana*, *K. insignis*, *V. saldanhae*, *C. moschata*, *D. trilobium*, *C. scabra*, *Calycorectes* sp.1 and *M. guianensis*. Although the order of importance is slightly different than for the IVI, the similarity between the two columns suggests that frequency had a smaller role on the importance of the species in terms of forest structure as a whole than both cover and density.

Table 5.4. Phytosociology (frequency by plot)

SpN	Botanical Name	Dens	RelD	Cover	RelC	Freq	RelF	IVI
1	<i>Euterpe edulis</i>	72	16.2	0.750	4.4	0.525	6.2	26.82
2	<i>Licania kunthiana</i>	11	2.5	0.467	2.8	0.200	2.4	7.60
3	Dead	14	3.1	0.694	4.1	0.028	0.3	7.58
4	<i>Dendropanax trilobium</i>	9	2.0	0.366	2.2	0.200	2.4	6.55
5	<i>Vochysia saldanhae</i>	7	1.6	0.577	3.4	0.125	1.5	6.47
6	<i>Cryptocarya moschata</i>	7	1.6	0.541	3.2	0.125	1.5	6.25
7	<i>Kielmeyera insignis</i>	5	1.1	0.666	3.9	0.100	1.2	6.25
8	<i>Calycorectes</i> sp.1	10	2.2	0.235	1.4	0.200	2.4	6.00
9	<i>Meriania robusta</i>	9	2.0	0.172	1.0	0.200	2.4	5.40
10	<i>Clethra scabra</i>	7	1.6	0.360	2.1	0.125	1.5	5.18
11	<i>Matayba guianensis</i>	6	1.3	0.356	2.1	0.125	1.5	4.93
12	<i>Ocotea divaricata</i>	5	1.1	0.331	2.0	0.125	1.5	4.56
13	<i>Sclerolobium rugosum</i>	5	1.1	0.347	2.1	0.100	1.2	4.36
14	<i>Cupania</i> sp.1	6	1.3	0.239	1.4	0.125	1.5	4.24
15	<i>Marlierea suaveolens</i>	6	1.3	0.199	1.2	0.125	1.5	4.00
16	<i>Mollinedia gilgiana</i>	6	1.3	0.215	1.3	0.100	1.2	3.80
17	<i>Cupania emarginata</i>	5	1.1	0.196	1.2	0.125	1.5	3.76
18	<i>Ormosia</i> sp. nov.	4	0.9	0.274	1.6	0.100	1.2	3.70
19	<i>Eugenia stictosepala</i>	6	1.3	0.097	0.6	0.150	1.8	3.69
20	<i>Rollinia laurifolia</i>	2	0.4	0.400	2.4	0.050	0.6	3.41
21	<i>Myrcia fallax</i>	4	0.9	0.174	1.0	0.100	1.2	3.11
22	<i>Pimenta pseudocaryophyllus</i>	4	0.9	0.151	0.9	0.100	1.2	2.97
23	<i>Amaioua intermedia</i>	4	0.9	0.200	1.2	0.075	0.9	2.97
24	<i>Clusia sturdantiana</i>	4	0.9	0.198	1.2	0.075	0.9	2.96
25	<i>Pseudoptadenia schumanniana</i>	3	0.7	0.227	1.3	0.075	0.9	2.90
26	<i>Coccoloba</i> sp.1	3	0.7	0.261	1.5	0.050	0.6	2.81
27	<i>Guapira opposita</i>	1	0.2	0.385	2.3	0.025	0.3	2.78
28	<i>Pouteria caimito</i>	2	0.4	0.288	1.7	0.050	0.6	2.75
29	<i>Myrceugenia kleinii</i>	3	0.7	0.198	1.2	0.075	0.9	2.73
30	<i>Trichilia lipidota</i>	6	1.3	0.133	0.8	0.050	0.6	2.73
31	<i>Alchornea triplinervia</i>	4	0.9	0.156	0.9	0.075	0.9	2.71
32	<i>Clusia lanceolata</i>	3	0.7	0.221	1.3	0.050	0.6	2.57
33	<i>Myrciaria floribunda</i>	4	0.9	0.081	0.5	0.100	1.2	2.56
34	<i>Cabralea cangerana</i>	4	0.9	0.075	0.4	0.100	1.2	2.52
35	<i>Calypttranthes lucida</i>	3	0.7	0.154	0.9	0.075	0.9	2.47
36	<i>Psychotria pubigera</i>	2	0.4	0.213	1.3	0.050	0.6	2.30
37	<i>Mollinedia salicifolia</i>	3	0.7	0.111	0.7	0.075	0.9	2.21
38	<i>Ocotea aciphylla</i>	4	0.9	0.069	0.4	0.075	0.9	2.19
39	<i>Posoqueria acutifolia</i>	3	0.7	0.101	0.6	0.075	0.9	2.16
40	<i>Myrceugenia</i> sp.1	3	0.7	0.099	0.6	0.075	0.9	2.15
41	<i>Duguetia salicifolia</i>	3	0.7	0.145	0.9	0.050	0.6	2.12
42	<i>Marlierea sylvatica</i>	2	0.4	0.182	1.1	0.050	0.6	2.12
43	<i>Vochysia</i> sp.1	2	0.4	0.160	0.9	0.050	0.6	1.99
44	<i>Eugenia</i> sp.1	3	0.7	0.072	0.4	0.075	0.9	1.99
45	<i>Ilex paraguariensis</i>	3	0.7	0.072	0.4	0.075	0.9	1.99
46	<i>Prunus myrtifolia</i>	3	0.7	0.062	0.4	0.075	0.9	1.93
47	<i>Eugenia curvatopeciolata</i>	3	0.7	0.049	0.3	0.075	0.9	1.85
48	<i>Myrocarpus frondosus</i>	2	0.4	0.126	0.7	0.050	0.6	1.79
49	<i>Brosimum</i> sp.1	3	0.7	0.036	0.2	0.075	0.9	1.77
50	<i>Bathysa mendoncaei</i>	3	0.7	0.068	0.4	0.050	0.6	1.67

5.6. Classification

In many cases it is difficult to establish whether the forest is primary or secondary on the basis of physiognomy alone. Due to the long period of time since the first European settlers had established in the region (Nicoulin 1996), areas that

show characteristics of a true primary forest may have been submitted to some degree of exploitation a few decades ago. The large number of trails that cut the reserve, as well as signs of extraction of timber or palm hearts even in some of the most inaccessible areas, are signs that only few, if any, areas can be considered as truly undisturbed primary forest. However, due to the dynamic nature of the tropical forest, after a few years it is hard to distinguish any sign of human disturbance in most areas.

The existence of clear boundaries between the montane and high montane formations is also difficult to establish. Even when it is possible to distinguish differences in physiognomy, both in the field and in aerial photographs, it is difficult to assert whether such differences correspond to real changes in the forest community structure. One way to test whether it is possible to identify, characterise and map the boundaries between the different forest types is by analysing floristic data from forest plots established at different locations, searching for both similarities and discontinuities in the data. The analysis of these data can help to demonstrate whether it is possible to identify discrete boundaries between different forest communities within the montane formation, between the montane and high montane formations, or between primary and old-secondary forests.

The results of the TWINSPLAN classification (Hill, 1979a), based on species abundance data (see Section 4.2.4) are shown on Figure 5.4. The first division (eigenvalue 0.88) revealed two distinct groups, with plots 1, 7, 9 and 10 in one group, and plots 2, 3, 4, 5, 6 and 8 in the other. A second division (eigenvalue 0.76) further divides the first group, with the plots 1 and 7 separated from the plots 9 and 10. On the other side, plot 8 is segregated from the other plots. A third division of the right-hand group separates plots 5 and 6 from plots 2, 3, and 4, while a final division further segregates plot 2 from plots 3 and 4.

The results from the classification appear to demonstrate the occurrence of at least two distinct types of forest communities. The first group is represented by plots 1, 7, 9, and 10. They all have in common location in the middle or the upper parts of the slopes and, apart from plot 7, location above 1300m. Another common feature is the absence of *Euterpe edulis*, the species with highest IVI in the overall analysis.

The second group, represented by the remaining forest plots, is more heterogeneous. However, the classification divisions can give us some clues. Plot 8, segregated from the others in the second division, was located in an area with visible signals of past disturbances, with fewer epiphytes, higher light penetration, and occurrence of known primary or early secondary species, such as *Cecropia hololeuca* and *Alchornea triplinervia*. This forest is called a *capoeira* by locals, a name used in most of Brazil to indicate secondary forests in general. In contrast, although there were signals of some degree of disturbance in some of the other plots, particularly 3 and 5, they still maintain the overall physiognomy of primary forest.

The next division segregates the plots located in a flat alluvial terrace (5) and valley bottom (6) from those located on middle slopes (2, 3, and 4). This suggests a differentiation between riverine/bottom valley forests and slope forests, probably related to a number of factors such as soil drainage, nutrient levels, depth and texture, or even light availability (considerably lower on narrow valley bottoms, compared to the slopes).

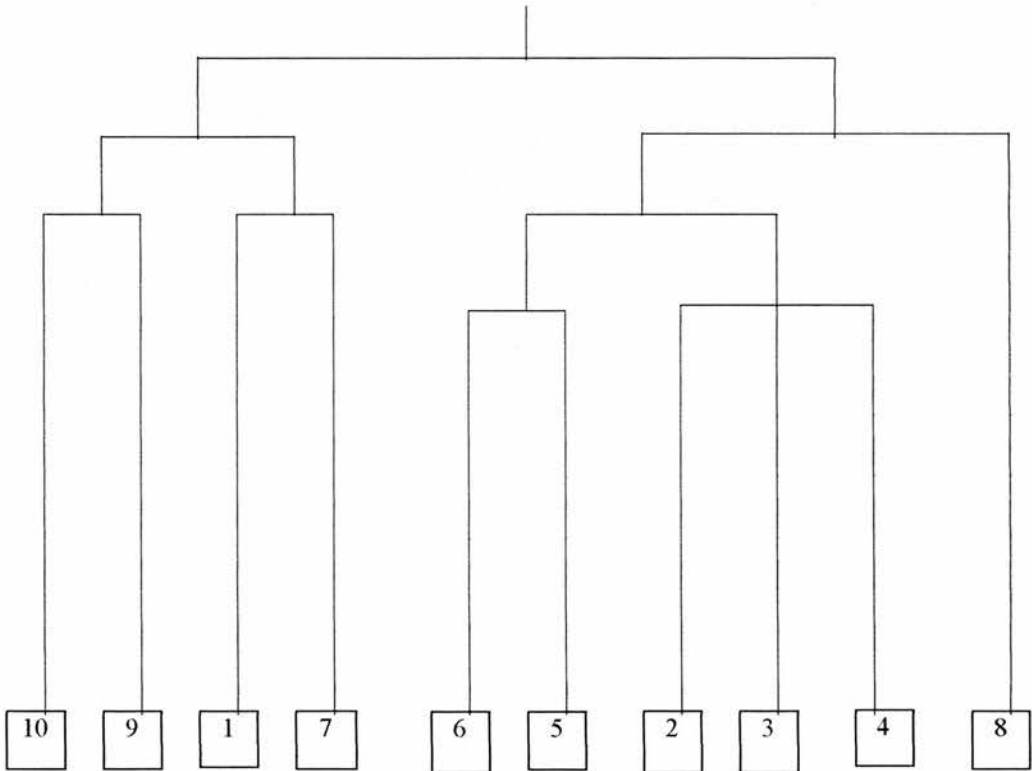


Figure 5.4 Dendrogram of the TWINSpan classification of forest plots, based on species abundance, showing the first division into two main groups.

The result of TWINSpan classification seems to support the occurrence of at least two or even three discrete community types of forest. They suggest also that the forest structure may be controlled by a gradient of environmental factors, related to the altitude and relief.

5.7. Indirect Ordination

The results of the Detrended Correspondence Analysis (DCA), performed by the program DECORANA (Hill, 1979b) are shown in the Figure 5.5. Figure 5.5a shows the position of the plots along the first two ordination axes. As expected, the results show some resemblance to the results of TWINSpan classification, which is achieved firstly by an ordination of the plots. The species loading values on this ordination is then used to further divide the stands. Therefore, the sequence of the stands along the first axis of DCA ordination must be similar to TWINSpan.

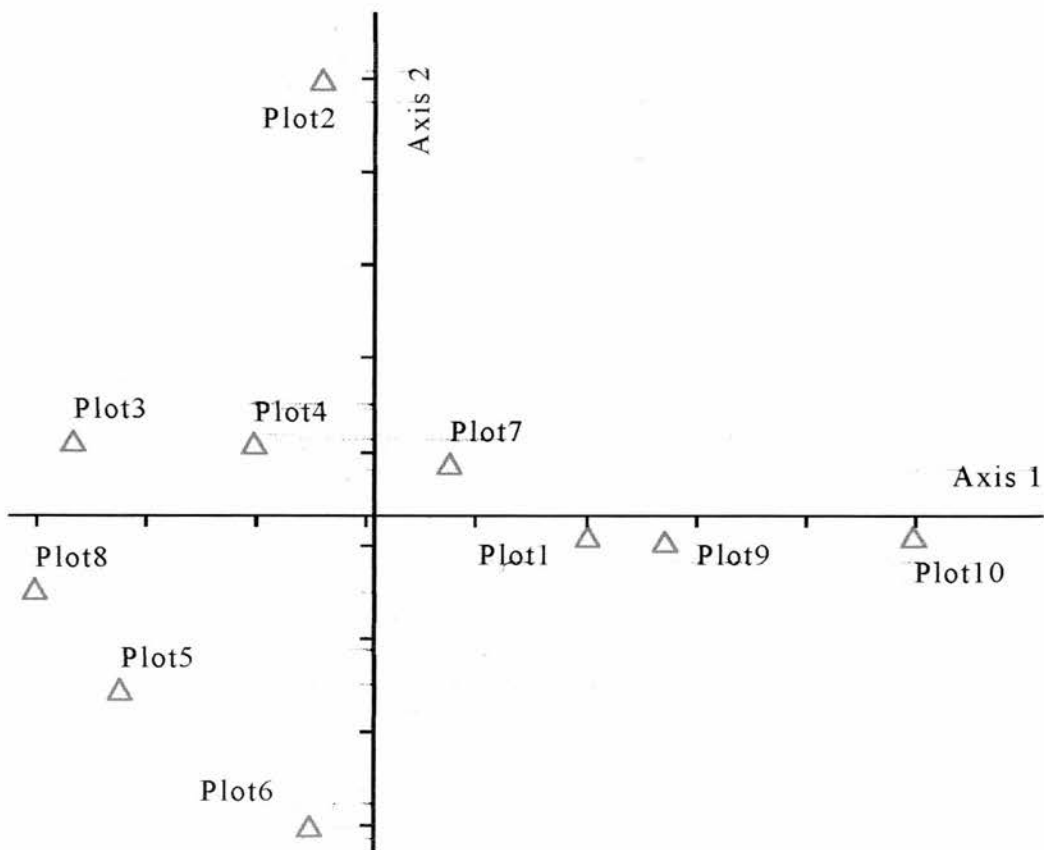


Figure 5.5a DCA ordination, axes 1 x 2, showing two main clusters (plots 1, 7, 9, 10 on the right, the remaining plots on the left-hand side) along the first axis.

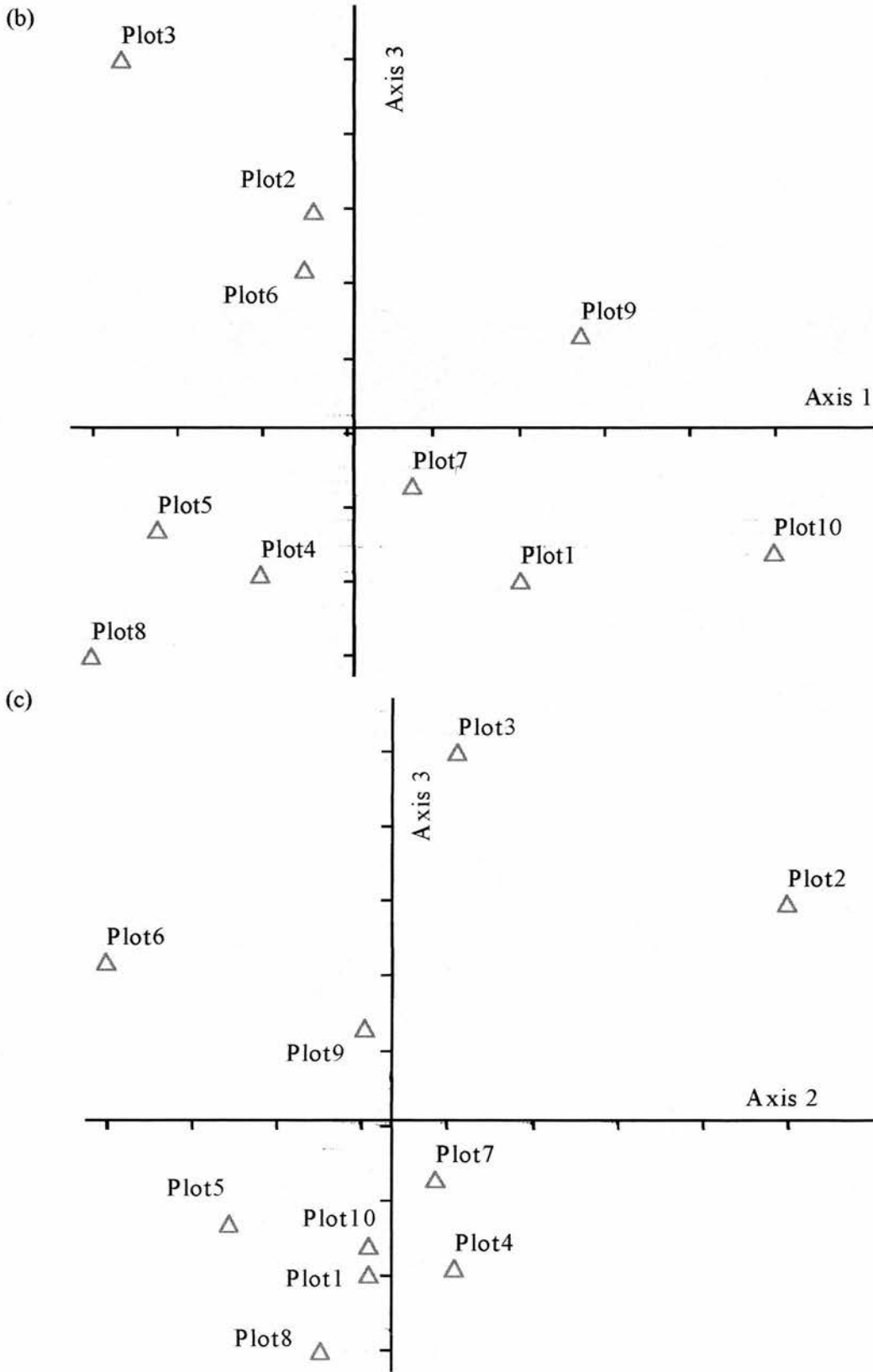


Figure 5.5bc DCA ordination of forest plots, (b) axis 1x3, and (c) axis 2x3, showing further divisions of the two main clusters along axes 2 and 3, that might be related to soil properties and moisture.

The first axis apparently refers to an altitudinal gradient, with the higher altitude plots grouped in one extreme. The eigenvalue accounted for by the first axis (0.75) refers to the amount of variability that could be explained by this axis. The other plots, although located at the other end of the first axis, show a much more scattered pattern, linked to their position on the second axis.

The interpretation of the second axis is much more difficult. It would appear to relate to a gradient associated with soil characteristics, either moisture, texture or chemical properties. The position of the plots along the axes 2 and 3 (eigenvalues 0.42 and 0.13 respectively) suggests gradients related to the location on the relief and soil characteristics. Axis 2 appears to be related to a moisture gradient, with both lower slope and high altitude plots located in one side of the diagram, opposed to the mid-slope, lower altitude plots, possibly on well drained soils. Axis 3 could be related to both physical and chemical properties of soils. To investigate whether these as well as other environmental factors influence the forest composition, an alternative technique, the direct gradient analysis, can be applied.

With the exception of plot 8, which has clear characteristics of secondary forest, and plots 5 and 6, where the influence of drainage is more evident, the plots could not be distinguished solely on their physiognomy. However, the results from both TWINSpan classification and DCA ordination do suggest the existence of discontinuities in the data or groupings of plots.

Considering the results of DCA and TWINSpan, combined with the location of the plots along the relief, the forest plots can be classified into four groups. The first group is clearly related to the montane forest formation, represented by plots 2, 3 and 4. Plots 5 and 6 also belong to this formation, but represent a more specialised habitat (riverine forest), characterised by the influence of soil drainage. Plot 8 also belongs to the montane formation, but shows a strong influence of human disturbance. The remaining plots correspond to a transition (plot 7) between the montane and the high montane forest formation (plot 1, 9 and 10) of the IBGE classification system, or the Atlantic top-slope forests, according to Leitão-Filho (1993) and Mantovani *et al* (1993). Plot 10 particularly was established near a considerable area of low forest along the mountain ridge (see Plate 5.1 and Figures

4.3 and 8.1). The physiognomy of this area clearly corresponds the concept of high montane or cloud forests (Veloso *et al*, 1991, Webster, 1995).

Summary

The montane forest, characterised by an evergreen dense, closed canopy is the dominant vegetation type of the Macaé de Cima Reserve. The high montane forest, which is characterised by smaller trees and high abundance of epiphytes, occurs on the top portion of the mountain slopes. Changes in the forest physiognomy appear to correspond with an increase in the organic matter content of the soils and decrease in soil depth. Secondary forests occur mainly on medium and lower slopes, on the central and northern parts of the reserve.

As a whole, the forest has an average density of 1112 trees/ha, with an average basal area of 43 m²/ha, an average total height of 14m, and an average volume of 171.3 m³/ha. The size distribution histogram suggests a well-balanced forest structure, with an advanced level of natural regeneration.

A total of 445 trees were measured in the 10 sampling plots, representing a total of 164 species. Myrtaceae had the greatest number of species, followed by Lauraceae, Leguminosae, Melastomataceae, Monimiaceae, Rubiaceae, Clusiaceae, Moraceae and Sapindaceae. The ten most important species were, in decreasing order, *Euterpe edulis*, dead trees, *Licania kunthiana*, *Vochysia saldanhae*, *Cryptocarya moschata*, *Kielmeyera insignis*, *Calycorectes* sp.1, *Dendropanax trilobium*, *Ocotea divaricata*, and *Matayba guianensis*. The palm *E. edulis* has the highest density, with a total of 72 individuals, equivalent to 180 trees/ha.

The TWINSpan classification revealed the occurrence of at least two discrete community types of forest. The DCA ordination confirmed the existence of a strong gradient along the first axis related mainly to altitude. The second axis appears to be related to a moisture gradient, and the third to soil properties. Considering the results of both analyses, the forest plots can be tentatively classified into four groups, related to riverine forest (1), old secondary (2) and primary (3) forest, all three within the montane forest formation. The last group represents the high montane forest formation (4), and also includes the montane-high montane transition (ecotone). With the exception of the second, these forest types can be considered as

representative of the relatively undisturbed SE Brazil Atlantic (upper) montane rainforests in general, characterised by very steep relief, varied catenary sequences and closed forest vegetation. The relationships between the structure and composition of the forest and the physical environment will be examined in more detail in the next chapter.

CHAPTER 6. Forest-Physical Environment Relationships

6.1. Introduction

In this chapter, the patterns of relationship between variations in the forest structure and aspects of the physical environment will be investigated through multivariate analysis techniques. Ordination techniques will be used to identify the relationships between several environmental variables, and how they are related to the forest heterogeneity. The main objective is to determine to what extent these variables influence the structure and floristic composition of the forest at the local scale.

6.2. Environmental Parameters

Soils

In order to investigate whether there is a direct relationship between the structure and composition of the forest and aspects of the physical environment, the first step is to select what seem to be the most relevant parameters, as judged from previous evidence. The objective is to investigate whether there is any correlation between different environmental parameters in order to avoid unnecessary analytical work and possible auto-correlation that could mask patterns of relationships between the vegetation and the physical environment.

Soils are one of the primary factors that affect which plant species grow in a particular location (Richards 1996; Whitmore, 1998). Despite the advances in the study of processes and interactions between tropical soils and forests (Jordan, 1985; Medina & Cuevas, 1994; Sollins *et al.*, 1994; Parker, 1994), the relationships between soil parameters and the structure and composition of the Atlantic forest are still poorly understood (Leitão-Filho, 1993; Rodrigues & Shepherd, 1992). In order to investigate the patterns of relationship between the soil characteristics of specific sites and forest structure and composition, soil samples were collected in all natural forest plots (plots 1-10). Soil samples were also taken in the plots located in a *Eucalyptus* plantation, on the Reserve's border (plots EI and EII).

The parameters estimated in the soil analyses were pH in water, levels of aluminium (Al), calcium plus magnesium (Ca+Mg), aluminium plus hydrogen (Al+H), sodium (Na), potassium (K), phosphorus (P), cation exchange capacity (CEC), percentage of carbon (%C), and size particle classes (clay, silt, fine sand and sand). The results of the soil analyses are shown in Table 6.1. The methods of soil analysis are presented in the Appendix 1.

Table 6.1 Mean levels for soil parameters of the field plots. Chemical parameters are cmol/kg (P in ppm). C and particle size class values are percentages.

Plot*	pH	Al	Ca+Mg	H + Al	Na	K	CEC	P	% C	Sand	Fine Sand	Silt	Clay
2	3.6	1.6	0.6	13.5	0.08	0.22	14.40	3	3.90	21	7	48	24
3	3.6	2.1	0.5	10.9	0.05	0.24	11.69	2	2.81	42	12	24	22
4	3.9	1.5	0.3	8.4	0.06	0.16	8.92	2	2.47	46	15	23	16
5	3.9	1.6	0.3	11.4	0.08	0.16	11.94	2	3.72	50	1	27	22
6	3.9	1.8	0.4	13.5	0.04	0.17	12.24	2	3.13	72	10	12	6
7	3.7	1.8	0.4	12.6	0.02	0.18	13.19	3	3.21	38	15	28	20
8	3.7	4.1	0.5	12.9	0.04	0.22	13.64	5	3.38	40	12	22	26
9	4.0	1.9	0.5	13.5	0.03	0.24	14.28	2	3.80	47	12	25	16
10	3.8	1.7	0.6	14.7	0.04	0.19	15.52	4	4.07	55	13	18	14
E1	4.0	2.5	0.3	15.7	0.08	0.32	16.40	8	4.48	40	11	23	26
E2	3.7	2.0	0.3	11.2	0.04	0.24	11.78	4	2.83	50	9	19	22
Avg	3.8	2.0	0.4	12.0	0.05	0.21	12.66	3.3	3.34	44.8	10.9	24.8	19.5
STDEV	0.14	0.75	0.12	2.6	0.020	0.046	2.69	1.8	0.68	12.2	3.9	9.6	7.1
VAR	0.02	0.57	0.01	6.8	0.0004	0.002	7.22	3.3	0.47	148.3	15.3	92.9	51.0

* Due to the lack of sufficient material for analysis there are no soil data for plot 1

The mean results of the soil analyses revealed a common pattern of low pH, with a narrow range varying from 3.6 to 4.0, characteristic of very acid soils. The soils also had low to medium levels of aluminium, varying from 1.6-4.1 cmol/kg. The levels of Ca+Mg were within the 0.3-0.6 cmol/kg range. Levels of K are within the 16-32 cmol/kg range, while P values vary from 2-8 ppm. CEC values were in the 8.9-16.4 range, and were mostly influenced by levels of H + Al. Considering all samples, the higher values of K, P, CEC (mostly H+Al) and C% were found in plot EI. Its pH (4.0) was also the highest, together with plot 9. The occurrence on plot EI of signs of a recent fire, which could have released mineral elements from the soil litter, is a possible explanation for this result. The data as a whole show a common pattern of high acidity and low fertility, which is often the case for soils originating from highly weathered crystalline rocks in areas with high rainfall (i.e., dystrophic soils).

The percentage of carbon varied from 2.5-4.5%, with an average value of 3.3%. Considering only the natural forest samples, the maximum value of C was 4.1%. In terms of organic matter, the content varied from 4.3-7.72 %, with an average of 5.92 %. These are relatively high values, which possibly suggest a strong influence of nutrient recycling by the forest on the local soils and a low decomposition rate (low temperatures + high moisture content).

Turning to soil texture, the clay content varied from 6-26%. The silt percentage range was higher, varying from 12-48%. Sand particles were separated into two classes, with the fine sand range (0.02-0.06 mm) varying from 1-15%, and (coarse) sand (0.02-2.00 mm), varying from 21-72%. If combined into a single class, the proportion of sand varied from 28 to 82%, figure that characterise most soils as sandy.

Other Environmental and Geographical Parameters

A summary of environmental, geographical and forest structural data for all the sampling plots is shown on Table 6.2. The ten plots located in natural forest covered all the Reserve's three sub-basins: Macaé (2 plots), Flores (4) and Bonito (4) rivers. The slopes varied from 10-45 degrees, characterising a very steep relief. Altitude varied between 950-1520m asl., covering most of the altitudinal range of the Reserve. Most plots faced northwards, while only three plots faced the south. The position of the plots covered a gradient from terrace to low, middle and the top parts of the slope.

6.3. Analysis of Environmental Parameters

Both geographical and environmental parameters, including soil properties, were analysed by Principal Components Analysis (PCA), in order to investigate possible correlations between the variables (Greig-Smith, 1983). As well as correlating variable parameters, PCA also identifies which parameters carry the most relevant information, i.e., are responsible for a largest part of any environmental heterogeneity. These parameters can be then used as environmental variables in the direct gradient analysis to investigate possible relationships with forest structure.

Table 6.2 Summary of environmental parameters of the field plots in the Macaé de Cima Reserve. Forest structural data (basal area/ha, average height, canopy height, number of species and number of trees) extracted from Table 5.1.

Environment Parameters	Natural Forest Plots										Eucalyptus Plots	
	1*	2	3	4	5	6	7	8	9	10	EI	EII
Basin	Flores	Bonito	Bonito	Bonito	Bonito	Flores	Flores	Macaé	Flores	Macaé	Macaé	Macaé
Altitude	1300	1040	1020	950	1150	1020	1150	1080	1200	1520	1130	1100
Relief Pos.	MidTop	MidTop	Mid	MidLow	Terrace	TerrLow	MidTop	Mid	Mid	MidTop	Mid	Mid
Exposure	S	NW	W	S	SE	NW	NE	NW	NE	NW	NW	N
Slope	30	30	20	40	10	10	30	20	40	20	30	45
Avg. Height	14.50	13.59	12.05	13.69	13.03	13.98	15.38	13.64	14.88	15.47	18.73	15.72
Canopy	4.18	3.98	2.81	4.28	3.88	4.04	5.31	3.95	5.13	5.03	5.60	4.28
BA/ha	48.6	50.8	41.5	40.0	39.1	33.6	57.2	44.1	36.7	38.4	56.8	42.2
N. Sp.	31	22	20	24	27	30	28	24	29	23	1	1
N. trees	45	28	43	41	49	41	51	62	54	30	15	18
pH	-	3.6	3.6	3.9	3.9	3.7	3.7	3.7	4.0	3.8	4.0	3.7
Al	-	1.6	2.1	1.5	1.6	1.8	1.8	4.1	1.9	1.7	2.5	2.0
Ca+Mg	-	0.6	0.5	0.3	0.3	0.4	0.4	0.5	0.5	0.6	0.3	0.3
H+Al	-	13.5	10.9	8.4	11.4	13.5	13.5	12.9	13.5	14.7	15.7	11.2
Na	-	0.078	0.052	0.061	0.078	0.039	0.070	0.022	0.039	0.030	0.078	0.039
K	-	0.220	0.240	0.159	0.159	0.159	0.179	0.220	0.240	0.189	0.320	0.240
P	-	3	2	2	2	2	4	5	2	4	8	4
CEC	-	11.4	11.69	8.92	11.94	12.24	14.15	13.64	14.28	15.52	16.4	11.78
C%	-	3.9	2.81	2.47	3.72	3.13	3.28	3.38	3.8	4.07	4.48	2.83
Sand	-	21	42	46	50	72	38	40	47	55	40	50
FineSand	-	7	12	15	1	10	14	12	12	13	11	9
Silt	-	48	24	23	27	12	28	22	25	18	23	19
Clay	-	24	22	16	22	6	20	26	16	14	26	22

* Soil data for plot 1 are not available

PCA Analysis of Soil Data

A PCA factorial analysis was performed first with the soil data (chemical and physical parameters), including those of the *Eucalyptus* plots. The correlation matrix produced in the analysis is shown in Table 6.3. The factor plot diagram is shown in Fig. 6.1. The first two axes were responsible for 56.2 % and 30.8% (87 % in total) respectively of the total variance.

Both plot and correlation matrix reveal the existence of a high correlation between % C and levels of CEC and H+Al ($r^2=0.91$). Good correlation was also found between P and K (0.70), H+Al (0.64), and consequently CEC (0.63). The PCA ordination revealed that Al^{++} levels can explain a large part (39.5%) of the environmental variation within the soils, with an eigenvalue of 5.13. Next comes C, with 18% of the variance, and an eigenvalue of 2.34, Ca+Mg (13.9%, eigenvalue 1.81), CEC (9.8%, eigenvalue 1.27), clay (7.3%, eigenvalue 0.95), fine sand (4.1%,

eigenvalue 0.53) and H+Al (3.4%, eigenvalue 0.44). These parameters in combination explain 96.1 % of the total variance within the soils. This means that all the other parameters combined were responsible for just 3.9% of the total variance, i.e., they add little information to any analysis of correlation between the local soils and the forest vegetation.

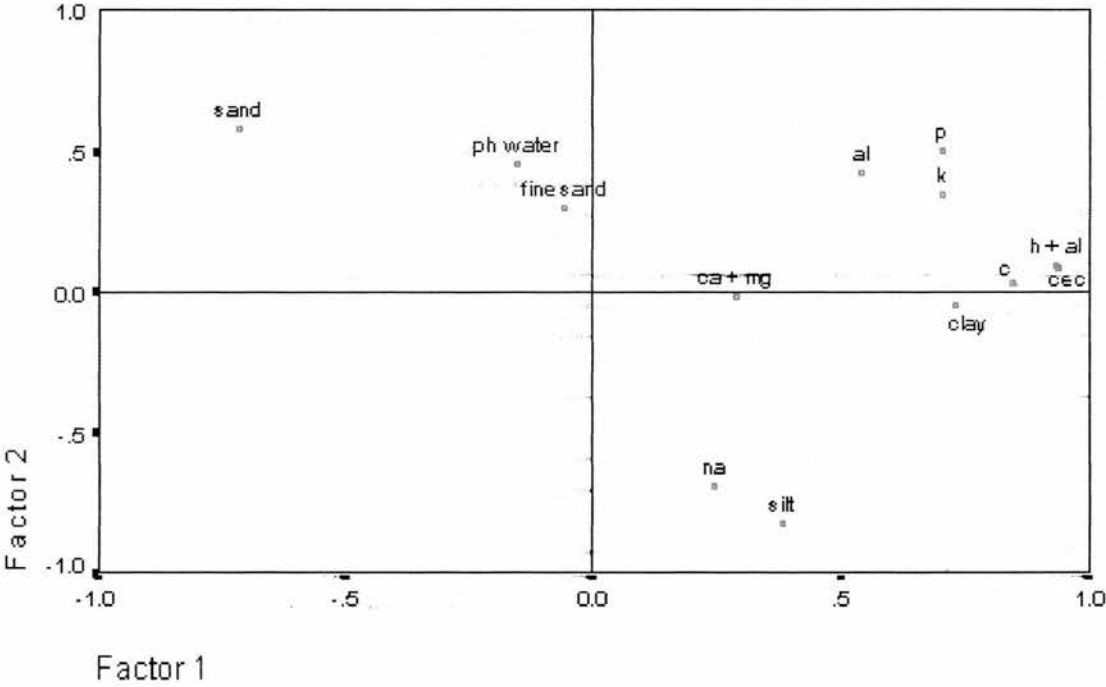


Figure 6.1 PCA factor plot, axes 1x2. Chemical parameters show greater variation along the first axis, while the size classes vary mainly along axis 2.

A second PCA analysis was carried out to investigate how far the sampling sites are representative of the local soil variability, as well as their relationship to the soil mapping units (see Table 3.2). The dataset (see Appendix 3 and 4) included data from soil profiles (EMBRAPA, 1992; Radambrasil, 1983) as well as from soil samples taken on the two PMA plots (Guedes-Bruni *et al.*, 1997; Pessoa *et al.*, 1997).

The first axis of PCA, with an eigenvalue of 0.76, accounted for 84.5% of the total variance. This means that the loadings of both sites and soil parameters along axis 1 can explain most of the relationships amongst the sites. An overview of the ordination diagrams of both sites (Fig. 6.2a) and soil parameters (Fig 6.2b) can help

to explain these relationships. The sites with a higher value along the first axis can be associated to higher values of Ca+Mg, K, Na, Al, pH, P and C. Plots 2 and Pma 1 can be associated to the Br2 profile. Plots 3, 4, 5 7 and 9 are closely related to profile Br1, while plots 8 and EI are closer to profile Br3. Plot EII is closer to Br1 in the first axis and in an intermediate position along axis 2. The position of plots 6 and 10 might be related to a high content of sand. They also appear to be related to Br1 in relation to the axis 2.

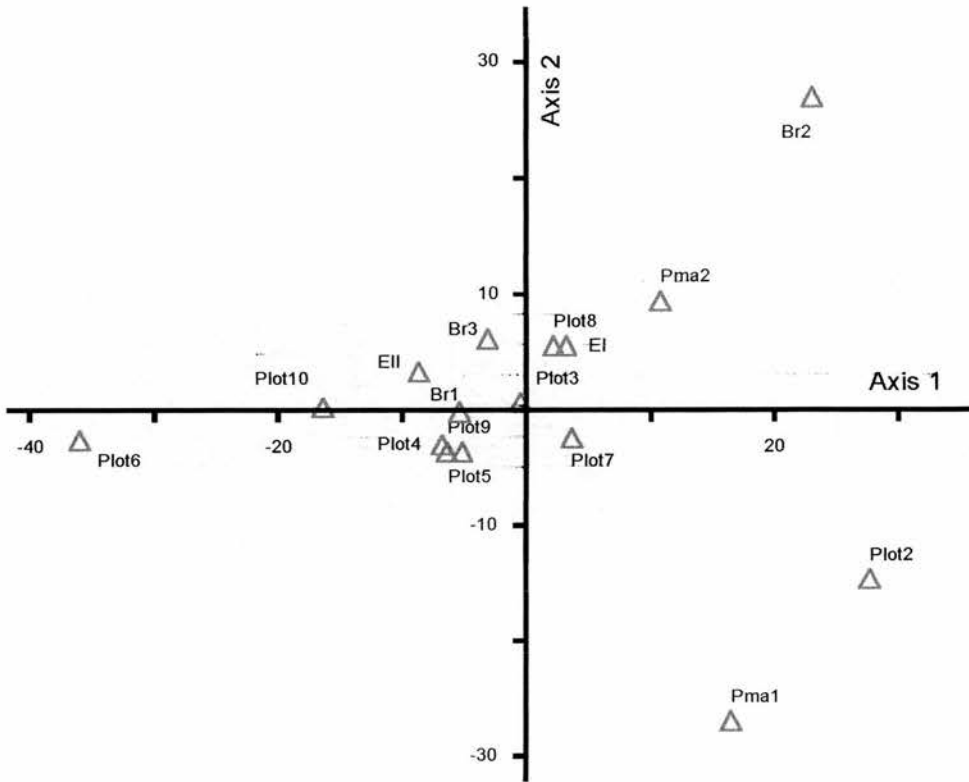
These results show that, at least in terms of top-soil physical and chemical properties (0-20cm), most sampling sites can be related to either the allic (Ca27 unit) and humic (CH) cambisols, soil types that cover most of the Macaé de Cima area (CNPS-EMBRAPA, 1992; Radambrasil, 1983). Plot 2 and Pma1 appears to have similar soil characteristics, which might be related to humic latosols (LVH1a unit). Plot Pma2 can be either associated to this last group, or with plots 8 and EI.

PCA Analysis of Environmental Data

A further PCA analysis was performed, including a set of forest structural, environmental, geographical and soil data (Table 6.2). Due to the lack of soil data, Plot 1 was excluded from the analysis. The resulting correlation matrix is shown on Table 6.4 while the ordinations are shown on Figure 6.3. The ordination axis angle was rotated through 15 (Fig. 6.3a) and 45 (Fig. 6.3b) degrees respectively, to improve the visualisation of the resulting clusters. The first three axes showed eigenvalues of 6.67, 4.49 and 2.84 respectively, accounting for 65.7 % of the total variance.

The first diagram shows some similarities with the ordination of forest plots based on quantitative ecological data produced by DCA (Fig. 5.5), with plots 7, 9 and 10 clustered together in one side of the diagram, and plots 2, 3, 4, 5 and 6 on the other side. Plot 8 is also isolated from the others. This suggests that the environmental factors showed some degree of correlation with the first axis, which appears to be linked to variation in altitude. The second axis appears to be related to the soil pH, while the third axis is apparently negatively correlated with levels of Al.

(a)



(b)

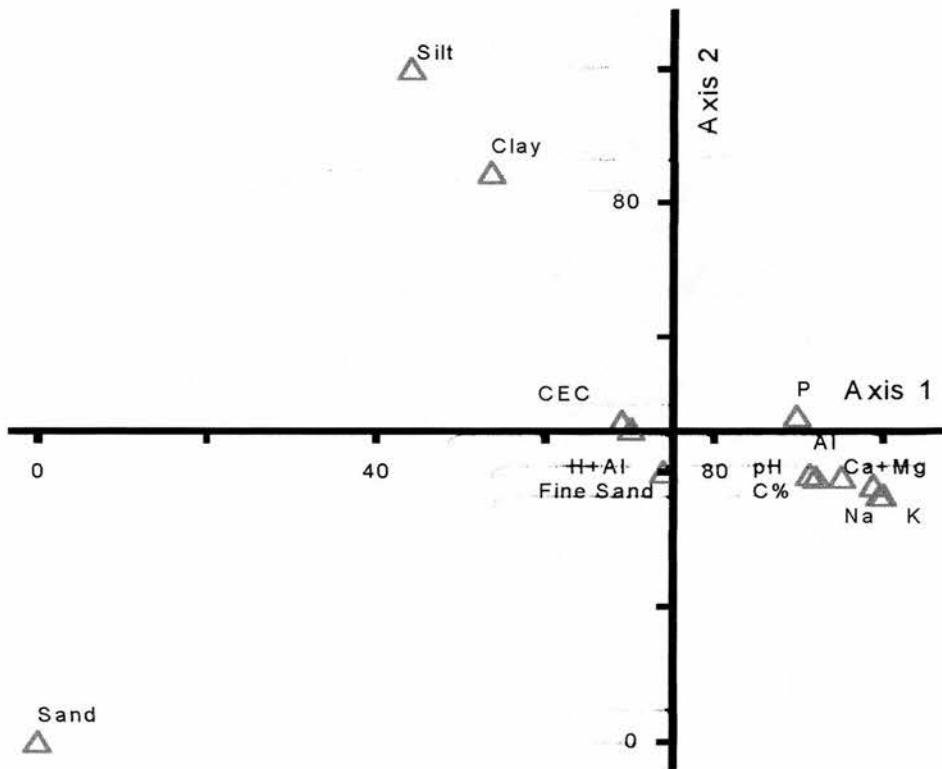


Figure 6.2 PCA ordination (axes 1x2) of sites (a) and soil parameters (b). Sample data include the two PMA plots and soil profiles (Br) from the RadamBrasil/Embrapa soil surveys. Again chemical parameters are related to axis 1, while particle size classes are related to axis 2.

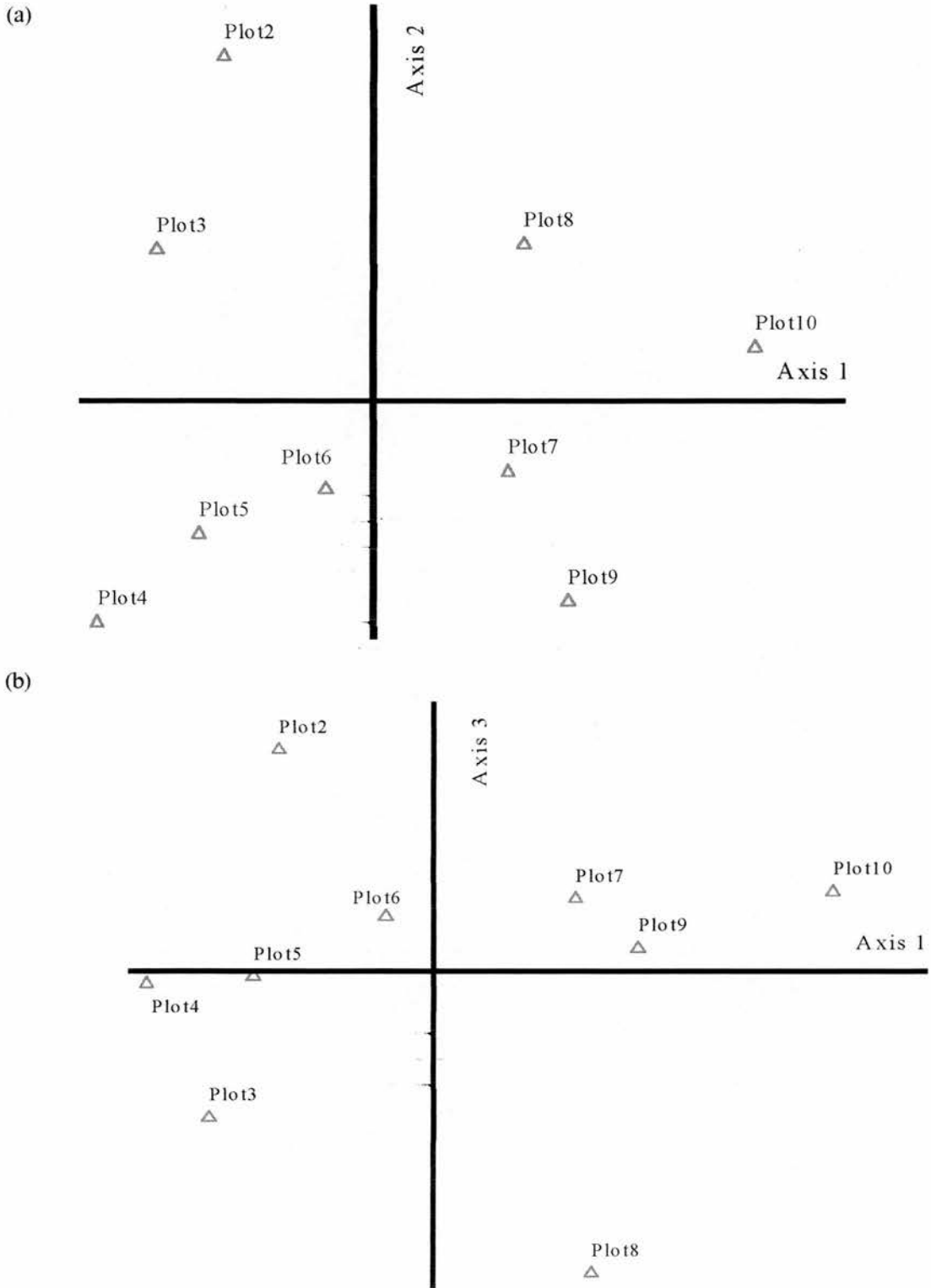


Fig. 6.3 PCA ordination diagrams of forest plots based on environmental data, axes (a) 1x2, and (b) 1x3. Both diagrams show two main clusters, according to the plot loadings along axis 1. On the left, plots 4, 5 and 6 appear in a intermediate position, while on the right plots 7, 9 10 appear to be closely related. Plot 8 is isolated from the others, which might be related to disturbance or soil properties.

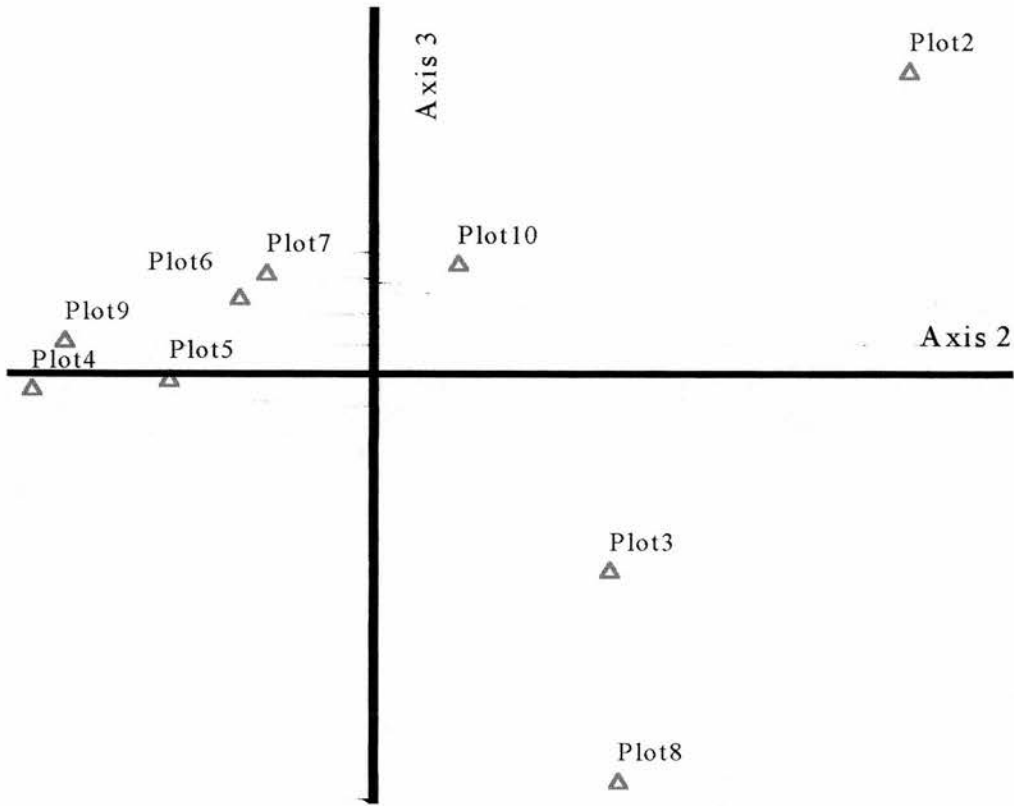


Fig. 6.3c PCA ordination diagrams of forest plots, based on environmental data, axes 2x3, showing the distance between plots 2 (axis 2), 3 and 8 (axis 3) from the other plots, which might be related to soil properties (texture, Al), disturbance, density or biomass.

The matrix on Table 6.4 shows the correlation coefficients among all the environmental factors utilised in the PCA ordination. All coefficients with a value higher than 0.6 are underlined. The highest coefficients, except clear auto-correlation such as between height and canopy or sand and clay, were between altitude and Al ($r^2 = -0.96$), BA and K (0.96), N.sp and %C (0.96), clay content and slope (0.94) and relief position (0.92). These, as well as other significant correlations, appear to reveal a strong influence of both altitude and relief on soil parameters. They also show that some soil parameters appear to be directly related to variations on forest structural parameters.

6.4. Direct Ordination – CCA

The existence of relationships between the forest structure and composition and the selected environmental parameters was investigated by use of the direct ordination technique Canonical Correspondence Analysis-CCA (Ter Braak, 1988). As CCA can not handle more variables than the number of plots, the analyses were performed separately for the environmental and soil parameters. The results of the direct ordination are show on Figures 6.4 (environmental) and 6.5 (soil) respectively. The Pearson and Kendall correlation indices are shown on Table 6.5.

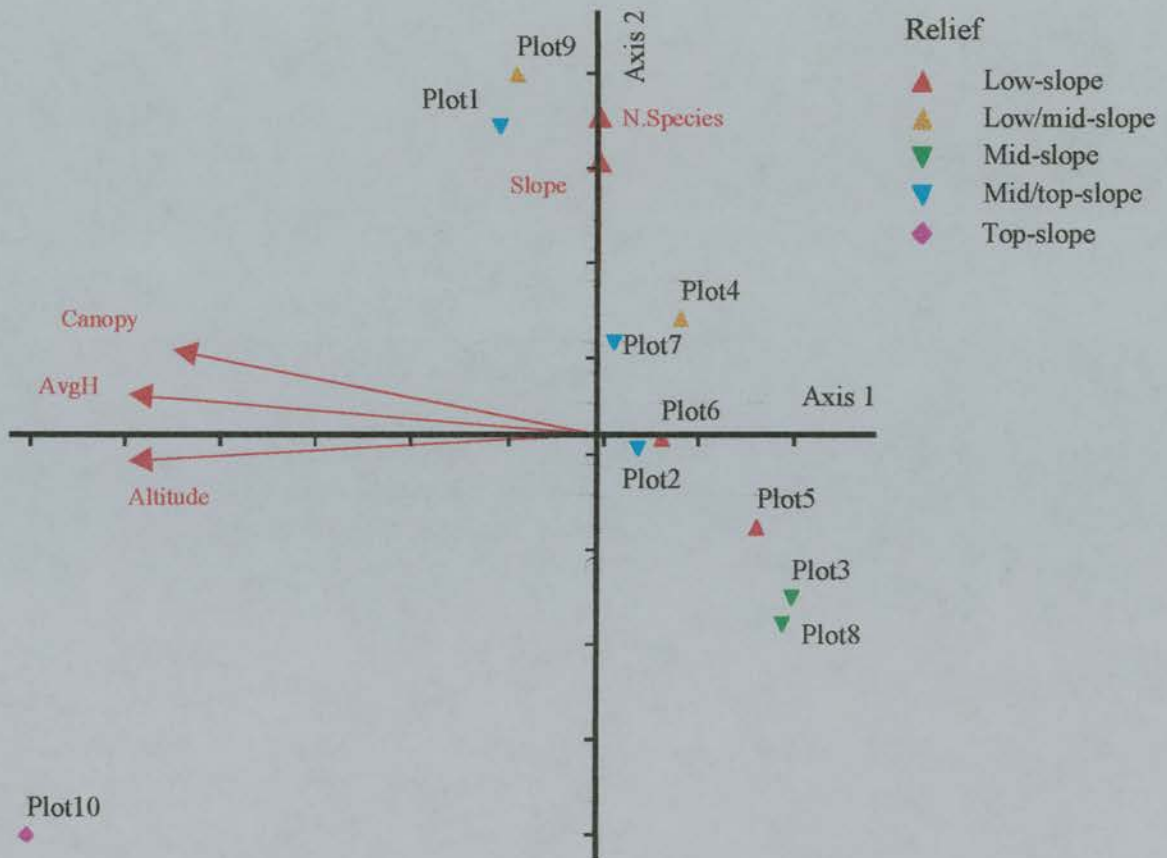


Figure 6.4a CCA ordination of the forest plots and environmental variables (arrows), axes 1x2. Plots on the right hand side are negatively correlated to altitude, canopy and height (axis 1); on the upper side plots are positively correlated to slope and the number of species (axis 2).

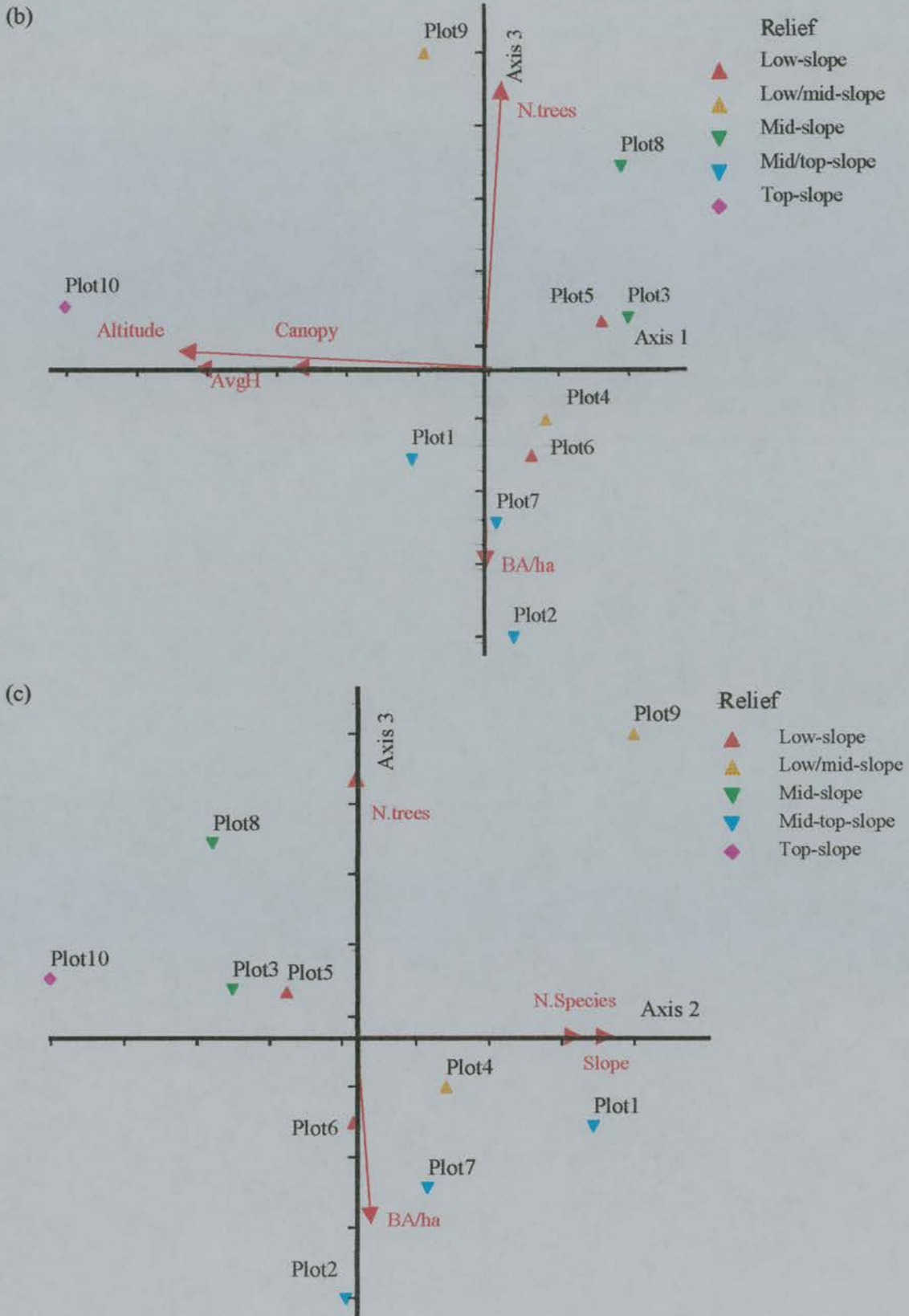


Figure 6.4bc CCA ordination of ecological x environmental data, axes 1x3 (b), and 2x3 (c). It shows the positive correlation with number of species and slope (axis 2); and negative correlation between density and basal area (axis 3).

Table 6.5 Pearson and Kendall correlations of the environmental variables with the three CCA ordination axes (N=10)

Axis	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Altitude	<u>-.882</u>	<u>.777</u>	-.659	-.202	.041	-.023	.215	.046	.159
Slope	-.118	.014	-.221	<u>.639</u>	.408	.515	.022	.000	-.025
AvgH	<u>-.735</u>	<u>.541</u>	-.689	.207	.043	.289	.010	.000	-.067
Canopy	<u>-.609</u>	.371	-.556	.271	.073	.422	.091	.008	-.022
BA/ha	.105	.011	.022	.171	.029	.022	<u>-.550</u>	.302	-.422
N.Species	-.060	.004	-.360	<u>.660</u>	.436	.494	.029	.001	-.090
N.trees	.175	.031	.135	.066	.004	.000	<u>.784</u>	.614	.405
Al	.325	.106	.250	-.476	.227	-.296	.478	.229	.432
Ca+Mg	-.168	.028	-.072	<u>-.558</u>	.312	-.454	.187	.035	.215
H+Al	-.087	.008	-.276	<u>-.510</u>	.260	-.276	.212	.045	.184
K	.161	.026	.092	-.386	.149	-.230	.348	.121	.322
P	-.119	.014	.000	<u>-.681</u>	.464	-.511	.228	.052	.153
CEC	-.117	.014	-.200	<u>-.528</u>	.279	-.289	.369	.136	.422
C	-.095	.009	-.244	-.499	.249	-.333	.237	.056	.200
Sand	-.115	.013	.000	-.458	.210	-.138	.465	.216	.460
Clay	.430	.185	.523	-.454	.206	-.386	.141	.020	.114

The ordination biplot along the two first axes (Figure 6.4a) revealed the existence of a negative correlation ($r = -0.88$) between altitude and the first ordination axis, with the plots located above 1150m placed on the left side of the diagram. Both height ($r = -0.74$) and canopy ($r = -0.61$) also showed a negative correlation with the first axis. Of the other parameters, both slope ($r = 0.64$) and the number of species ($r = 0.66$), an indicator of diversity, showed a positive correlation with the second axis. In relation to relief, the ordination diagram revealed a gradient on both axes, with the low-slope plots generally on the right and lower side, and the middle-top slope plots on the left and top parts of the diagram.

The diagram of the ordination along axes 1 and 3 (Fig. 6.4b) highlighted more clearly the negative correlation of altitude, height and canopy in relation to the first ordination axis. The third axis showed a positive correlation with density ($r = 0.78$), and an negative correlation with basal area ($r = -0.55$), a parameter directly related to forest biomass. Again, the ordination revealed a pattern related to relief, i.e. the position of the plots along the slope. The ordination along axes 2 and 3 (Fig. 6.4c) showed even more clearly the relationship between both plots and environmental variables along the

ordination space. This relationship has already been outlined in the central Brazil cerrados and dry forests (Furley & Ratter, 1988; Furley *et al.*, 1988).

The diagram ordination of both soil parameters and plots in relation to the first two axes (Fig. 6.5a), showed plots 1, 7, 9 and 10 located on the left side, on inverted positions along the first axis in comparison with Fig. 6.3a. In relation to the second axis, plot 10 was isolated from the other three plots. The biplot diagram also highlighted the existence of a negative correlation between P ($r = -0.68$) and the second axis. The position of plots 1, 2, 6, 7 and 9 along this axis appear to indicate also a moisture gradient related to their geographical location, along the south side of the Reserve (see Fig. 4.3), an area with higher rainfall.

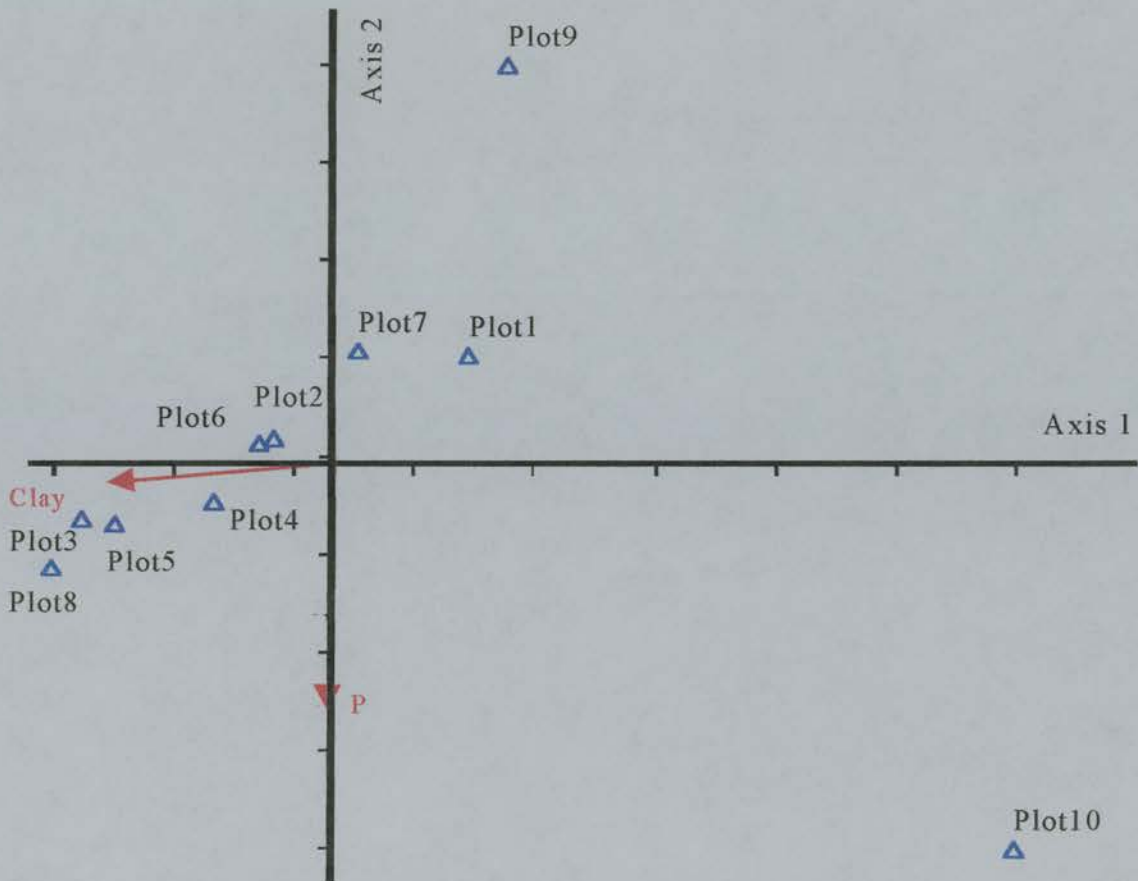


Figure 6.5a CCA ordination of ecological x soils data (axis 1x2), showing a positive relationship between plots on the left side and clay content (axis 1), and a negative relationship between plots on the upper side and levels of P (axis 2).

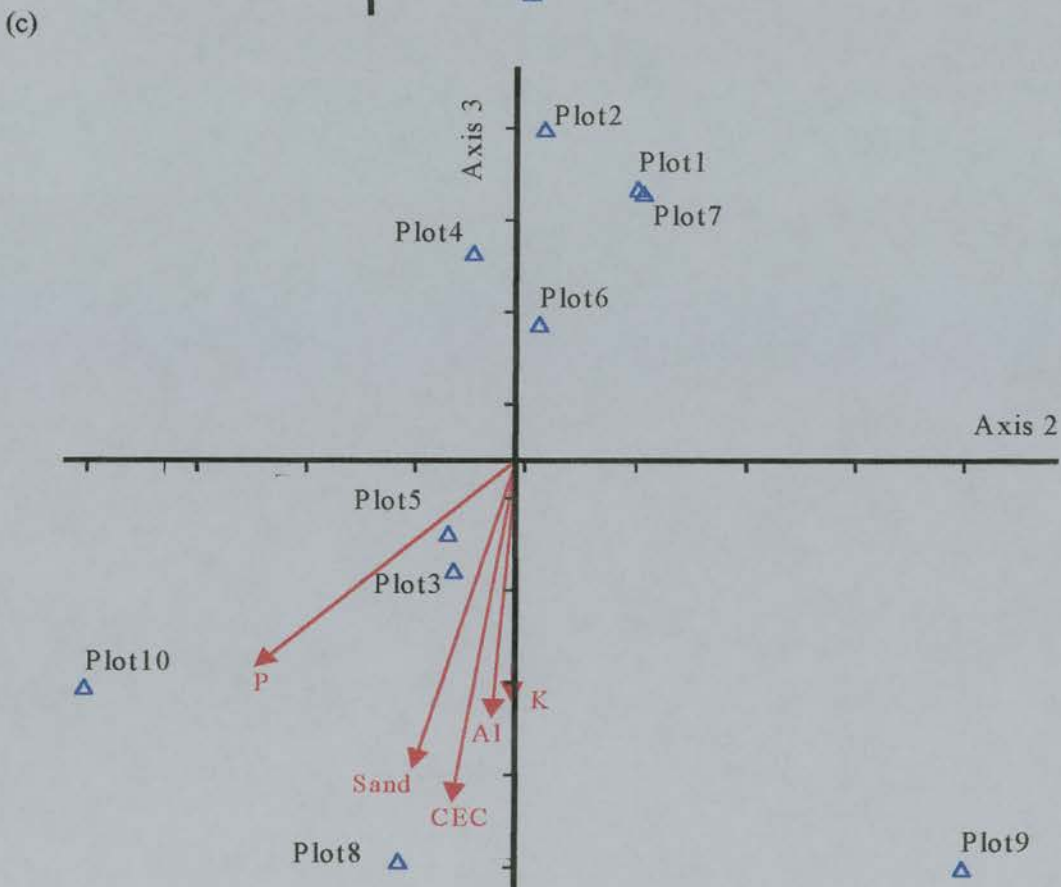
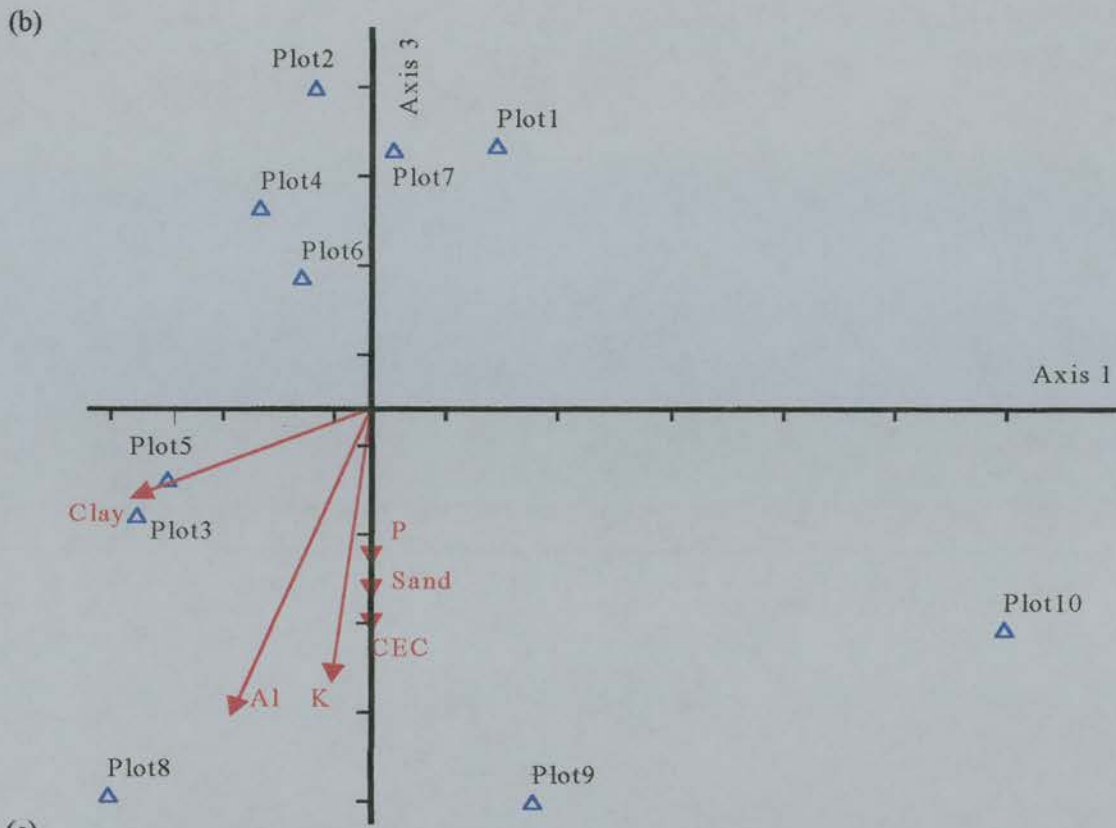


Figure 6.5bc CCA ordination of ecological x soils data, (b) axes 1x3 and (c) axes 2x3, showing the negative correlation of Al, K, P, CEC and sand with axis 3.

On the biplot ordination along axes 1 and 3 (Fig. 6.5b), the second group of plots is split into two groups, located on both halves of the axis 3. This pattern is also highlighted on the ordination along axes 2 and 3 (Fig. 6.5c). The diagram revealed a negative correlation between the second axis and levels of Ca + Mg ($r = -0.56$), H + Al ($r = -0.51$) and CEC ($r = -0.53$). Plots 1, 2, 4, 6 and 7 were located in opposition to all those parameters, suggesting a negative correlation with them. On the other hand, plots with strong (8) or light (3 and 5) signs of disturbance are positively correlated with these parameters, as well as higher altitude plots (9 and 10).

6.5. Discussion – Forest-Physical Environment Relationships at Local Scale

The results of the PCA analysis of environmental data and the CCA ordination of vegetation and environmental data indicate a relatively similar pattern to that of the TWINSpan classification and DCA ordination of the forest plots (Chapter 5). The first pattern to emerge from the analysis is that variations in forest structure and composition are strongly related to differences in altitude. Both PCA and CCA ordinations have also shown that site conditions are related to two main characteristics linked to the relief, position and slope.

Altitude represents a combination of the influence of several environmental factors (Austin, 1989), especially those related to climate, such as moisture, temperature and radiation. The combined effect of altitude and relief is likely to increase the spatial variation of these factors, not only in relation to aspect (i.e., N-S exposure), affecting the incidence of radiation, rainfall and winds, but also in relation to soil characteristics.

Despite the protection provided by the continuous forest cover, pedogenetic processes occur continuously in tropical humid areas (Thomas, 1994; van Wambeke, 1992). Temperature also affects weathering, emphasising the direct effect of altitude on pedogenesis (Buol *et al.*, 1989). The high degree of slope, allied to the local high rainfall, with some extreme summer peak events, promotes occasional landslides even under a forest cover, with a great amount of mass movement downslope. Subsurface flow of both particles and dissolved nutrients also occurs continuously across the soil catena (Bruijnzeel, 1989). Therefore, both chemical and physical characteristics of the soils are strongly related to the combined effect of altitude and relief (Grubb & Tanner, 1976).

Soil characteristics not only influence the forest structure directly (Austin *et al.*, 1972; Baillie *et al.*, 1987; Grubb, 1989; Webb, 1969), but can also be affected by forest ecological and hydrological processes that occur at local and landscape levels, such as nutrient absorption, rainfall interception, and litter production (Bruijnzeel, 1989; Buol *et al.*, 1989; Jordan, 1985; Kimmins, 1997). The local physical environment, namely soils and landforms, has been found to affect forest structure in other neotropical areas (Clark & Clark, 1996; Grubb & Tanner, 1976; Jordan, 1985; Lieberman *et al.*, 1985; Lugo & Scatena, 1995).

The results from PCA did show high positive (CEC and C%) and negative (Al) correlations between soil parameters and altitude. Both slope and the position of the site on the relief are correlated with clay content and Ca+Mg levels. The CCA ordination showed a strong influence on both soil and environmental variables on the forest composition. Both analyses suggest a combined effect of these variables on the structure and composition of the Atlantic montane forest.

The occurrence of soils with a high content of organic matter on the mountain ridges, which resembles peat (*mor*), have been reported for other tropical montane forests (Grubb & Tanner, 1976; Grubb, 1977; Whitmore, 1989). They seem to correspond to humic cambisols according to the Brazilian soil classification system (humitropepts in the U.S Soil Taxonomy) (Radambrasil, 1983). The CCA results suggest some relationship between the occurrence of these soils and the high montane forests. Part of the ecosystem nutrients may be locked up in the undecayed litter and unmineralised humus, unavailable to plants (Grubb, 1977). Further research is needed to assess to which extent differences in moisture during the dry season, nutrient levels or nutrient cycling in these soils influence directly the montane forest physiognomy and composition (Grubb, 1989; Whitmore, 1989).

Variations in forest structure have been related to both soil drainage and nutrient levels, in seasonal riverine (Oliveira-Filho *et al.*, 1995) and gallery (Silva-Jr, 1995) forests of central Brazil. Differences in forest physiognomy and composition were related to soil and landform variations along an altitudinal gradient (870-1170m) in a transitional montane semideciduous/ombrophilous forest (Serra do Japi, see Chapter 7), in São Paulo (Rodrigues & Shepherd, 1992). The variation in vegetation appeared to be

related to a gradual increase in Al, fine sand and occurrence of pebbles, and a decrease in CEC and soil depth with altitude.

Human disturbances such as clear-cutting and fire are also considered to affect soil properties, at least over the short term (Jordan, 1985). Clear-cutting, followed by burning of dead wood, can release a considerable amount of nutrient previously unavailable to plants. The removal of the forest cover, as well as the temporary decrease in input of soil organic matter can also increase the erosion potential, with consequent loss of nutrients. The signs of fire in one of the *Eucalyptus* plots could be related to higher values of pH, P, Al and CEC. Plot 8, located in a secondary forest area, showed the highest level of Al and P of the natural forest plots. It also showed the second lowest basal area, despite having the highest density (62 trees). Basal area, a surrogate for forest biomass, showed a high correlation to K (0.93), and also to Al and soil texture. The plot with lowest basal area (plot 6) also showed the lowest proportion of clay (6%), as well as a low level of K. Therefore, the lower biomass might be related not only to disturbance, but also to soil texture and Al levels. This idea would need to be followed up in future research.

The results of both PCA and CCA ordinations, combined with the TWINSpan classification and DCA ordination (see Chapter 5), appear to support the initial hypothesis that the complex mosaic composed of different plant communities can be related to site characteristics. The overall patterns of relationships between the forest and the physical environment revealed by both classification and ordination procedures have been used to establish some general rules concerning the forest ecosystem in Macaé de Cima. These rules can be used to predict, for example, which plant communities or biomass values are more likely to be found at a particular combination of soil and slope characteristics at a given altitude (see discussion in Chapter 9).

CHAPTER 7. Biogeographical Analysis of Atlantic Forest Areas

7.1 Introduction

The biogeographical links between the different areas or regions within the Atlantic forest domain are still far from well-understood (Oliveira Filho & Ratter, 1995; Prance, 1992). In this chapter, the position of Macaé de Cima in the Atlantic forest will be investigated by analysing its floristic and environmental relationships with several other forest areas located within the Atlantic forest domain. An attempt will be made to assess the extent to which floristic similarities between Macaé de Cima and other areas analysed by both multivariate classification and ordination techniques are related to environmental and/or geographical variables. The patterns revealed by the analyses can then help to clarify these links.

7.2. Atlantic Forest Areas

The objective of using multivariate classification and ordination analytical methods was to investigate whether the Atlantic Forest in the SE region of Brazil can be compartmented into different segments or vegetation types, characterised by specific floristic and/or environmental conditions. The inclusion of data from neighbouring states could also help to determine whether the region's forests are part of a continuous gradient along the total range of the Atlantic Forest, or constitute a distinct floristic unit within the Atlantic Province, as well as clarifying floristic links with the Paranaense Province (Cabrera & Willink, 1973; Prance, 1992).

Most areas from where floristic data were obtained (see Fig. 7.1) were located in southeastern Brazil, covering the states of Rio de Janeiro (RJ), São Paulo (SP), Minas Gerais (MG) and Espírito Santo (ES). A few more areas located in the southern states of Paraná (PR) and Santa Catarina (SC), as well as the southern portion of Bahia (BA) were also included (Table 7.1). The data used are derived from both floristic and quantitative ecological surveys. Although most data come from published sources, some unpublished data were also used.

The final matrix of species *per* area (presence/absence), after the elimination of doubtful taxa and a thorough check for possible synonymies, consisted of a total

of 2122 woody tree and shrub species. After eliminating species that occurred in only one area (unicates), which provide no basis for comparison (Oliveira Filho & Ratter, 1995), a final matrix with a total of 1353 species occurring in at least two or more areas was used in both classification (TWINSPAN, UPGMA) and ordination (DCA, CCA) analyses. The complete matrix will be lodged in both the RBGE and the Institute of Geosciences-UFF libraries.

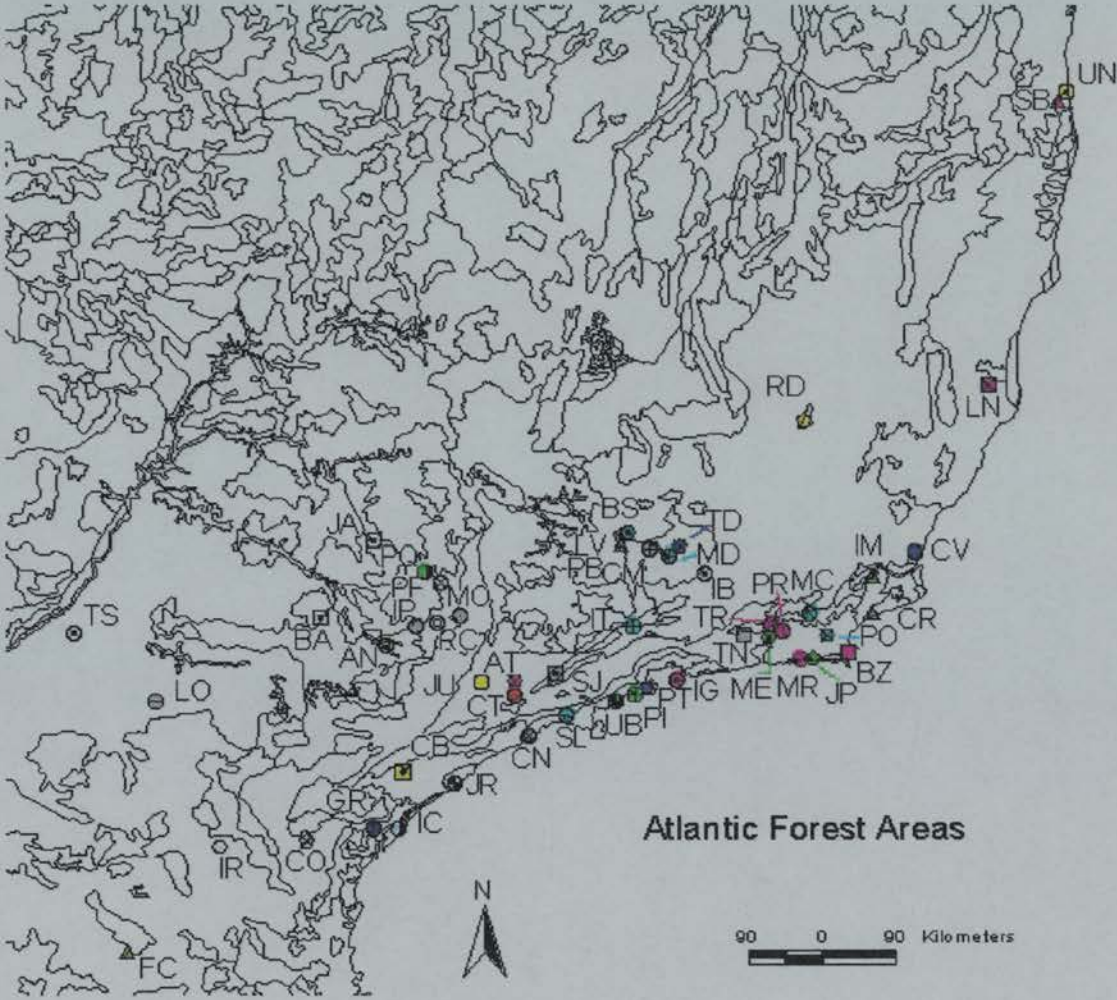


Figure 7.1 Location of the Atlantic forest areas used in the biogeographical analysis (Key in Table 7.1). Lines are boundaries between vegetation types, extracted from the IBGE vegetation map (see Fig. 3.2).

Table 7.1 List of the Atlantic forest areas used in the analyses. Vegetation types according to the IBGE classification system, modified by Oliveira-Fillho & Ratter (1995)

N	Code	Veg	Forest Area	Source
1	PT	Db	APA Cairuçu Parati (RJ)	Marques, 1997
2	IM	Db	Mata Imbé Campos (RJ)	Moreno <i>et al.</i> , 1988
3	CV	Fb	Mata Carvão S.J. Barra (RJ)	Silva, 1997
4	BZ	Fb	Búzios Cabo Frio (RJ)	Araújo <i>et al.</i> , 1988
5	MR	Pa	APA Maricá (RJ)	Silva & Oliveira, 1989
6	CT	Dm	PE Cantareira (SP)	Baitello & Aguiar, 1982; Baitello <i>et al.</i> , 1992
7	CB	Dm	PE Carlos Botelho (SP)	Custodio-Filho <i>et al.</i> , 1992
8	CN	Db	Cubatão (SP)	Leitão Filho 1993; Mendonça <i>et al.</i> , 1992
9	IB	Dml	PE Ibitipoca (MG)	Fontes, 1997
10	PI	Db	PE S. do Mar Picinguaba (SP)	Cesar & Monteiro, 1995
11	SL	Dm	PE S. do Mar Salesópolis (SP)	Mantovani <i>et al.</i> , 1990
12	JR	Db/s	EE Juréia (SP)	Mantovani, 1993; Tabarelli <i>et al.</i> , 1993
13	FC	Mm	FN Caçador (SC)	Silva <i>et al.</i> , 1997
14	CO	Mm	CNPF Colombo (PR)	Oliveira & Rotta, 1982
15	UN	Db	RB Una (BA)	Lobão & Souza, 1993
16	GR	Db/s	APA Guaraqueçaba (PR)	Roderjan & Kuniyoshi, 1988
17	TR	Dm	Teresópolis (RJ)	Davis, 1945; Veloso, 1945; IBDF, 1984
18	IT	Dm	PN Itatiaia (RJ)	Brade, 1956; Segadas-Viana, 1965
19	CR	Pa	APA Carapebus Macaé (RJ)	Henriques <i>et al.</i> , 1986; Zaluar, 1997
20	PR	Db/s	EE Paraíso Guapimirim (RJ)	JBRJ, 1993
21	TN	Ds	RB Tinguá N. Iguaçu (RJ)	Rodrigues, 1996
22	ME	Db	Faz. UEB Magé (RJ)	Guedes, 1992
23	PO	Db	RB Poço das Antas (RJ)	JBRJ, 1993; Scarano <i>et al.</i> (unpublished)
24	IG	Db/s	RB Praia do Sul I. Grande (RJ)	Araújo & Oliveira, 1988
25	JP	Pa	RE Jacarepiá Saquarema (RJ)	Sá, 1992
26	MC	Dm	RE Macaé de Cima (RJ)	This study; Lima & Guedes-Bruni, 1997
27	LV	Fm	ESAL Lavras (MG)	Oliveira-Filho <i>et al.</i> , 1994b; Oliveira-Filho <i>et al.</i> , 1997
28	PB	Fm	RB Poço Bonito, Lavras (MG)	Gavilanes <i>et al.</i> , 1992a; Oliveira-Filho <i>et al.</i> , 1994a
29	BS	Fm	Macaia Bom Sucesso (MG)	Carvalho <i>et al.</i> , 1995 Oliveira-Filho <i>et al.</i> , 1994e
30	CM	Fm	Camargos Itutinga (MG)	Vilela <i>et al.</i> , 1994; Oliveira-Filho <i>et al.</i> , 1994e
31	MD	Fm	Madre de Deus de Minas (MG)	Gavilanes <i>et al.</i> , 1992b; Oliveira-Filho <i>et al.</i> , 1994f
32	TD	Fs	Serra S. José Tiradentes (MG)	Oliveira-Filho & Machado, 1993
33	RD	Ds	RF Rio Doce (MG)	CETEC, 1982; Silva Jr. <i>et al.</i> , 1994
34	SB	Db	Southern Bahia (BA)	Harley & Mayo, 1980; Mori <i>et al.</i> , 1983
35	LN	Db	RF Linhares (ES)	Jesus, 1988; Jesus & Garcia, 1992; Peixoto & Gentry, 1990
36	AN	Fs	Faz. Barreiro Rico Anhembi (SP)	Assumpção <i>et al.</i> , 1982; Cesar & Leitão-Filho, 1990
37	AT	Fm	PM Grota Funda Atibaia (SP)	Meira Neto <i>et al.</i> , 1989; Grombone <i>et al.</i> , 1990
38	BA	Fs	RE Bauru (SP)	Cavassan <i>et al.</i> , 1984
39	IP	Fs	APA Corumbataí Ipeúna (SP)	Mantovani <i>et al.</i> , 1986; Rodrigues, 1991
40	JA	Fs	UNESP Jaboticabal (SP)	Pinto, 1989; Marchiori <i>et al.</i> , 1992
41	JU	Fm	Serra do Japi Jundiá (SP)	Leitão Filho, 1992; Rodrigues <i>et al.</i> , 1989
42	MO	Fs	RB Mogi-Guaçu (SP)	Gibbs & Leitão Filho 1978; Gibbs <i>et al.</i> , 1980; Mantovani <i>et al.</i> , 1989
43	PF	Fs	RE Porto Ferreira (SP)	Bertoni <i>et al.</i> , 1982; Bertoni & Martins, 1987
44	RC	Fs	Rio Claro (SP)	Pagano & Leitão Filho, 1987; Pagano <i>et al.</i> , 1987
45	PA	Fs	PE S. Rita Passa Quatro (SP)	Bertoni <i>et al.</i> , 1988; Martins, 1993
46	TS	Fs	PE M. do Diabo T. Sampaio (SP)	Campos & Heinsdijk, 1970; Baitello <i>et al.</i> , 1988
47	SJ	Fs	FR S. J. Campos (SP)	Silva, 1989
48	UB	Db	EE Ubatuba (SP)	Silva & Leitão Filho, 1982
49	IC	Db/s	PE Ilha do Cardoso (SP)	Barros <i>et al.</i> , 1991; Melo & Mantovani, 1994
50	LO	Fs	PE Mata Godoy Londrina (PR)	Soares-Silva & Barroso, 1992;
51	IR	Mm	FN Irati T. Soares (PR)	Galvão <i>et al.</i> , 1989

7.3. TWINSPAN Classification

The first division of the TWINSPAN classification (Fig. 7.2) has produced two large groups. The group on the right side of the dendrogram includes all but two areas of RJ, three areas (PI, CT and UB) located in SP, and the areas located in ES and BA. The next division separated coastal (*restinga*) areas of RJ from the lowland and slope forest areas. In this second group, the next division formed a 'NE Atlantic' group with the one RJ (CV), and the ES and the BA areas. Further division on the second group resulted in one cluster with two SP areas, whereas the other two final groups included all areas but one (PI) located in RJ.

The left side of the dendrogram included two areas of RJ (MC and IT), together with all the MG, PR and SC, and most of the SP areas. The first division within this group isolated one PR area (LO), while a further division produced two large groups. The right side includes all dense forests, two mixed and one semideciduous (SJ) forest, whereas the left side contains all the remaining semideciduous forests located in MG and SP, and one mixed forest of PR (IR). The next division of the right side group isolates a MG area (RD) from the others. The next division separates the two mixed forests from the others. A further division separates the high altitude areas of RJ and MG, whereas the last division separates the coastal areas from the more interior slope and mountain forest areas of SP. The first division of the semideciduous group separates the submontane (Fs) from the montane (Fm) forest areas. A further division on the montane group separates the MG areas from the mixed forest (IR) and the SP areas. The submontane group is further subdivided into smaller clusters of three and four areas each, all located in SP.

An overview of the TWINSPAN classification reveals that, although confirming the separation of the coastal rainforests from the seasonal semideciduous forests located in SP, MG and PR, the two biomes are closely related floristically. It also shows clearly the existence of two separate formations, the submontane and montane semideciduous forests, a pattern already revealed in other studies (Fontes, 1997; Oliveira Filho & Ratter, 1995).

Another pattern that emerges is the existence of clear links between the high montane rainforest areas of RJ and both the subtropical rainforests of coastal SP and

PR, and the mixed *Araucaria* forests. On the other hand, the dendrogram shows that the northern coastal forests of SP are closely related to the lowland and submontane forests of RJ. It also shows that although the arboreal *restinga* forests are clustered together, they are also closely related to the adjacent lowland rainforest areas. Finally, TWINSpan clustered together a lowland forest of northern RJ (CV) with the lowland forests of ES and BA, which suggests the existence of close links between these two regions.

7.4. UPGMA classification

The Atlantic forest areas were also classified by use of an agglomerative cluster classification, Unweighted Pair-Group Method using Arithmetic averages, or UPGMA (Kent & Coker, 1992; van Tongeren, 1995). The Sørensen Coefficient of Community was used as a measure of similarity between the areas. The resulting matrix was then used as a measure of the distances between the areas in the classification. Being an agglomerative hierarchical method, UPGMA clusters the areas successively, according to their floristic similarities. Therefore, the levels of clustering are more relevant than the position of the areas along the classification dendrogram (Fig. 7.3).

The UPGMA dendrogram reveals strong geographical and physiognomic links between the areas. The semideciduous forest areas again appear to form a closely related group, with the areas clustered together at high levels of similarity. The separation between the submontane and the montane formations is also maintained. The two areas clustered at lower levels of similarity are located further South (LO) and in a transition area (IB) between the evergreen and seasonal forests (Fontes, 1997; Ururahay *et al.*, 1983). The semideciduous forest group is later clustered with a group that includes most lowland, submontane and montane rainforest areas of RJ and SP. These areas form two separate clusters, joined together at a lower level of similarity. The next clustering includes two additional montane areas of RJ (IT and TR).

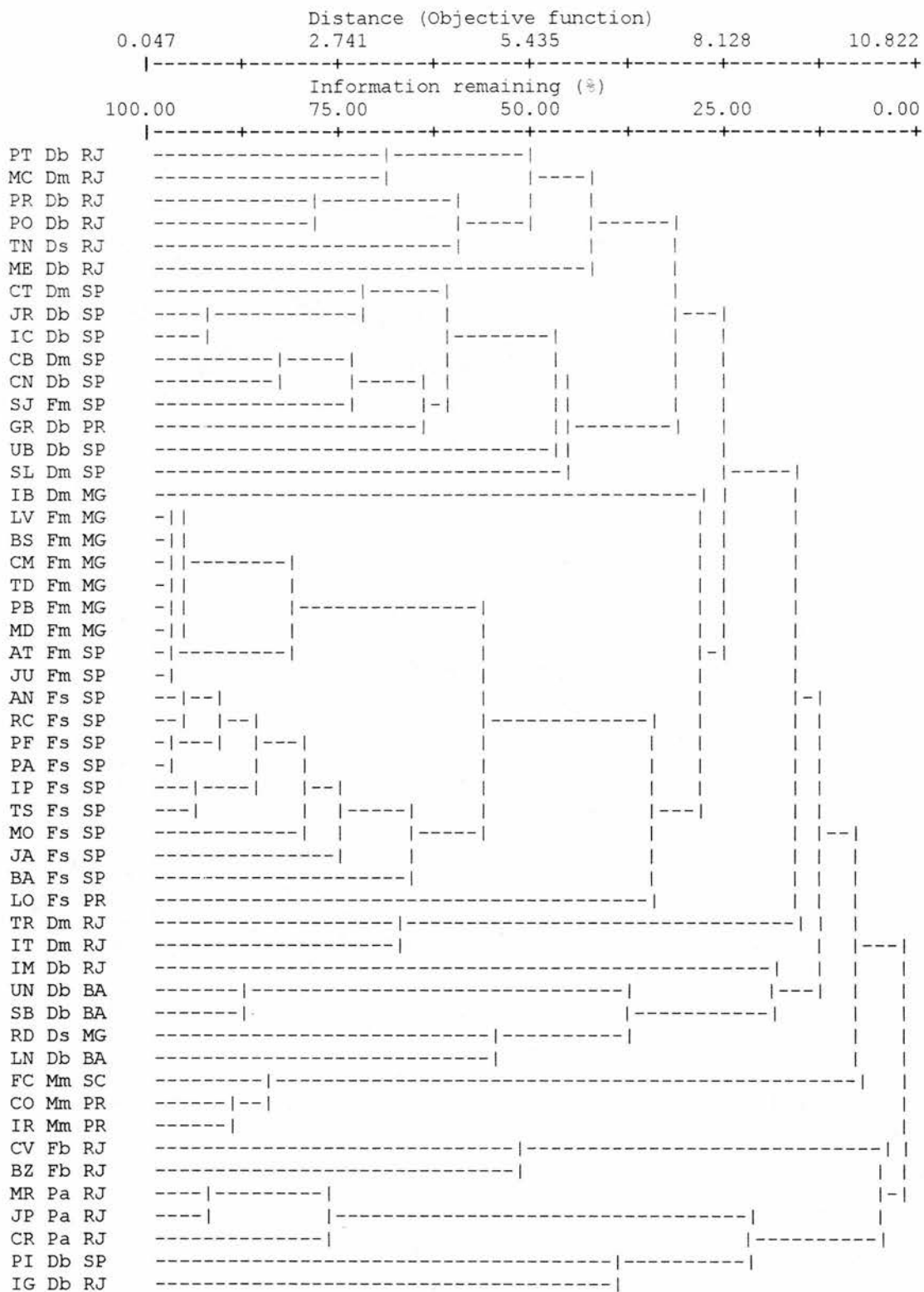


Figure 7.3 Dendrogram of the UPGMA classification, based on the Sørensen Coefficient of Community as a measure of similarity (codes are given on Table 7.1). The scale on the top shows the similarity distance (hierarchy) in absolute and percentage values, which indicates that the similarity among areas and/or groups decreases as the level of clustering moves from left to the right.

The next level brings together a cluster formed by the BA areas, the ES (LN), one MG (RD) and one RJ (IM) area, with the latter joining the group at a lower level. At the next stage the three mixed forest areas are separated out, showing a high level similarity among them. Finally, the dendrogram distinguishes a group formed by the two coastal dry forests, the *restinga* and two coastal lowland wet forest areas with *restinga* plants also included in the dataset (IG and PI).

Although the results of the UPGMA are quite similar to the TWINSpan classification, they show some differences. The NE Atlantic group includes the RD and IM areas, whereas CV is clustered with BZ and the *restinga* areas. IB, which appeared by TWINSpan in a dense montane forest cluster, is clustered with the semideciduous forests by the UPGMA. However, its similarity to these areas appears at an intermediate level between the semideciduous and the dense forest groups, whose clustering is joined by other montane dense forest areas (IT and TR) at the next clustering level. Both the mixed *Araucaria* and the coastal *restinga* forests show a lower degree of similarity to the other areas than indicated by TWINSpan, which supports their position as distinct forest formations.

On the whole, both classification procedures have shown similar patterns. The main clusters are related to the submontane and montane semideciduous forests, montane or subtropical moist forests, coastal submontane and lowland tropical forests, including a separated 'NE Atlantic' group, coastal *restinga* and subtropical mixed *Araucaria* forests. A few areas are clustered with different groups, which can be related to an ecological (ecotone) or floristic transition. Differences in sampling intensity might affect the classification results, especially in UPGMA (Greig-Smith, 1983; van Tongeren, 1995).

7.5. DCA ordination

Indirect ordination DCA (Hill, 1979) was applied to the Atlantic forest dataset in order to investigate the clustering patterns further, to discover whether the different forest areas formed groups that could be identified along the environmental space represented by the ordination axes. The resulting ordination diagrams are shown on Fig. 7.4. The colours indicate the forest formation, according to the modified IBGE classification (see Table 7.1).

The ordination along the two first axes (Fig. 7.4a) showed at least six main clusters, which appear to be related to both geographical location and climate. On the right side of the first axis are the areas located close to the coast, with a hotter and wet climate. On the left side are both the areas located at higher altitude, including the mixed *Araucaria* and dense forests, and the semideciduous forest areas of the interior of MG, SP and PR. The second axis reveals the geographical cluster composed by the Southern BA-ES forests and its links with both RD (MG), CV and also BZ (both in RJ). The more seasonal areas are located above the centroid, whereas most rainforest areas are located below. This axis also separates the montane from the submontane seasonal forests.

(a)

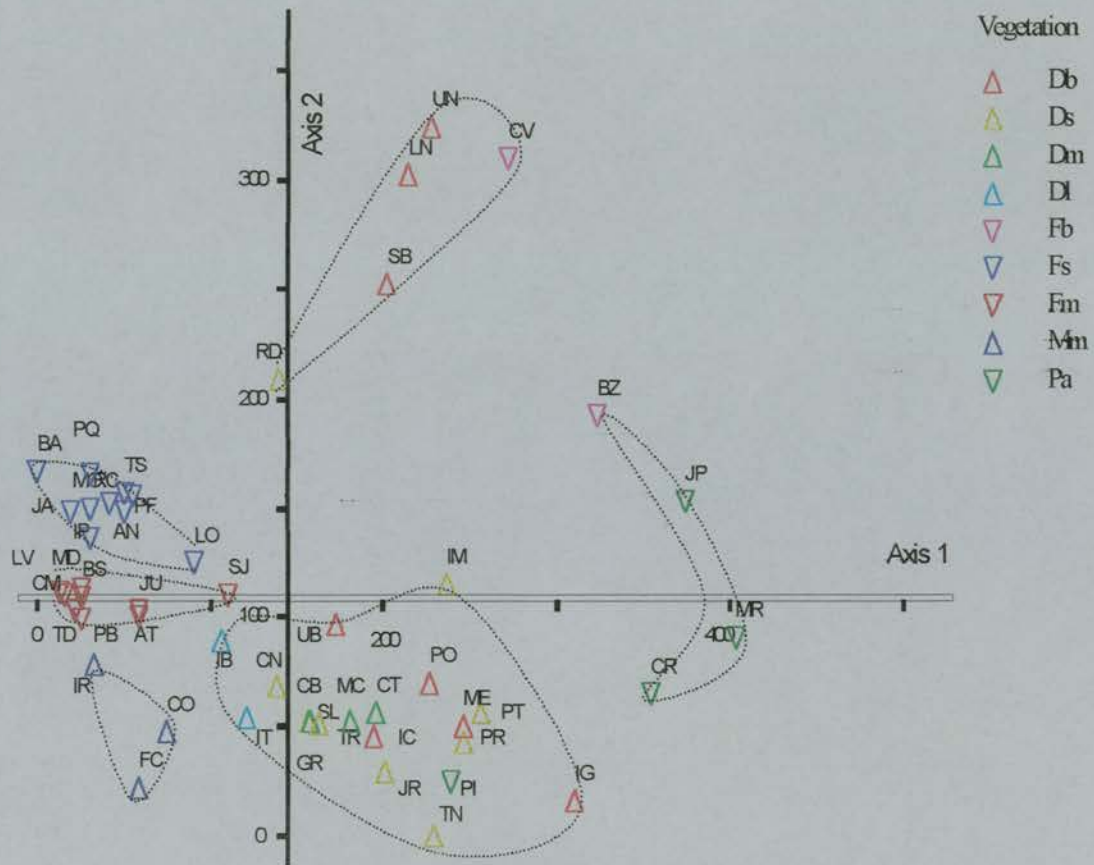


Figure 7.4a DCA ordination (axes 1x2), shows six main clusters related to climate and geographical location: NE areas on upper right, restinga on centre-right, tropical rainforest on lower right, *Araucaria* forest on lower left, semideciduous montane forest on centre-left and submontane on upper left side of the diagram. Colours represent vegetation types, according to the modified IBGE classification (See Table 7.1).

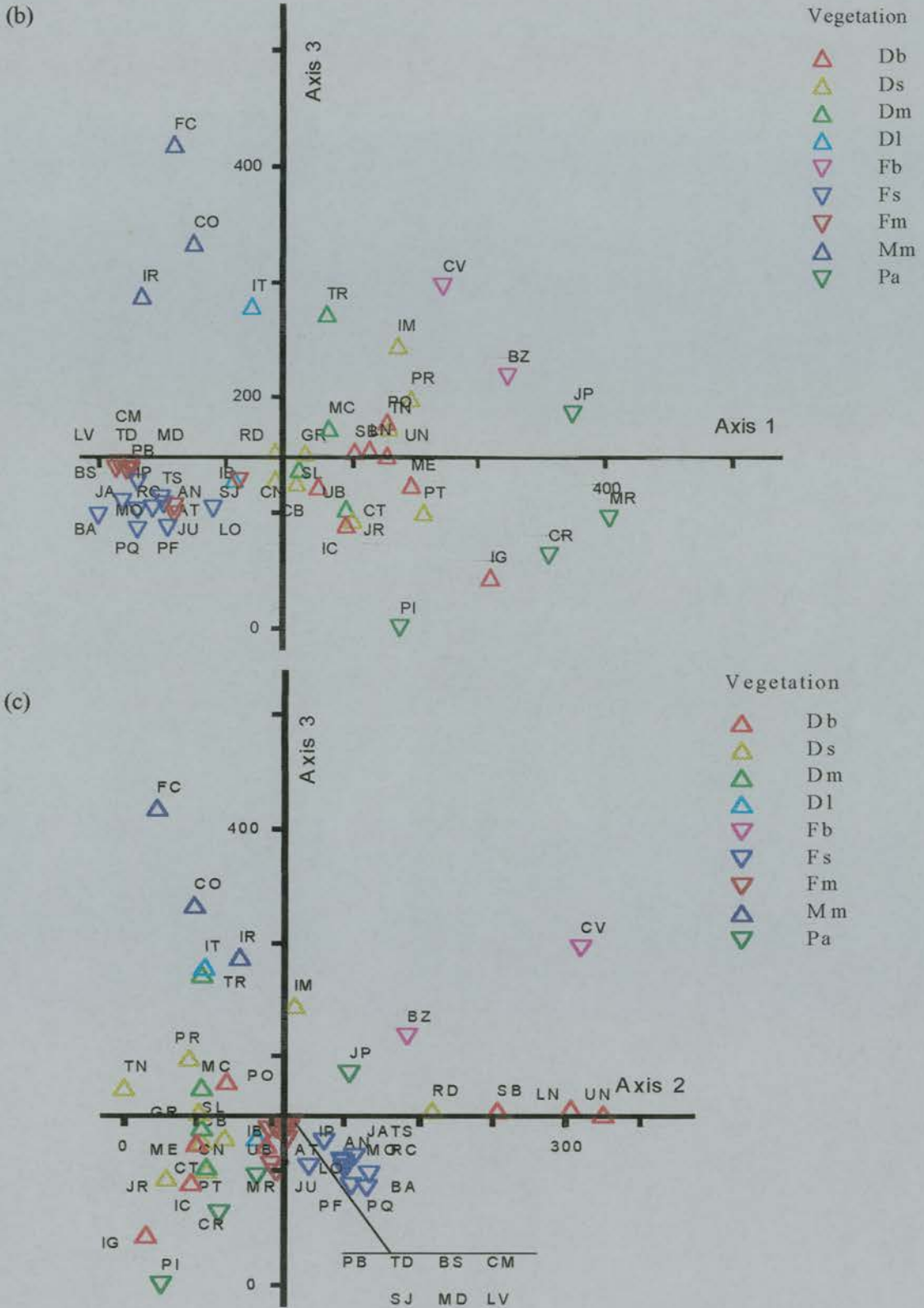


Figure 7.4bc DCA ordination, axes (b) 1x3 and (c) 2x3. The semideciduous forests are clustered together closer than in (a), with links with NE Atlantic, lowland seasonal and montane moist forests. Axis 3 (c) appears to separate further the coastal moist lowland from the submontane, montane and *Araucaria* forests (left side).

The diagram in Figure 7.4b (axes 1x3) resembles an inversion of Fig. 7.4a, with the three *Araucaria* forest areas clustered together with IT (RJ) on the upper left side, and the seasonal forest areas in the lower part of the diagram. On the right side, the coastal areas of RJ are clustered together, distributed on both sides of the third axis centroid. Most moist forest areas are clustered on the centre-right part of the diagram. Three areas are for some reason isolated on the upper half of the right side, TR, IM and CV (RJ). PI was also isolated on the lower half, although equally far from IG, PT, JR and IC, all coastal rainforest areas of SP and RJ.

The ordination along axes 2 and 3 (Fig. 7.4c) highlights more or less the same clusters identified in the previous diagrams. This time, the montane semideciduous areas occupy the centre of the diagram, with the submontane areas on the lower part of the right side. The upper part of the same side contains the same cluster of southern BA-ES areas, added by RD (MG) and CV (RJ). On the left side, the upper part reveals the cluster formed by the *Araucaria* forests, plus IT and TR (RJ). Most moist forest areas are located along the centroid (axis 3), while the lower part shows a cluster formed by several coastal areas.

An overview of the three diagrams allows some preliminary conclusions. As expected, the first ordination axis reveals a pattern similar to that of the TWINSPAN classification (Kent & Coker, 1992). The ordination provide a good separation of the tropical, coastal lowland and lower slope moist forests from the more subtropical forests located at higher altitudes and/or latitudes. It also shows some recurring patterns in all diagrams, related to clusters of the *restinga* forests, the *Araucaria* forests with some montane/high montane moist forests, the submontane and montane semideciduous forests, and the NE portion of the Atlantic rainforest. The distinction between the lowland, submontane and montane rainforests is not so clear, with some areas as components of different clusters, according to the different combinations of the ordination axes, which also occur for areas located in the transition between the moist and the seasonal forests. These patterns can be further confirmed or clarified by the direct ordination.

7.6. CCA ordination

A second objective of this chapter was to investigate how the patterns revealed by both ordination and classification procedures can be related to environmental and/or geographical factors. Therefore, a second matrix containing several environmental and geographical variables of the areas (see Table 7.2) was used in the direct ordination Canonical Correspondence Analysis-CCA (Ter Braak, 1986). The parameters adopted in the CCA analysis were either quantitative (value) or qualitative (state), and referred to geographical location (lat/long), altitude, climate (Köppen climatic type, annual average rainfall and temperature), geology, relief and soil. Whenever the parameters were not available from the original references, they were either obtained or estimated from other sources, including thematic maps (EMBRAPA, 1981; IBGE, 1993a,b; Radambrasil, 1983).

The Pearson and Kendall correlation values of the environmental variables (Table 7.3) revealed that the first axis is positively correlated to both longitude and temperature and negatively correlated to altitude. Latitude was positively correlated with the second axis, while rainfall showed a negative correlation with the third axis. The patterns shown on the CCA ordination biplots (Fig. 7.5abc) can illustrate these correlations in a clearer way.

The ordination diagram along the two first axes (Fig. 7.5a) shows a clear division of the areas along the first axis related to the main climatic types. The first axis centroid separated most areas with A climate from those with a C climate, on the right and left side of the diagram, respectively. The diagram also separated most areas with a Cw climate, located above the second axis centroid, from the areas with the climate type Cf. A cluster located on both sides of the first axis centroid included areas with both Af and Cf types. The remaining areas were separated in three main clusters. Most wet coastal forests from northern SP and RJ (Af and Am climates) are clustered below the second axis centroid. A second cluster, located along the second axis centroid, includes the *restinga* forests plus the lowland coastal forests from northern RJ (Aw climate). The remaining cluster includes the southern BA forests (Af climate), plus a little wider apart an area from northeastern MG (RD) and the ES area (LN, both with Aw climate), which can be also related to their latitude (all below 20° S).

Table 7.2. Environmental parameters of the Atlantic forest areas

N	Code	Forest Area	Veg Class	Latitude	Longitude	Altitude	Climate	Rainfall	Temp	Geology ¹	Relief ²	Soil ³
1	PT	APA Caiuru (RJ)	Db/s	23°16'	44°40'	200	Af	2390	22.5	2	2	9
2	IM	Mata Imbé (RJ)	Db	21°45'	41°40'	150	Aw	1400	22.0	3	3	1
3	CV	Mata Carvão (RJ)	Fb	21°25'	41°05'	30	Aw	917	22.8	4	5	6
4	BZ	Búzios/Cabo Frio (RJ)	Fb	22°50'	42°00'	50	Aw	820	22.8	2	2	12
5	MR	APA Maricá (RJ)	Pa	22°52'	42°38'	20	Aw	1355	23.0	1	1	10
6	CT	PE Cantareira (SP)	Dm	23°22'	46°26'	900	Cf	1570	20.0	3	4	4
7	CB	PE Carlos Botelho (SP)	Dm	24°32'	47°57'	700	Cf	1800	18.0	3	6	4
8	CN	Cubatão (SP)	Db	23°55'	46°15'	100	Af	2767	23.0	3	3	7
9	IB	PE Ibitipoca (MG)	Dm/l	21°42'	43°53'	1450	Cw	1532	18.0	3	4	8
10	PI	PE S. do Mar Picinguaba (SP)	Db	23°22'	44°48'	30	Af	2624	21.2	3	1	11
11	SL	PE S. do Mar Salesópolis (SP)	Dm	23°37'	45°45'	1000	Cf	1750	18.0	1	3	7
12	JR	EE Juréia (SP)	Db/s	24°33'	47°15'	200	Af	2195	21.2	3	3	12
13	FC	FN Caçador (SC)	Mm/l	26°52'	51°37'	1100	Cf	1614	16.6	3	6	2
14	CO	CNPQ Colombo (PR)	Mm	25°20'	49°14'	920	Cf	1400	16.5	8	3	13
15	UN	RB Una (BA)	Db	15°10'	39°03'	50	Af	1918	23.6	3	5	12
16	GR	APA Guaraqueçaba (PR)	Db/s	25°10'	48°20'	200	A/Cf	1940	20.5	2	2	7
17	TR	Teresópolis (RJ)	Dm	22°25'	43°00'	880	Cf	1703	17.8	3	3	8
18	IT	PN Itatiaia (RJ)	Dm/l	22°25'	44°50'	1400	Cf	2300	14.0	7	3	13
19	CR	APA Carapebus (RJ)	Pa	22°15'	41°40'	20	Aw	1134	22.4	1	1	10
20	PR	EE Paraisópolis (RJ)	Ds	22°29'	42°53'	200	Am	2250	22.0	3	3	8
21	TN	RB Tingüá (RJ)	Ds	22°34'	43°24'	400	Am	2268	21.7	3	3	8
22	ME	Faz. UEB Magé (RJ)	Db	22°35'	43°02'	40	Aw	2050	21.9	3	2	10
23	PO	RB Poço das Antas (RJ)	Db	22°33'	43°17'	50	Aw	1600	22.8	4	2	12
24	IG	RB Praia do Sul (RJ)	Db/s	23°10'	44°17'	200	Af	2314	22.5	2	2	8
25	JP	RE Jacarepiá (RJ)	Pa	22°52'	42°38'	20	Aw	960	23.0	1	1	10
26	MC	RE Macaé de Cima (RJ)	Dm/l	22°25'	44°31'	1225	Cf	2193	17.7	3	3	8
27	LV	ESAL Lavras (MG)	Fm	21°13'	45°00'	925	Cw	1517	19.6	3	9	7
28	PB	RB Poço Bonito (MG)	Fm	21°20'	45°00'	1150	Cw	1493	19.3	3	9	2
29	BS	Bom Sucesso (MG)	Fm	21°09'	44°54'	825	Cw	1517	19.3	3	9	8

Table 7.2 continuation.

N	Code	Forest Area	Veg class	Latitude	Longitude	Altitude	Climate	Rainfall	Temp	Geology ¹	Relief ²	Soil ³
30	CM	Res. Camargos (MG)	Fm	21°22'	44°37'	917	Cw	1517	19.6	3	9	12
31	MD	Madre de Deus de Minas (MG)	Fm	21°29'	44°22'	925	Cw	22.8	20.0	2	9	8
32	TD	Serra S. José Tiradentes (MG)	Fm	21°01'	44°14'	900	Cw	1600	19.0	3	9	8
33	RD	RF Rio Doce (MG)	Ds	19°40'	42°35'	450	A/Cw	1450	22.0	2	8	8
34	SB	Southern Bahia (BA)	Db	15°20'	39°10'	50	Af	2000	23.6	4	5	5
35	LN	RF Linhares (ES)	Db	19°12'	40°07'	40	Aw	1183	23.6	4	5	5
36	AN	Faz. Barreiro Rico (SP)	Fs	22°40'	48°10'	500	Cw	1200	20.0	7	6	14
37	AT	PM Grota Funda (SP)	Fm	23°10'	46°25'	1200	Cf	1600	16.0	3	4	11
38	BA	RE Bauru (SP)	Fs	22°19'	49°04'	570	Cw	1283	21.4	7	6	2
39	IP	APA Corumbatai (SP)	Fs	22°25'	48°45'	600	Cw	1200	20.0	7	6	5
40	JA	UNESP Jaboticabal (SP)	Fs	21°15'	48°20'	560	Cw	1720	21.3	6	6	2
41	JU	Serra do Japi (SP)	Fm	23°11'	46°52'	1020	Cf	1355	19.2	3	4	1
42	MO	RB Mogji Guaçu (SP)	Fs	22°16'	47°10'	595	Cw	1280	20.2	6	7	12
43	PF	RE Porto Ferreira (SP)	Fs	21°49'	47°25'	580	Cw	1200	20.0	6	7	2
44	RC	Rio Claro (SP)	Fs	22°22'	47°28'	630	Cw	1360	19.6	6	7	3
45	PA	PE S. Rita Passa Quatro (SP)	Fs	21°40'	47°38'	630	Cw	1526	21.4	6	7	2
46	TS	PE M. do Diabo (SP)	Fs	22°30'	52°20'	300	Cw	1382	22.3	7	6	2
47	SJ	FR S. J. Campos (SP)	Fm	23°05'	45°55'	840	Cf	1500	18.0	3	4	1
48	UB	EE Ubatuba (SP)	Db/s	23°27'	45°04'	105	Af	2500	21.0	3	3	8
49	IC	PE Ilha do Cardoso (SP)	Db/s	25°10'	48°00'	150	Af	2300	21.2	3	3	1
50	LO	PE Mata Godoy (PR)	Fs	23°27'	51°15'	700	Cf	1632	21.0	8	6	2
51	IR	FN Irati (PR)	Mm	25°26'	50°24'	870	Cf	1450	17.5	6	6	1

Geology codes: Quaternary (1); Quaternary + Pre-Cambrian (2); Pre-Cambrian (3); Tertiary Barreiras (4); Cretaceous (6); Jurassic (7); Permian/Carboniferous (8)
² Relief Unit codes: Quaternary unconsolidated sedimentary deposits, marine coastal plain (1); Plio-Pleistocene unconsolidated sedimentary covers, coastal plateaus (2); Barreiras formation (5); Scarps and reverses of Serra do Mar (3); Scarps and reverses of Serra da Mantiqueira (4); Basins with central plateau of the Paraná Basin (6); Peripheral Depression of the Paraná Basin (7); Rio Doce depression (8); Canastra-Alto Rio Grande plateau (9).
³ Soil types codes (See key on Appendix 3): LV (1); LE, LR, TR, Tb (2); LV + LE, LE + Ae, A + LV (3); PV + LV (4); PV (5); PA (6); C + PV (7); C, C + R (8); C + LV (9); HG, HP (10); AQ (11); PV + R, PV + AQ (12); LH, CH (13); HG + LV (14).

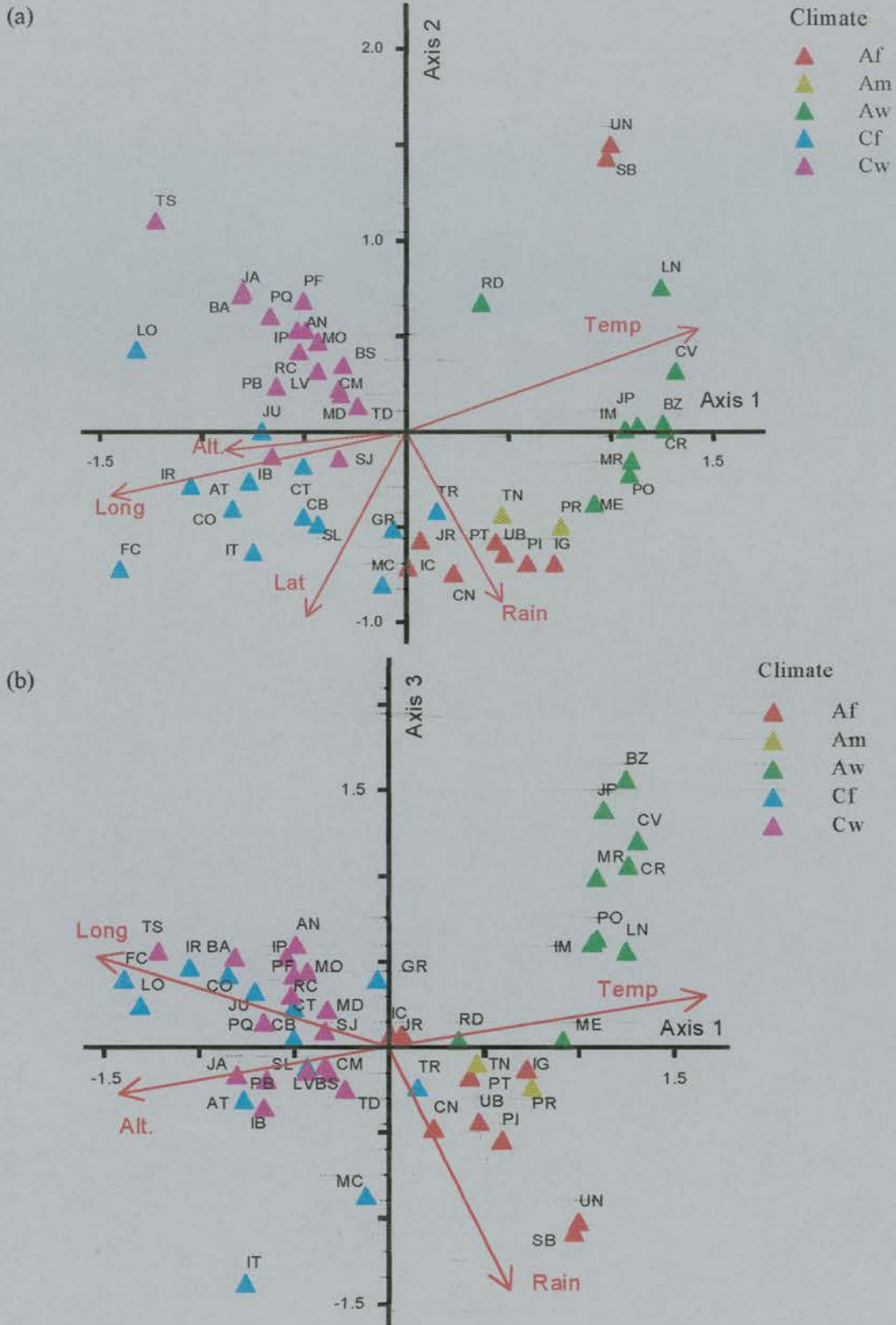


Figure 7.5ab CCA ordination of the Atlantic forest areas, (a) axes 1x2 and (b) 1x3. Arrows represent correlation between the axes and environmental and geographical variables: temperature, longitude and altitude (axis 1), latitude (axis 2), and rainfall (axis 2 and 3). The colours highlight the relationship of the main clusters with climate.

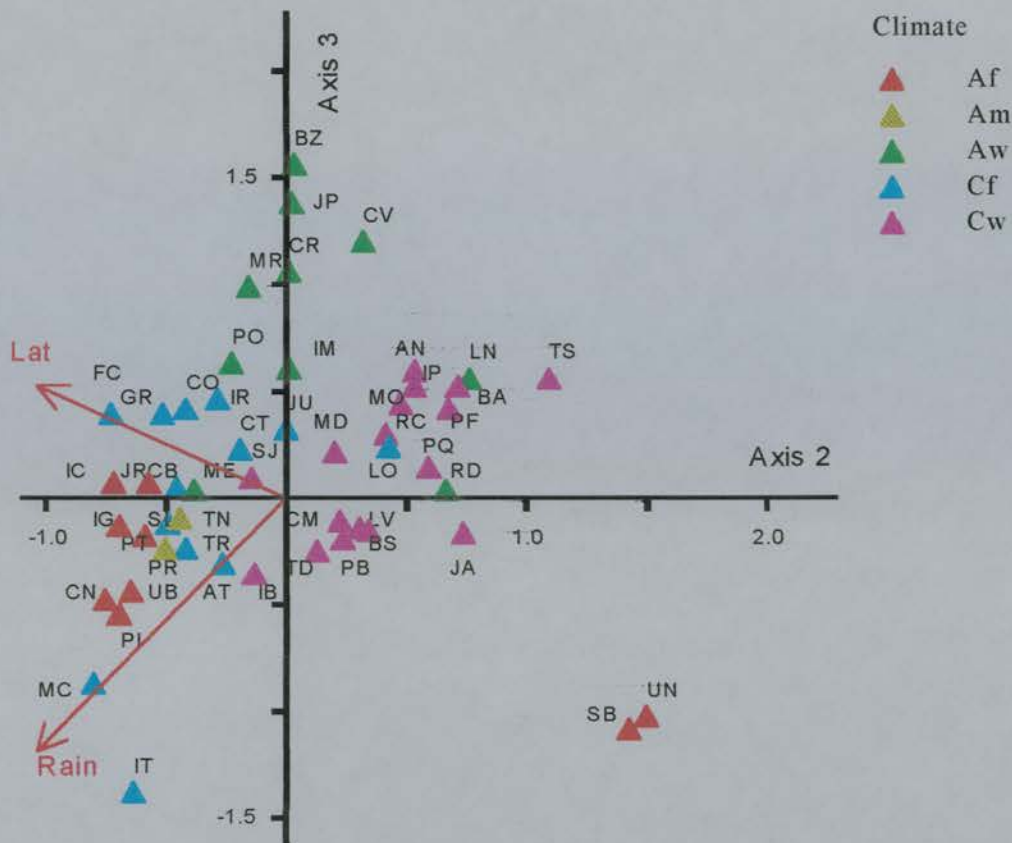


Figure 7.5c. CCA ordination of the Atlantic forest areas, axes 2x3. The arrows emphasise the position of the areas along a N-S gradient (lower right to upper left side), and a lower (upper right) to higher rainfall (lower left) gradient.

Table 7.3 Pearson and Kendall correlations with CCA ordination axes (N= 51)

	Axis 1		Axis 2			Axis 3			
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Lat	-0.423	0.179	-0.198	<u>-0.717</u>	<u>-0.514</u>	-0.500	0.322	0.104	0.103
Long	<u>-0.869</u>	<u>0.754</u>	-0.670	-0.029	0.001	0.027	0.110	0.012	0.135
Alt	<u>-0.781</u>	<u>0.610</u>	-0.590	-0.075	-0.006	-0.061	-0.340	-0.115	-0.240
Rain	0.061	0.004	0.036	-0.560	0.314	-0.502	<u>-0.719</u>	<u>0.517</u>	-0.584
Temp	<u>0.704</u>	0.495	-0.540	-0.310	-0.096	-0.181	0.306	0.093	0.176

The diagram on Fig. 7.5b (axes 1 and 3) shows a pattern related to the total annual rainfall. The areas with Aw climate were located above the third axis centroid, whereas areas with Af and Am climates were located below. On the left side, two high altitude areas from RJ (MC and IT) are separated from the other areas,

which form a large cluster along the third axis centroid. A distinct cluster can also be identified on the upper left side, including the mixed *Araucaria* and two seasonal forests (LO and TS). It is probably related to their longitudinal position (above 49° W), as longitude showed a good correlation with the first axis (see Table 7.3).

The last diagram (axes 2 and 3, Fig. 7.5c) again shows a clear distinction between the southern BA areas and two high mountain areas of RJ (MC and IT) from other areas with similar climate types. The lowland and *restinga* forests of RJ are again clustered on the central upper part of the diagram. The large cluster on the second diagram, formed by areas with close values along the third axis, splits into several smaller clusters. The seasonal montane semideciduous forests are located on the lower part of the right side, while the submontane forests are on the upper part of the same side. This cluster also included two dense forest areas (RD and LN, climate Aw) which were previously clustered with the southern BA forests. This can probably be related to both their latitude and a relatively drier climate. The centre left part of the diagram shows a cluster that includes the lowland and submontane forests of RJ and SP, plus a few montane areas (TR, CB and SL). Two montane semideciduous (AT and IB) are in a transitional position between this cluster and the cluster formed by the montane semideciduous forests of MG. On the upper left side, two lowland/submontane (GR) and montane (CT) dense and two montane semideciduous (SJ and JU) forest areas are clustered with the *Araucaria* forests, which might be linked to both a C climate and latitude.

The first diagram (Fig. 7.5a) is perhaps the one that allows a better interpretation of the results of the CCA ordination. The first two axes carry most of the information about the total variation along the environmental space (eigenvalue of 0.45 and 0.36 respectively). This can be better understood by examining Table 7.3. Four of the five variables show relatively strong correlation with axes one and two. Rainfall, the variable which shows the greatest correlation with axis three, also shows some correlation with the second axis ($r = -0.56$). Therefore, the relationships of the floristic composition of the areas with the environmental and geographical parameters, as well as among themselves, can be interpreted by examining the relative position of the areas along the ordination and environmental axes.

As already suggested above, the position of the areas along the first axis is clearly related to the climate type, either C on the left side, or A on the right side of the diagram. The high correlation of longitude, altitude and temperature with the first axis reinforces this interpretation. Altitude and temperature are two clearly negatively autocorrelated parameters ($r = -0.85$). The higher the altitude, the lower the average temperature, a parameter directly related to the differentiation between A and C climate types. The strong correlation of longitude can also be related to the climate. Due to the physiographical nature of SE Brazil, longitude values are directly correlated with the distance from the coast. Therefore, the first axis can be interpreted also as an E-W longitudinal axis, with a consequent increasingly longer dry season towards the west.

The vegetation classification of IBGE is based on both physiognomic and climatic aspects, with both altitude and the length of the dry or cold season adopted as criteria to distinguish between the different formations (Veloso *et al.*, 1991; see also Chapters 2, 3 and 8). A closer examination of the left side of the ordination diagram (Fig. 7.4a) reveals a gradient from the *Araucaria* (Mm) forests, through the montane moist forests (Dl and Dm), the montane seasonal (Fm), and finally the submontane seasonal forests (Fs). The submontane (Ds) and lowland (Db) moist forests (lower centre-right) are clearly separated from the higher altitude (lower left) areas. This side of the diagram also shows a coastal, longitudinal gradient, from the relatively colder areas of southern SP, through the wet forests of the Atlantic slopes (Serra do Mar) and lowland RJ, the drier northeastern coast of RJ (Pa, Fb), to the lowland moist forests of southern BA.

Although the other two diagrams (7.5b and 7.5c) in general show similar patterns of clusters, a few areas revealed a lack of consistency, i.e. were located in different clusters. LN and RD showed linkage to the southern BA forests (7.4a), to the lowland forests of RJ (7.4b), or to the submontane seasonal forests (7.4c); this could be related to a transitional nature of both areas. Macaé de Cima and IT are either linked to both the mixed *Araucaria* forests and the montane forests of SP (7.4a) or remain isolated (7.4b and 7.4c). On the last diagram (Fig. 7.4c), however, MC appears to be also linked to the coastal moist forests of SP (PI, CN and UB). The position of MC could be related to the extensive dataset used in the analysis, which

covered at least two formations (see Chapters 5 and 6). The same can be said of the GR area of coastal PR, which appears linked not only to the southern SP coastal areas (7.4a and 7.4b), but also to the montane seasonal forests (7.4b) and the mixed *Araucaria* forests (7.4c). The varying positions of two submontane seasonal forests appears to be related more to a geographical location, either further south (LO), or west (TS), in relation to the other areas of this formation. This suggests a climate with a colder or longer dry season, respectively.

CCA did not include non-quantitative or categorical variables in the correlation estimates (McCune & Mefford, 1997). However, some of the categorical data can be divided into two classes (0/1), which permits correlations to be made. Therefore, the climatic types (A/C) and subtypes (w/f, m subtype was included with f) were also introduced into the analyses as quantitative variables. The results (see Table 7.5) confirmed the high correlation between the floristic data and the main climate types ($r=0.89$).

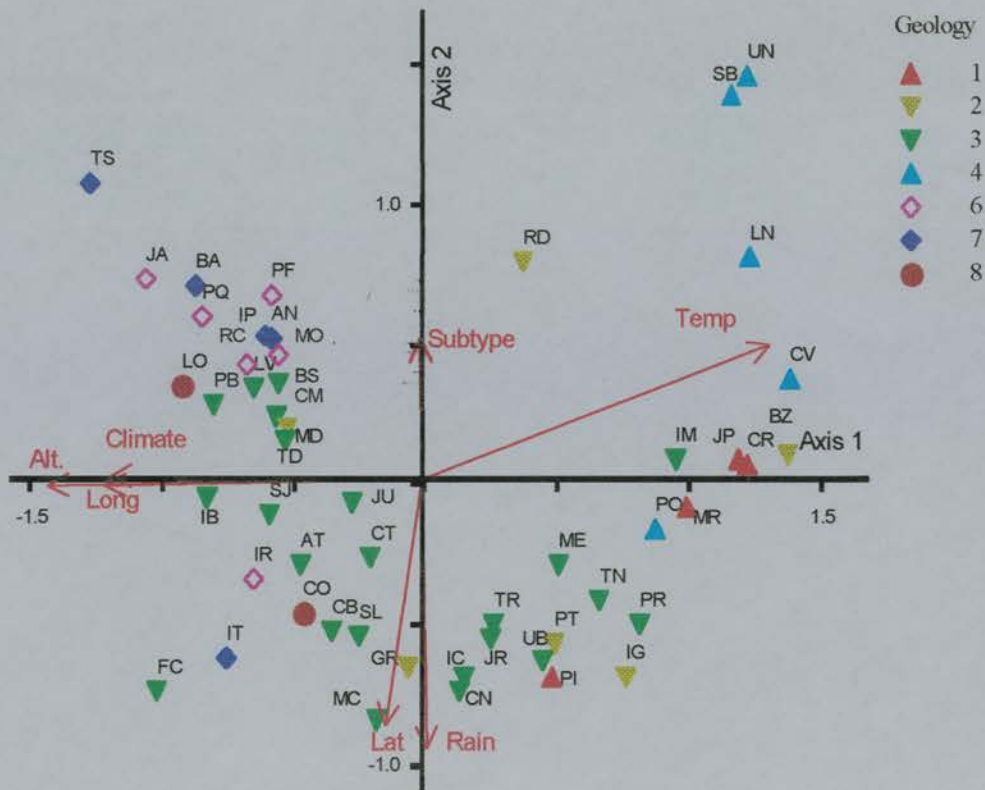


Figure 7.6a CCA ordination (axes 1x2), according to geology. It confirms the strong correlation between climate and the ordination axes 1 (main type) and 2 (subtype). The colour codes reveal a good correspondence between clusters and geology, highlighted by Quaternary (1), Tertiary (4), Pre-Cambrian (3), and Cretaceous (6) groups (Key on Table 7.2).

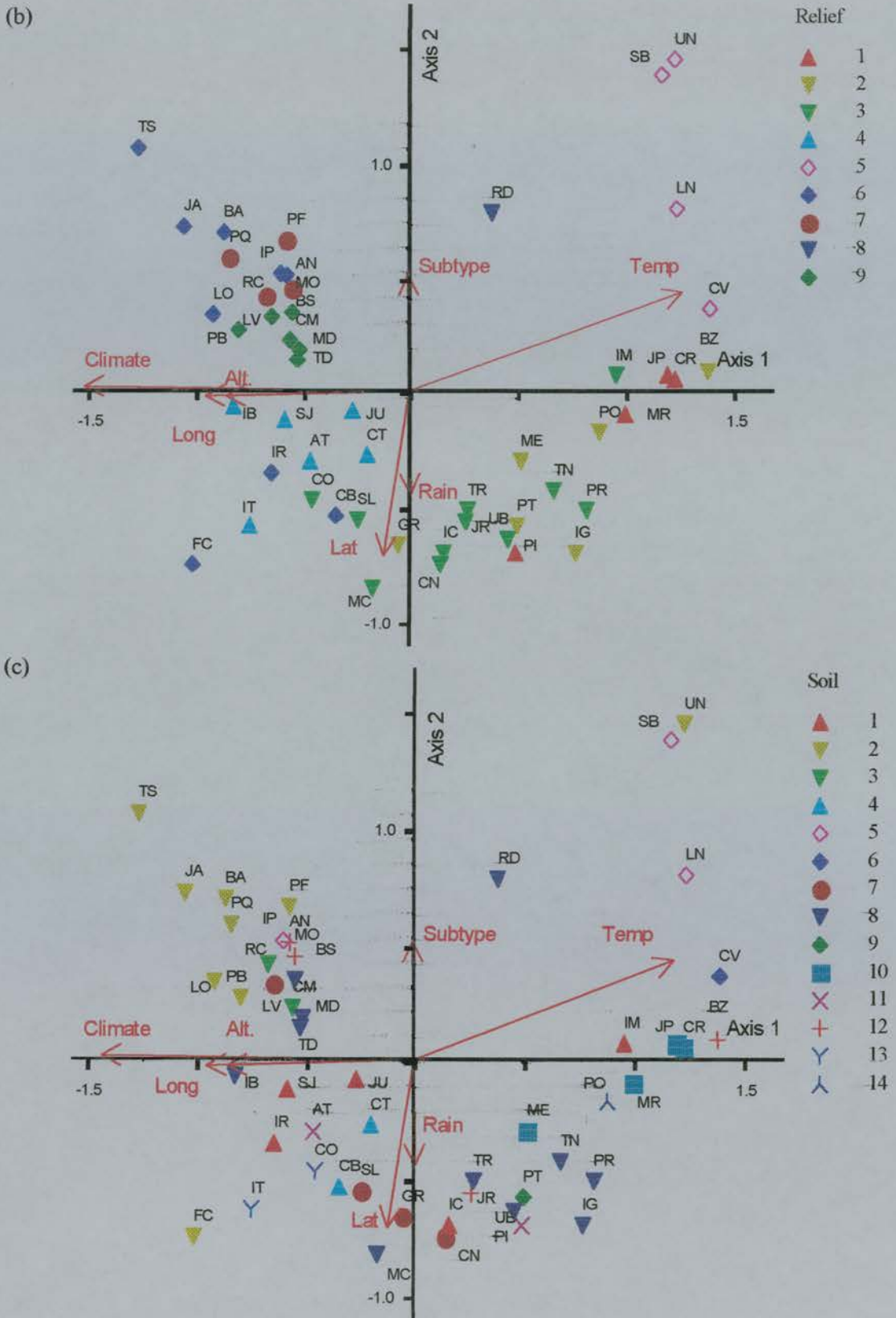


Figure 7.5bc CCA ordination according to (b) relief and (c) soil types (axes 1x2). The colour codes reveal a good correspondence between clusters and relief units, and in some cases soil types, such as eutrophic latosols (2) and hydromorphic (10) soils (Key on Table 7.2).

Table 7.4 Pearson and Kendall correlations with ordination axes, including distinction between the Koppen climate types and subtypes, N= 51

	Axis 1			Axis 2			Axis 3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Latitude	-0.304	0.093	-0.032	<u>-0.765</u>	<u>0.585</u>	<u>-0.550</u>	0.309	0.095	0.072
Longitude	<u>-0.795</u>	<u>0.632</u>	<u>-0.596</u>	-0.137	0.019	-0.037	0.100	0.010	0.112
Altitude	<u>-0.752</u>	<u>0.566</u>	<u>-0.500</u>	-0.141	-0.020	-0.102	-0.321	0.103	-0.226
Rain	0.082	0.007	0.062	<u>-0.547</u>	0.299	-0.475	<u>-0.723</u>	<u>0.523</u>	<u>-0.611</u>
Temp	<u>0.639</u>	0.408	0.449	0.374	0.140	0.229	0.299	0.089	0.197
Climate type	<u>0.888</u>	<u>0.789</u>	<u>-0.696</u>	0.081	0.007	0.123	-0.146	0.021	-0.078
Subtype	0.082	0.007	-0.119	<u>0.579</u>	0.336	<u>0.550</u>	<u>0.530</u>	0.281	0.429

The positions of the area along the two first axes (Fig 7.6) are similar to the previous diagram (Fig.7.5a), with basically the same main clusters. The diagrams show a good degree of correspondence between the clusters and the geology (Fig. 7.6a) and the relief units (Fig 7.6b). Most relief units are closely related to a common geological background. Although not as close, the ordination also shows a good correspondence between the clusters and soil types. These results show that both geology and relief, and in a lesser degree soil types, can help to explain the floristic links between the Atlantic forest areas.

7.7. Discussion

A general overview of the results of both classification and ordination of the Atlantic forest areas reveals some clear patterns that were repeated in all four techniques. The first aspect to be remembered is that the dataset used in the multivariate analyses included data from both floristic checklists and ecological quantitative surveys, with varying sampling intensities and geographical and environmental coverage. Although this can affect the results considerably, the use of different techniques, as well as of the environmental background data, should reduce the degree of uncertainty. As the geographical coverage of data collected by use of standard sampling methods is still very limited, this is an inevitable constraint. Due to the lack of both human and financial resources, this problem is not likely to be overcome in the near future.

The floristic patterns revealed in all analyses appear to be strongly related to both geographical and climatic variables. The characterisation of the areas according to the climatic types (Köppen classification) shows a good correlation with the floristic patterns, either at the main (types A and C) or secondary (types f, m and w) classes. The floristic links also show a good degree of relationship with both latitude and longitude. This can be probably associated with a decrease in the average temperature along the latitudinal (N-S) gradient, an increase in the length of the dry season along the E-W gradient, and also to the geographical distance between the areas. The CCA ordination reveals a clear longitudinal gradient along the coastal (rain) forest areas.

Altitude could also explain the floristic variation in part. The distinction between the seasonal submontane (< 750m) and montane (750-1300m) areas is apparent from all four techniques. This result reinforces what has already been found in other studies (Fontes, 1997; Oliveira-Filho & Ratter, 1995; Salis *et al.*, 1995; Torres *et al.*, 1997). Some seasonal forests appear also to be related either to high altitude Atlantic coast rainforests, or to the colder, mixed *Araucaria* forests. This group includes one area (IB) from MG, which, despite being located well within the seasonal forest region, has been described as a high-montane dense forest (Fontes, 1997). This can be explained by its location on a high altitude area along the eastern slopes of the Mantiqueira mountain ridge, characterised by a colder and wetter climate. Other high altitude areas from SP (AT, SJ, and JU) can also be included in this group, which could be perhaps be better characterised as a high altitude transition (ecotone) between the seasonal and evergreen montane forests.

Although the distinction based on altitude is also evident in the moist forest, the location of the areas within different altitudinal zones was not so clear-cut. Some areas show floristic links that appear to be independent of altitude, whereas others reveal a repeated pattern of relationships within the same altitudinal range in all analyses. This is more evident in most of the lowland and coastal tropical (A climate) forest areas. The contrasting results of the different methods might be related to both the altitudinal limit between the formations, and the altitudinal range of the data. The IBGE classification adopts either 50m (between 16-24° lat S) or 30m asl. (above 24° S), as the limit between the lowland and submontane, 500 or 400m asl. between the

submontane and montane, and 1500 or 1000m asl. between the montane and high montane formations (Veloso *et al.*, 1991). Oliveira-Filho and Ratter (1995) proposed the values of 250 and 750m asl. as a limit between the lowland, submontane, and montane forests respectively, which were adopted in this study. Fontes (1997) adopted the value of 1250m asl. as a limit between the montane and high montane formations. The classification of the Macaé de Cima forest plots (see Chapters Five and Six) shows that, although this value is approximately correct, local environmental conditions, related mainly to relief, can affect the altitudinal boundaries between the two formations considerably (Prance, 1992).

The results of the analyses do not allow precise or definitive values for the altitudinal limits between the rainforest formations for all SE Brazil to be established. The extensive altitudinal range of some data, covering two or perhaps even three formations, adds further noise to the analyses. The establishment of altitudinal limits between the coastal rainforests formations clearly needs further investigation. It could be based on data from quantitative surveys, covering all the altitudinal and latitudinal range. Nevertheless, even with these limitations of the dataset, some patterns of relationships appear to be more or less consistent.

The *restinga* forests of eastern RJ form a constant group that also include, in most cases, a coastal dry forest area (BZ), which is closely related both climatically and geographically. Another coastal semideciduous forest (CV) appears to be related either to this group or to the southern BA/ES forests. This can be partially explained by a greater distance from the other coastal forest areas and a similar geological setting with the 'NE Atlantic' group (Tertiary Barreiras formation).

The coastal lowland and submontane (lower-slope) rainforest areas form a heterogeneous group, whose floristic links appear to be related either to geographical (latitude) or environmental factors. The group can be subdivided into four groups. The first includes the areas located on the southern coast of SP, including GR (north PR), which appear to form a distinct group from those located on the state's northern coast or in RJ. This can be related to the influence of lower temperatures. This aspect is further supported by the links with some of these areas with higher altitude forests. GR, apart from being the most southern coastal area, includes trees from a wide altitudinal range (Roderjan & Kuniyoshi, 1988).

A second group includes the remaining coastal areas of SP, plus the wet slopes forest of RJ (climate Af and Am). This group also reveals links with both higher altitude areas (TR and MC) and the *restinga* forests. NT, PI, PT and IG, which are closely related both environmentally and geographically, were included in different clusters, according to the method. PT and IG included plants from both *restinga* and low-slope forests (Araújo & Oliveira, 1988; Marques, 1997), whereas PI, which was originally described as a *restinga* forest (Cesar & Monteiro, 1995), appears to be located on a *restinga*-lowland forest ecotone (F. Scarano, pers. comm.).

The third group includes the remaining lowland and lower slope forest of RJ, characterised by a Aw climate. This group reveals links with the former group, with the *restinga* forests and also with the southern BA/ES forests (CV, BZ and IN). Both geographical proximity and environmental (climatic) similarities can explain the first two links. Although the areas receive a considerably lower rainfall, in comparison with the former group, the proximity to the sea, with consequent high humidity could mitigate the effects of the high temperatures. Despite the lower precipitation during the winter months, in most of these areas there is not a real dry season sufficient to characterise seasonally deciduous behaviour of the forest canopy.

The fourth group includes the southern BA/ES forests. The two BA forest areas were clustered together in all techniques, including all the ordination (DCA, CCA) axes. LN however, is also linked to the northern RJ and even with the seasonal forests of SP/MG, which suggests a more intermediary, transitional nature. This group also includes in some analyses, the RD area of eastern MG, which can be perhaps explained by both geographical and environmental similarities. In the TWINSPLAN classification, RD occupied an intermediary position between the seasonal forests of MG/SP and the moist forests of the Serra do Mar slopes (coastal SP/RJ), whereas in the CCA ordination it was also clustered with the second group discussed above. This suggests a transitional nature for RD, emphasised by its climatic typology (A/Cw), which can be related to both its altitude and the distance from the coast.

The link between the northern RJ forests and the fourth group (southern BA and ES forests) is new information, which has not been previously detected, perhaps because of lack of reliable data (Oliveira-Filho & Ratter, 1995). Although there were

some indications of similarities, based on the distribution of particular taxa (Prance, 1979; 1992; Mori *et al.*, 1981), the southern BA/ES forests are normally considered to constitute a separated phytogeographical entity from the forests of SE Brazil. The existence of a hot, dry 'corridor' between the Doce and Paraíba do Sul river valleys (centre-south ES and northern RJ, see Figs. 3.1 and 3.2) is considered to provide a geographical and environmental barrier for both northward/southward expansion of taxa adapted to moister environments (Prance, 1979). However, the geology and relief similarities (Tertiary sedimentary plains, plus old-crystalline slopes) could also provide a relatively homogeneous environmental background, thus favouring the expansion of these taxa. The results of the analyses give some support to this last hypothesis, which must be further tested once more reliable data covering other areas of northern RJ, eastern MG, the entire ES and other southern BA areas become available.

The position of Macaé de Cima forest can also help to clarify both current and possible past biogeographical links. The analyses suggest close links with other rainforest areas of Rio de Janeiro, with montane and high montane areas of SP and MG, as well as with the mixed *Araucaria* forests. It appears also to be linked with the more southern coastal rainforests. The links between M. de Cima and the other areas can be related to mainly with a moist and/or cold climate, the relief and geology (slopes of the Serra do Mar mountain ridge, with mainly Pre-Cambrian crystalline rocks). The proximity of M. de Cima and other montane rainforests with the *Araucaria* forests also highlights the existence of close floristic links between the two forest formations. Both formations share many species, which perhaps could be adapted to a relatively wide range of climatic fluctuations, especially of temperature.

In summary, a tentative classification of the Atlantic forest areas used in this chapter is shown in Table 7.5. It is based on the results of the four multivariate analysis techniques, complemented by previous works on classification of southeastern Brazil forests, based on physiognomy, environmental and floristic data (Fontes, 1997; Oliveira-Filho & Ratter, 1995; Prance, 1989; Salis *et al.*, 1995; Torres *et al.*, 1997; Veloso *et al.*, 1991). The importance of the analysis results for the Atlantic forest biogeography, as well as for the forest management and conservation planning purposes will be further discussed in Chapters Nine and Ten.

Table 7.5 Classification of the Atlantic forest areas according to their physiognomic, floristic and environmental similarities (IBGE vegetation classes between brackets)

-
1. Dense, moist, evergreen forests of southeastern coastal Brazil
 - a) Lowland and lower-mid slopes of the Serra do Mar, northern SP and RJ, climate Af/m/w (Db/Ds): IG, PT, PI, UB, ME, PO, IM, PR and TN
 - b) Lowland and lower-mid slopes of the Serra do Mar, RJ, southern SP/northern PR, climate A/Cf (Db/Ds/Dm): JR, GR, IC, CN, CT, CB and TR
 - c) High altitude areas (> 1000 m), climate Cf (Dm/Dl): MC, IT, and SL
 - d) Lowland areas, southern BA/ES, climate Af/w (Db): UN, SB and LN
 2. Low thicket forests on coastal sand dune (*restinga*) and dry lands of eastern RJ, climate Aw (Pa/Fb): MR, CR, JP and BZ
 3. Transitional areas (ecotone), moist evergreen/seasonal semideciduous forests (ON)
 - a) High altitude areas of SP/MG, climate Cw (D/Fm): AT, SJ, IB and JU
 - b) Lowland-lower montane areas of eastern MG, northern RJ, climate A/Cw (Ds/Fb): RD and CV
 4. Seasonal semideciduous forests
 - a) Submontane areas (< 700m), west SP/PR, climate Cf/w (Fs): LO, AN, RC, BA, PF, PA, IP, JA, MO and TS
 - b) Montane areas (> 750m), southern MG, climate Cw (Fm): BS, CM, TD, LV, PB and MD
 5. Moist mixed *Araucaria* forests, highlands of PR/SC, climate Cf/w (Mm): FC, CO and IR
-

In the next Chapter, the spatial aspects of the forest-environment relationships within the study area will be investigated. The possibilities of using a spatial analysis approach for the study of the relationships between the Atlantic forest and the physical environment at broader scales will also be discussed.

CHAPTER 8. Spatial Analysis of the Macaé de Cima Reserve

8.1. Introduction

Land use and conservation planning deal with areas that vary from a few hectares to thousands of square kilometres. Therefore, the environmental data used in the planning process should reflect as far as possible the environmental variability across the spatial scales of interest to planners. At the same time, most detailed botanical and environmental information is normally only available at site level.

The spatial variation of vegetation across the landscape can be investigated by use of remote sensing tools and techniques. Both aerial photographs and satellite image systems can be used to analyse the spatial patterns and their relationships with the physical environment. Such analyses can be used for classifying and mapping the different vegetation types of a given area and for monitoring changes in the vegetation cover over time. Both offer invaluable information for forest management and conservation purposes. This chapter shows the results of the spatial analysis of the Macaé de Cima Reserve.

8.2. Land Cover Mapping

The land cover map of Macaé de Cima Reserve resulting from the interpretation of Black & White aerial photographs refers to the situation in 1970 (see Fig. 8.1). The land cover classes representing primary and secondary forests have been described in Chapter Five. The map extends beyond the Reserve boundaries, showing the extension of the land cover types reaching the main access roads. This helps to show the direction and extent of vegetation conversion into other land uses in the region.

The map shows that in 1970 most of the Reserve was covered by the montane forest formation, with a total area of 3846 ha (see Table 8.1). The next most important group is low or early growth secondary forest, covering 921 ha, and high or old growth secondary forests, which covered 807 ha. The mixed land use class, with a total area of 426 ha refers to those areas which included small areas of pasture

and agriculture along with secondary forests of varying degree of growth. Larger pastures covered 263 ha.

The high montane forest formation shows a relatively fragmented spatial pattern, with several small areas (10 ha in average) located on the tops of the mountains. These are well connected along the southern and eastern boundaries of the Reserves, which coincide with both the watershed divide and the municipal boundaries. A few small areas were classified as low forest. Although they can also be referred to as high montane forest, they show a different structure, with a much lower and more open forest canopy. Rock outcrops, which occur over a considerable part of the region, are mainly covered by sparse herbaceous vegetation.

Table 8.1. Land cover types in the Macaé de Cima Reserve (1970). Areas in ha.

Land Cover	Frequency	Sum. Area	Mean Area	Min. Area	Max. Area
Montane forest	2	3846.18	1923.09	956.58	2889.60
High-montane forest	33	351.01	10.64	0.28	34.57
Low forest	6	81.73	13.62	4.23	30.71
Rock outcrop	7	158.69	22.67	4.26	62.81
High-secondary forest	10	807.49	80.75	1.23	289.30
Low-secondary forest	18	920.95	51.16	0.87	199.91
Pasture	15	263.61	17.57	3.10	52.68
Mixed land use	8	426.42	53.30	10.54	109.49
Urban	5	25.38	5.08	0.00	12.55
Eucalyptus	1	2.06	2.06	2.06	2.06
Total/Avg	106	6883.51	217.99	98.32	368.37

The NW boundary represents a narrow urban area along the main road (RJ 116) that connects Nova Friburgo to the State's capital, Rio de Janeiro City. Finally, the map shows two *Eucalyptus* plantations, a small one near the Flores River, and a larger one along the main access road, near the Reserve boundary (see Chapter 6).

An overview of the map shows that the anthropogenic activities were concentrated on both sides of the access roads, along the Macaé and Flores rivers. The part of the Reserve belonging to the Rio Bonito basin appears to be in a better conservation state. This is probably related to difficulty of access at that time, as the only access road just reached the Reserve's eastern boundary. Apart from the facility of access, another important reason for the spatial pattern of human activities at the time is the local relief (see Section 8.3). As can be expected, both agriculture and pastures tend to concentrate on the lower to middle-slope areas.

REM Macaé de Cima Land Cover 1970

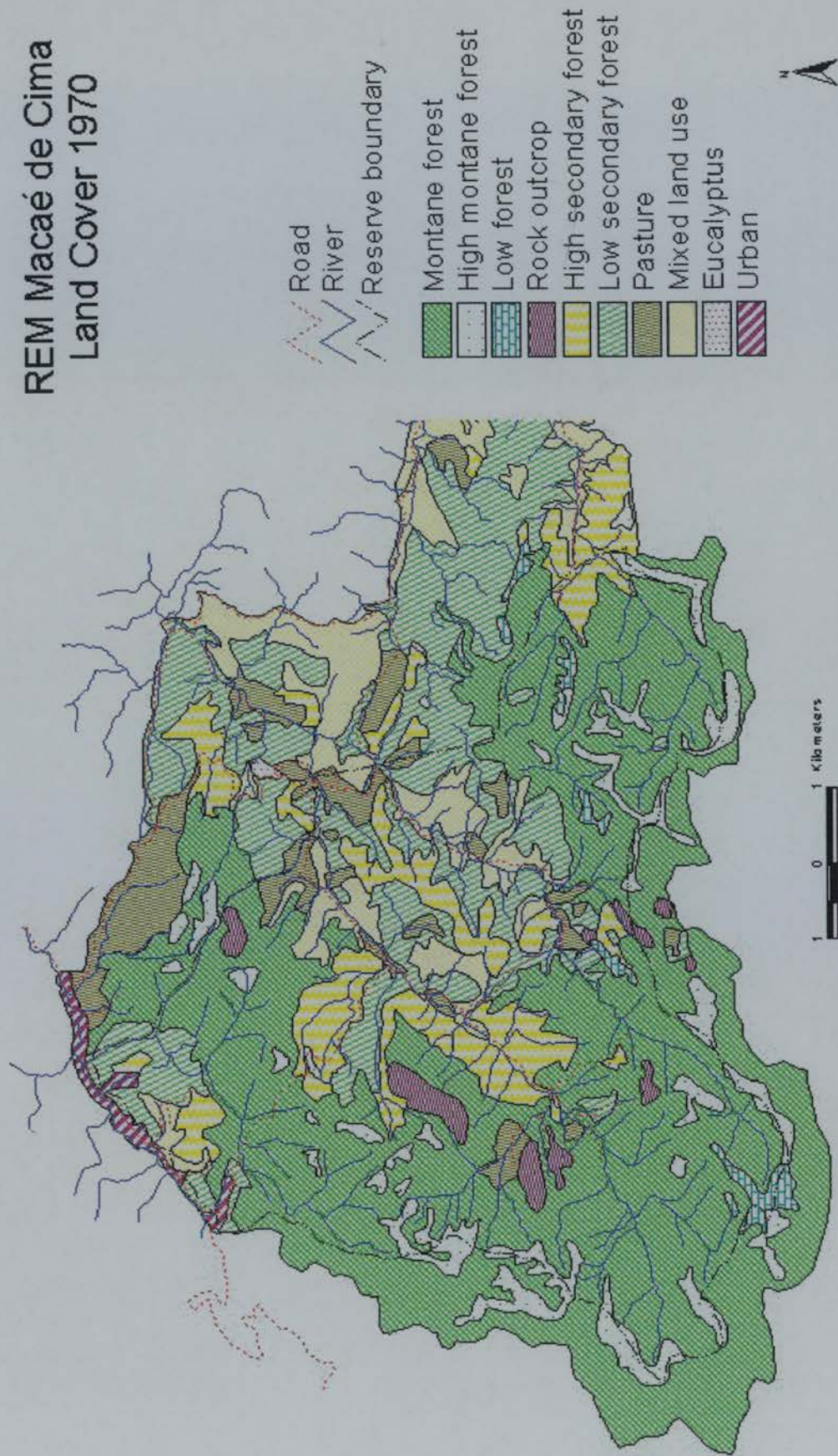


Figure 8.1 Land cover map of the Macaé de Cima Reserve, based on the interpretation of aerial photographs (1970)

Another important pattern, which is more apparent on the Landsat TM image (1996, see Section 8.4), is related to aspect. Most agricultural areas face northwards, reflecting a local, farm level trend, which can be related to the aspect (toward the sun). North facing areas receive more sunlight than those facing south especially during the winter, which is an important aspect in a region with a relatively cold and wet climate. This pattern also reflects a more regional trend, with an increase in agricultural land use from the colder and wet southern areas towards the warmer and drier northern areas, in a transition to areas originally covered by semideciduous forests (Ururahy *et al.*, 1983).

A further important aspect related to the relatively low intensity of agricultural land use in the area is soil fertility. The Macaé de Cima region in general consists of soils with a high acidity and low level of nutrients (see Chapter 6). However, the existing soil maps also show the occurrence of better soils in the drier and warmer areas north of the Reserve (EMBRAPA, 1992; Radambrasil, 1983).

As a whole, the map shows that agricultural land use and secondary forests of varying height covered significant portions of the Reserve in 1970. It also shows that, apart from well conserved forest areas located outside the municipal borders, two considerable areas of primary forests, including high montane forests (see Plate 5.1), were left outside of the Reserve boundary.

8.3. The Macaé de Cima Terrain

The landscape of the Macaé de Cima region is characterised by a steep relief, with narrow valleys and occurrence of granite rock outcrops (Radambrasil, 1983; Rosier, 1965, see Section 3.6). This can be analysed in a GIS using terrain-modelling techniques.

Digital terrain (DTM) or elevation (DEM) modelling is an important feature of most GIS. It permits an analysis of the terrain in combination with other spatial thematic data. One of the main utilities of DTMs is an estimate of the degree of slope, which is a fundamental aspect of land use planning. They can be used also as an input to environmental modelling, whenever terrain is an important factor (Goodchild *et al.*, 1993). The possibility of producing a three-dimensional image of the terrain is also an important utility of DTMs.

The analysis of the terrain of the Macaé de Cima Reserve was based on two different DTMs, using the TIN and TOPOGRID commands of the ArcInfo software. The TIN DTM is done by triangulation, producing a vector (lines) file. ArcInfo allows the visualisation of the DTM as a 3-Dimensional surface (Fig. 8.2), a grey or as a hypsometric surface, where the eleven altitudinal levels (80m intervals) are represented by different colours (Fig. 8.3). TIN also allows the estimating and mapping of the spatial distribution and area of different degrees of slopes. Figure 8.4 shows six classes of slopes for the Macaé de Cima region, expressed as percentage.

The TOPOGRID (Lattice) command works on a rectangular grid. The resulting DTM is stored as a raster (grid or pixels) file. The DTM based on the Lattice model (Fig. 8.5) shows the Reserve's terrain (buffer zone of 500 m) divided into ten altitudinal levels (80m intervals). TIN DTMs can also be converted from Lattice models, which can be represented as a grey surface, or also as a hypsometric surface (Figs. 8.3 and 8.6).

The precision of any DTM is related to the accuracy of the original data. Errors may arise from data input (digitising of contour lines) and also from the algorithms used in the transformation or interpolation of the data (triangulation or grid). The Macaé de Cima terrain characteristics make the use of the original contour line distance (20m) a difficult task, because of the amount of time required for digitising, as well as the proximity of one line to another in the more steep areas. The adoption of a 40m interval, although reducing the amount of labour, also reduced the accuracy on the terrain representation. The availability of updated topographic data in digital format and at a larger scale could improve considerably the Macaé de Cima DTM. Nevertheless, the results were considered to be compatible with the scale and objectives of the present work.

A visual comparison between the DTMs on figures 8.3 and 8.6 reveal a greater accuracy of TOPOGRID over TIN, with a better representation of the narrow valleys. The greater amount of computer time and memory needed are some of the constraints that are likely to become less important with the increasing power of computers. Both models provide a good view of the local terrain, and can be used as a basis for environmental studies and planning.



Figure 8.2 Three-dimensional view of the Macaé de Cima terrain (from SW towards the NE), based on a TIN DTM (approximate scale 1:105,000).



Figure 8.3. Hypsometric model of the Macaé de Cima terrain, derived from a TIN DTM (approximate scale 1:100,000). The colours represent eleven altitudinal levels (from 880m to > 1660m a.s.l., at 80m intervals).

REM Macaé de Cima

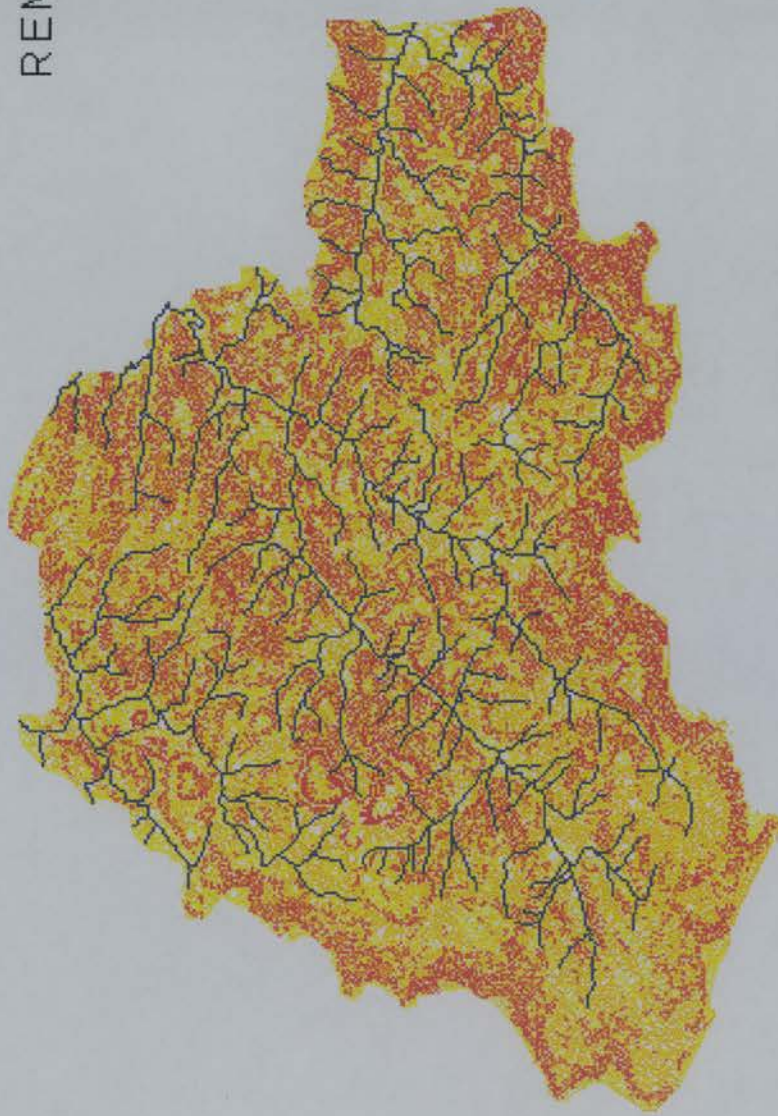


Figure 8.4 Map showing a plain view of the terrain of Macaé de Cima region divided into five slopes classes (%), estimated from a TIN DTM.

Dtm

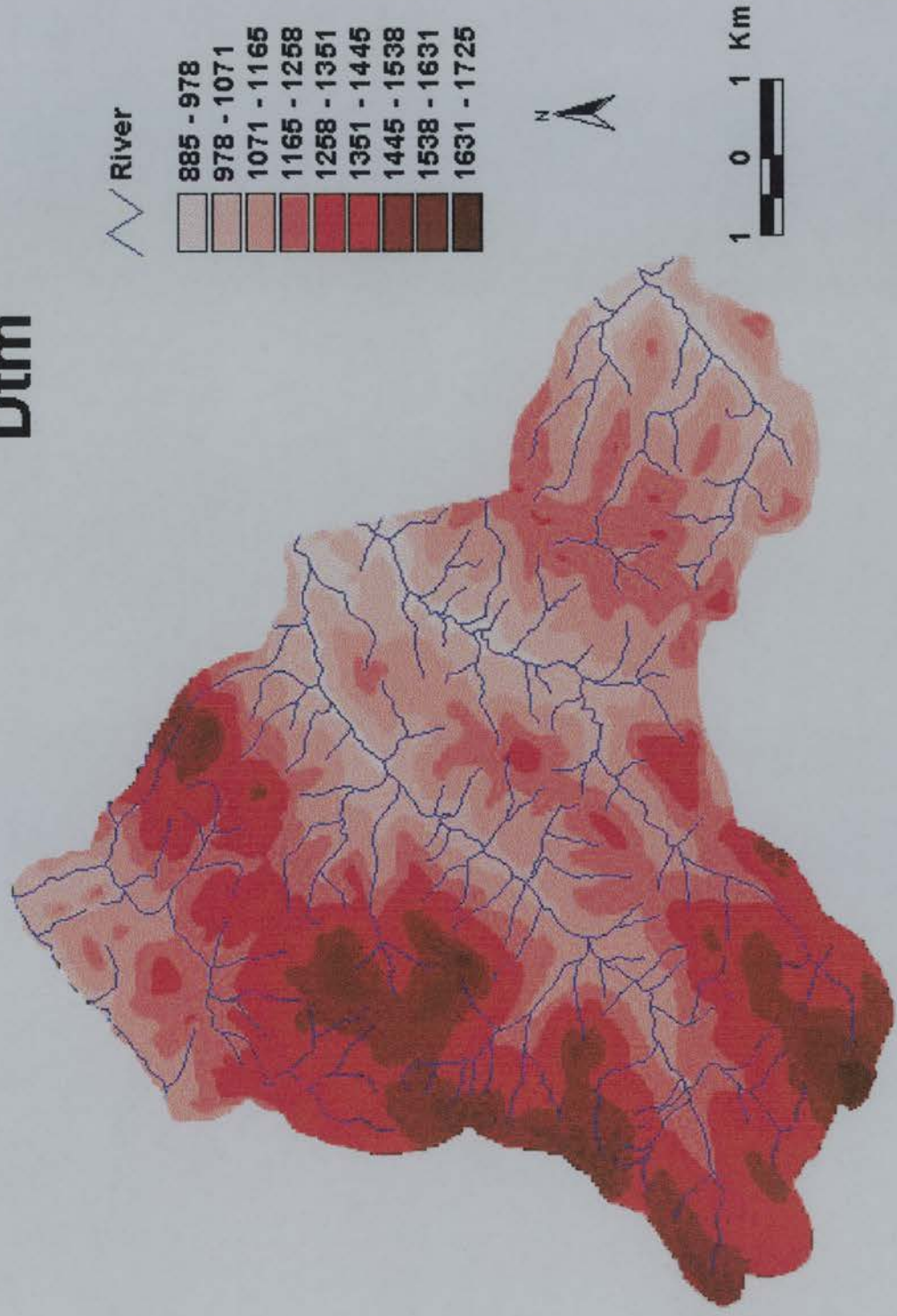


Figure 8.5 Map of the terrain of the Macaé de Cima Reserve showing nine altitudinal levels (meters), derived from a Lattice (TOPOGRID) DTM

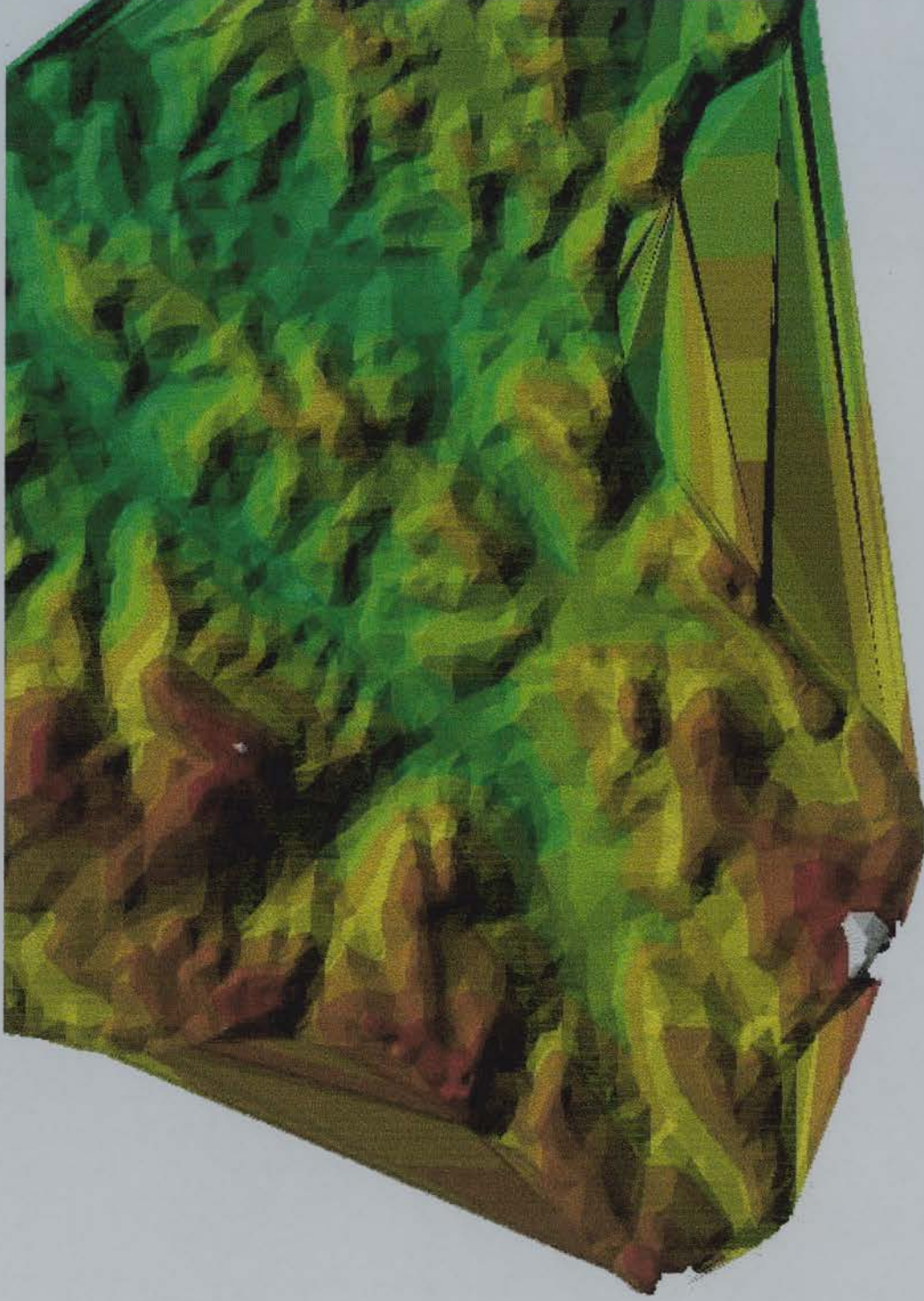


Figure 8.6 Hypsometric view in more detail of the terrain in centre south part of the Macaé de Cima Reserve, derived from a TIN DTM built from a Lattice (TOPOGRID), approximate scale 1:52,000. It shows a greater accuracy on the representation of the terrain, especially of the V-shaped valleys (the colours represent the same altitudinal levels as Fig. 8.3).

8.4. Digital Image Processing of Satellite Imagery

Both unsupervised and supervised classifications were performed on the Landsat TM image (1996), using the combination (RGB) of bands 4,5,2 (see Chapter 4). The result of the unsupervised classification is shown on Figure 8.7. Forest vegetation appears in different tones of green. The yellow represent open areas, either pastures or rock outcrops. The brown colour refers to other open areas, including also rock outcrops, pastures, agriculture or secondary vegetation on the early stages of growth. Areas in black are due to the shadow, on the SW steep slopes of the higher mountains.

Although the unsupervised classification could separate fairly well the forest from the non-forest vegetation, the distinction between different types of forest is not clear. The dark green tones refer mainly to primary or high, old growth secondary forests, with the light green representing areas with low secondary forest. However, a close look on the image reveals that the relief could mask the differences. The northern and top slopes receive more sunlight. Therefore, similar forests could be showing different degrees of reflectance, according to aspect. On the other hand the northern slopes are more likely to be cleared for agriculture than the southern ones. Comparing the classified image with the land cover map (Fig. 8.1), the areas with dark green tones can be classified either as primary or high secondary forest. However, areas in light green could be low or high secondary, and even primary forest, depending on their aspect and position on the slope.

Some rock outcrops did not show up on the image, or appeared covering a much smaller area than suggested by the land cover map (Fig. 8.1). This can be explained by the fact that low, herbaceous vegetation, which shows a similar reflectance to pastures or low secondary vegetation covers most rocks. The size of the rock outcrops might have also been overestimated in the interpretation of the aerial photographs.

The *Eucalyptus* plantation near the northern Reserve border appears in brown, undistinguished from the open areas. The unsupervised classification also did not distinguish the small urban area along the RJ 116 road. Finally, the classification was not able to distinguish the montane from the high montane forest formation. The result of the structural analysis (see Chapter 5) revealed that both formations have

similar basal areas and average canopy height, properties that are associated with biomass and cover, aspects that more strongly affect vegetation reflectance (Spies, 1994). The two forest types could be distinguished on the aerial photographs only based on 'texture'. Montane forest showed a more rugged texture, due perhaps to the effect of the steep relief, an irregular canopy, and the occurrence of forest gaps of varying size.

The land cover map resulting from the supervised classification (Maximum Likelihood) is shown in Figure 8.8. The provision of a training set, based on areas where the land cover was known (urban, pasture, *Eucalyptus*, primary and secondary forest) did provide a clearer result. There was a better distinction between the non-forest cover types when compared with the unsupervised classification. Urban areas and rock outcrops (dark blue) and the *Eucalyptus* plantation (light grey) could all be distinguished.

The distinction between different types of forest (light blue and grey), including differentiation between primary and high, old-growth secondary forests was again masked by the effects of the relief. Also, several pixels scattered across the Reserve area were incorporated into the *Eucalyptus* class (dark grey). The fieldwork did reveal the occurrence in many areas of both *Eucalyptus* and conifer trees (*Pinus*, *Araucaria*), scattered or along the roads and fields, as windbreaks or living fences. However, their occurrence was exaggerated by the classification. This might be explained by the influence of their canopy in the average reflectance value within a single pixel, or by the reflectance similarity with other objects. The location of some of the pixels suggests a higher similarity with natural or secondary forest vegetation that can be related to a single or a group of native tree species.

The digital classification of the Landsat TM image confirmed both the strengths and limitations of the sensor for forest mapping. An important limitation is related to the relative small size of features in relation to the minimum pixel size (currently 30x30m). The relatively small size of many of the farms which also affects the size of agricultural fields and interventions in the natural vegetation, make it very difficult to map and characterise these areas.

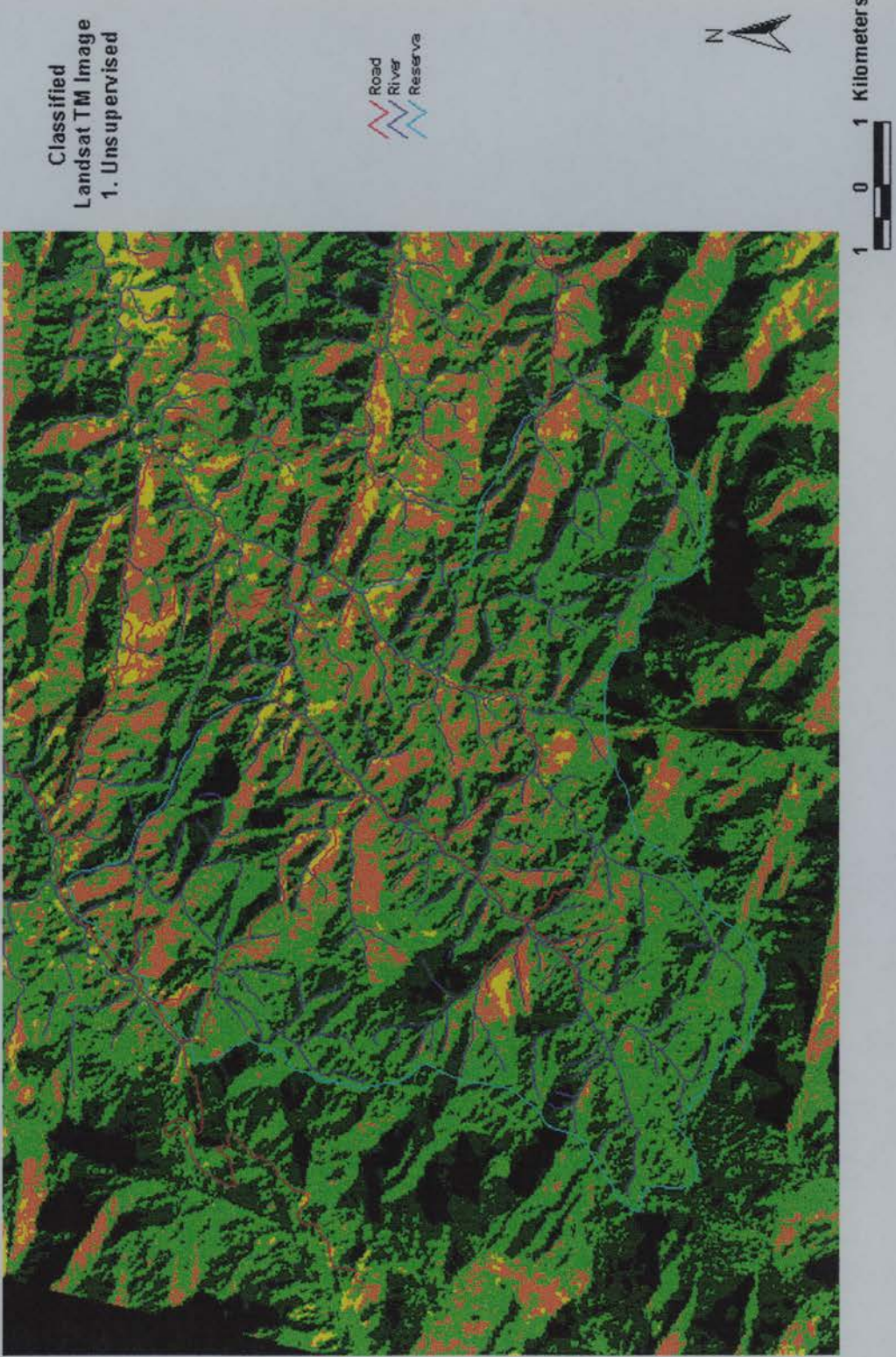


Figure 8.7 Unsupervised classification of Landsat TM image. Open areas in brown and yellow, forest in different tones of green, shadow in black.

Landsat TM
Supervised classification

Reserva



1 0 1 Kilometers

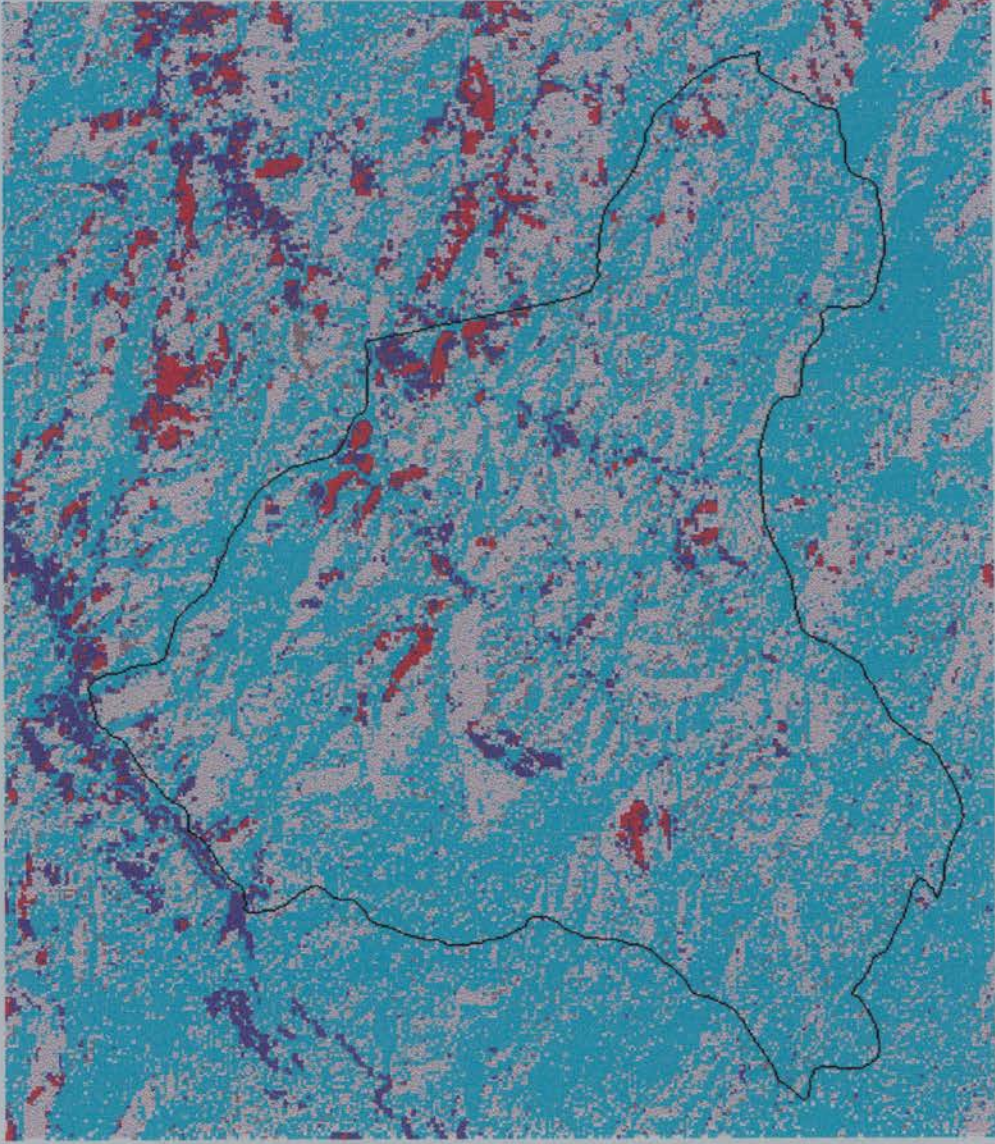


Figure 8.8 Supervised classification of Landsat TM image, showing open areas in dark blue and red, forests in light blue and light grey and *Eucalyptus* in dark grey.

Another important limitation refers to the difficulties in classifying the different forest types, including secondary forests. Great advances in the classification of secondary forest with different ages or canopy heights have been obtained in relatively flat areas of the Amazonia, with a recent and well known history of human intervention (Foody *et al.*, 1996, 1997; Lucas *et al.*, 1996). Differences in vegetation related to drainage (Mertes *et al.*, 1996) or seasonality (Garcia & Alvarez, 1994) can also be detected. However, the detection of different forest types on closed canopy forests on hill terrain is a much more difficult task (Foody, 1996; Hill, 1995; Kalliola & Syrjanen, 1991)

Differences in the reflectance levels of the Macaé de Cima forests on the other hand are strongly affected by the steep relief of region, with occurrence of large shadows and different colour intensities related to aspect. It is difficult to detect whether the pixel values reflect real differences in the forest canopy structure or are simply the effect of different degrees of illumination. The effect of relief could be mitigated by use of sophisticated techniques for topographic normalisation, which was beyond the objective of this work. The availability of new sensors in the next few years, with greater levels of spatial resolution could improve considerably the current situation. The use of images based on a radar sensor (Palme *et al.*, 1996) is also another promising area that might be better explored.

Despite these limitations, the possibility of detecting areas with strong human impact, as well as the temporal scale of the repeating imagery, allowing a continuous monitoring with standard data, are important advantages that must be taken into account. The facility of integrating satellite images with other spatial thematic data stored in a GIS is also an important factor. The overlay of digital thematic data with the satellite image can be used to improve the classification. Conversely, satellite data can be used to improve and/or update spatial thematic data (see Section 8.5 and 9.5). The increasing availability and accuracy of Global Positioning Systems (GPS) can considerably increase the accuracy on the location of ground control points. This can improve not only the geometrical correction of image, as well as the combined use of image and field ecological and environmental data in the spatial analysis.

The use of the structural data from the forest plots in the analysis of the image data was not possible due to the relatively small variation of the forest structure.

There were also difficulties in locating the different sites accurately, using low precision handheld GPS or maps (see Chapters 4 and 5). However, these data still can be used in combination with data from new, additional plots. This could improve the spatial distribution of the ecological data, thus reflecting more accurately the heterogeneity of the Macaé de Cima forests. New and more accurate (differential) GPS could also be used to locate more precisely the current plots. These data could then be used to analyse the correlation of the forest structure with the image reflectance values, considerably improving the forest classification and mapping (Lewis, 1998).

In summary, the main achievements of the digital analysis of Landsat TM image were the detection of changes in the land use, notably the distinction between forest and non-forest areas, including the separation of monocultural forest plantation (*Eucalyptus*) from the natural forest. The main constraints at present are the lack of precisely located coordinates (GPS technology) and the relatively coarse spatial resolution of the Landsat TM in relation to the Reserve area. However, the results do indicate a greater potential of the TM sensor for mapping and monitoring at slightly broader spatial scales (see Section 8.6), especially when viewed against the probable improvements in resolution over the next decade. Digital image processing is likely to become a tool of increasing relevance and practical value.

8.5. Landscape Ecology of Macaé de Cima

The integrated analysis of the Macaé de Cima landscape combined the results of the analysis of relationships between the forest vegetation and the physical environment at local scale (Chapters 5 and 6) with the spatial analyses described in the previous sections of this chapter. This included an overlay analysis of the land cover (1970) and classified image (1996) maps, the terrain (DTM) maps and other thematic maps (vegetation, soil, geomorphology, geology) available for the area. An overview of the results of both local and spatial analyses was the basis for the design of a Landscape Ecology map of the Macaé de Cima Reserve (Fig. 8.9), according to the descriptive approach of the landscape ecological analysis (Jongman *et al.*, 1995; Vink, 1983; Zonneveld, 1995).

The results of the both PCA and CCA ordinations (Chapter 6) revealed the existence of correlations between the site environmental characteristics (soil parameters, relief) and the forest vegetation. Unfortunately, there are no soil data available at scales equivalent or approximate to the other spatial data. The available data (EMBRAPA, 1992) show only broad soil classes (see Table 3.2). The solution adopted was to use these classes in combination with the geological maps and the terrain models in order to refine the information on the spatial distribution of the main soil types. This resulted in the establishment of a physical setting, which reflects the topological relationships between the main parameters of the physical environment, and between them and the vegetation (Zonneveld, 1988d, 1995).

The map legend reflects a hierarchical classification of the Macaé de Cima landscape (van Gils, 1989, Zonneveld, 1988d, 1995), with the ecological or land cover classes grouped according to geology. The main classes refers to the geological mapping units (see Appendix 3 for description) Santo Eduardo (1), São Fidelis (2), Desengano (3), Paraíba do Sul Complex (4) and Holocene deposits (5). The vegetation or land cover classes were then divided according to the main mapping units (see Table 3.2 and Appendix 3 for soil classes description).

The Landscape Ecology map should be seen as a first approximation. Additional pedological and geomorphological information, based both on the existing and additional field data, would allow a better definition and characterisation of land units. Additional vegetation data could also shed more light on the understanding of the relationships between the vegetation and the local physical environment. However, it could be used immediately for an initial zoning of the Reserve, as a part of a management plan, which must include measures for the protection of the areas in a good state of conservation. Such a plan could also improve the management practices in the disturbed areas, including control of fire and of selective extraction of forest products, and of hunting.

To illustrate how the spatial information could be used in the Reserve planning, an exercise was carried out, based on the current Brazilian Forest Law (Decree No. 4771, 1965), and on a theoretical extension of the edge effect on forest-agriculture field borders. The Law prescribes the conservation along river courses of areas with a size proportional to the river width. The minimum value of 20 m was

adopted in the exercise. The extent of the edge effect on tropical forests depends on several factors, including land use history and the organisms affected. The value of 100 m was adopted as an approximation, based on theoretical and empirical evidence from Atlantic forests (Laurence, 1991; Waldhoff & Viana, 1993).

The first procedure adopted was to overlay both buffer zones on the Landscape Ecological map (see Fig. 8.10). The resulting layer shows the spatial distribution of the river buffer zones in relation to the land units. This helps to select priority areas for protection or restoration (inside agriculture areas). The map also shows the extent of forest areas that might be affected by the edge effect. Most of them are covered by secondary forest, but areas of primary montane forest might also be affected. These areas may have a lower conservation value for several interior forest species.

The exercise can illustrate some of the steps in which the spatial database could be used for the Reserve zoning, according to certain criteria (see Fig. 8.11). The areas of greater priority in terms of protection (Zone 1) include all the high montane forests. Montane forests located in high steep relief and shallow soils could also be selected, by use of the DTM. In this zone any type of extraction of forest products should be forbidden, and human access should be restricted, to avoid impacts on wildlife. The remaining montane forest areas (Zone 2) should also be conserved, although some type of limited extraction in a sustainable basis (e.g. palm heart from *Euterpe edulis*) could be allowed.

The areas with secondary forests could be used as buffer zones between the disturbed and the natural areas (Zone 3). The type and intensity of management should depend on the forest structure and composition, location on relief, and distance from Zone 1 and 2. The 100 m wide buffers surrounding intensive land use (agriculture, pasture, urban, Zone 5) areas should have priority for monitoring, to avoid or reduce possible impacts of fire, invasion by domestic animals, etc, the natural vegetation and wildlife. Activities with potential low impact on the natural environment such as fish farming (trout), ecological tourism or rock climbing (Zone 3), could be allowed, but carefully monitored. Smallholder agriculture, including agroforestry, should be restricted to areas already disturbed, on the foothills and on better soils (red-yellow Latosol, LV).

REM Macaé de Cima Landscape Ecology Map

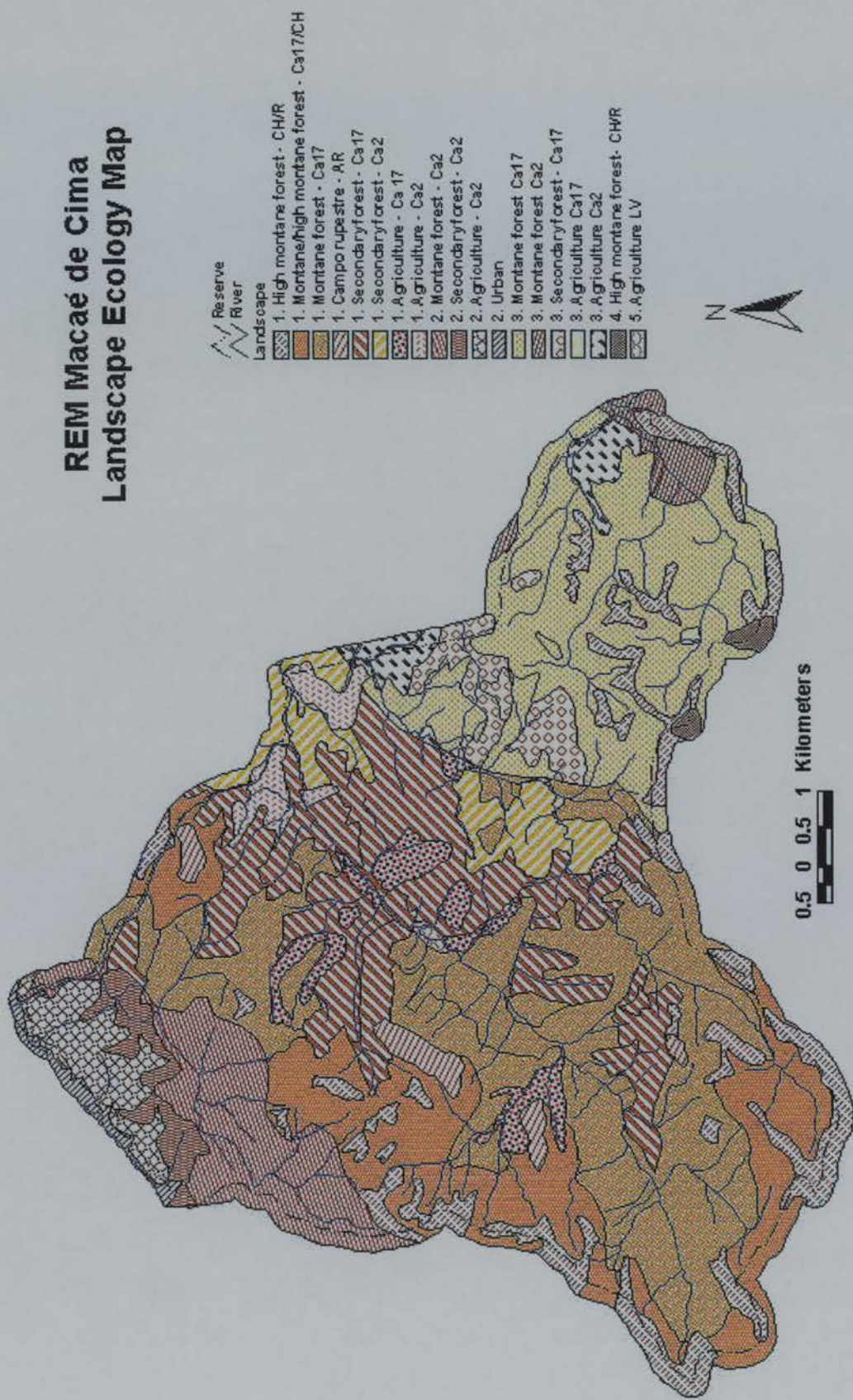


Figure 8.9 Landscape Ecology map of the Macaé de Cima Municipal Ecological Reserve, showing the spatial distribution of the proposed Land Units.

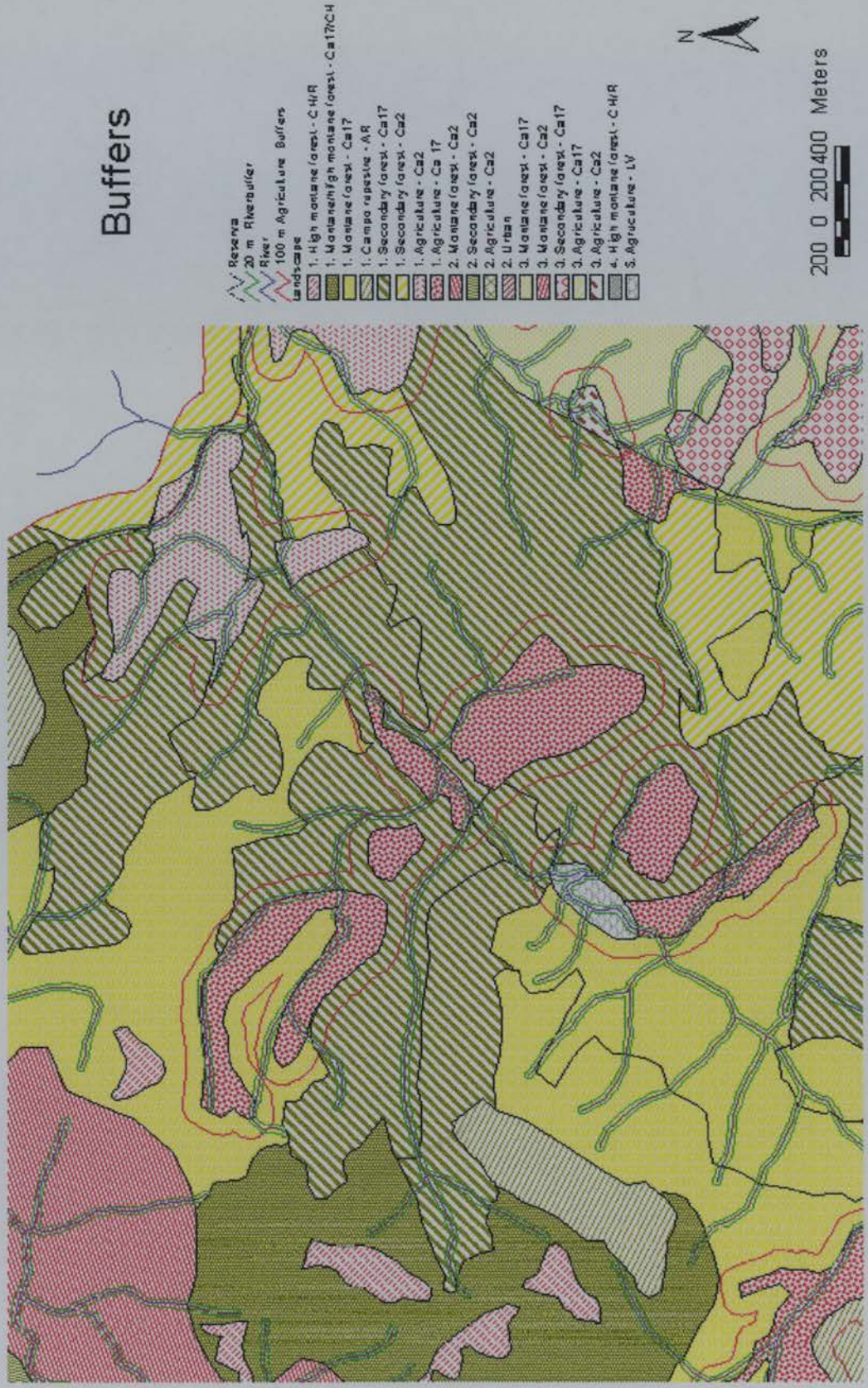


Figure 8.10 Detailed (zoom) view of some of the proposed Land Units on the central part of the Reserve, combined (overlay) with buffer zones along the river courses (20 m each side), based on the current Forest Code, and forest edge zone (100 m wide), surrounding agricultural areas.

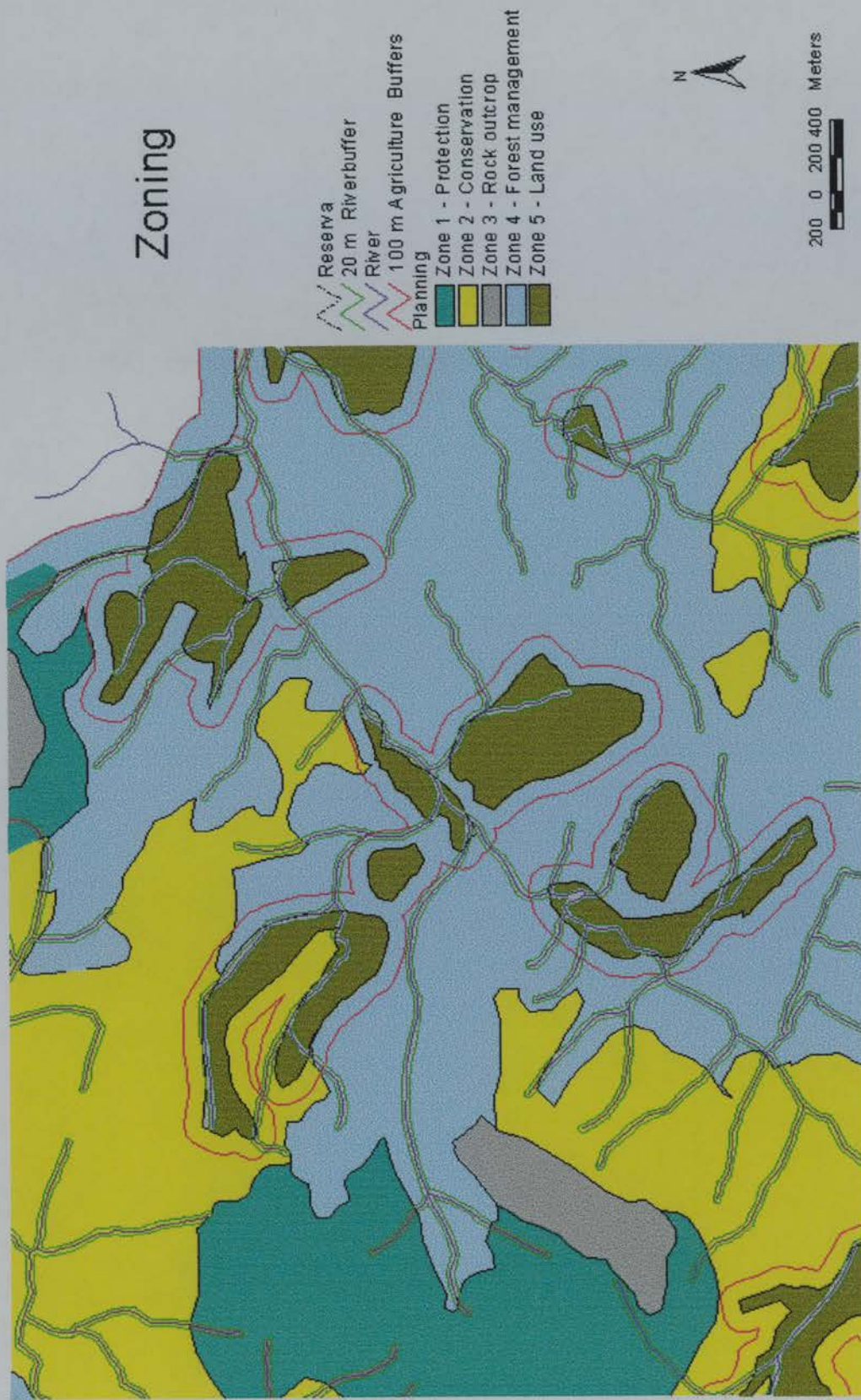


Figure 8.11 Detailed (zoom) of the resulting Zoning on the same area as Fig. 8.10, including the buffer zones along river courses, and the forest edge zone (100m wide), surrounding agricultural areas.

8.6 Land cover of the eastern region of Rio de Janeiro

The previous sections have shown the potential for ecological research and land use planning of tools that deal explicitly with spatial data. The approach used in the spatial analysis of the Macaé de Cima forest could be used in other areas with similar environments in Rio de Janeiro State or within the Atlantic forest region. This approach could also be adapted for studies at a regional level, or broader scale. Data from sites that represent different types of environment could be employed to investigate the relationships between the vegetation and the physical environment (see Chapter 7). The results of these analyses could be used in combination with thematic spatial data, in order to investigate the spatial variability of vegetation at a broader scale.

To help to illustrate how this approach could be implemented, a spatial analysis was carried out at a regional level, covering the eastern region of the Rio de Janeiro State (see Fig. 3.3). The reasons for selecting this particular area were the availability of a good spatial environmental dataset for the area at a uniform scale (1:250,000), including the full scene Landsat TM imagery. In addition to Macaé de Cima, three other areas (Poço das Antas, Jacarepiá and Búzios) included in the biogeographical analysis (see Table 7.1) are located in the region. Four additional areas (Teresópolis, Paraíso, Maricá and Carapebus) are located just outside the map area. The region includes several conservation units including the Poço das Antas Biological Reserve, home of the endangered primate Golden Lion Tamarin (*Leontopithecus rosalia*), Jacarepiá and Massambaba Environmental Protection Areas, and the Pau Brasil Reserve, in Cabo Frio. Therefore, the region is suited to illustrate how an integrated analysis of the landscape can be carried out at a broader spatial scale.

An overview of both spatial environmental data and the floristic data from the eight areas reveals a significant heterogeneity in the physical environment and vegetation in the region. The original vegetation cover included alluvial, lowland, submontane and montane dense and semideciduous forests, *campo rupestre*, *restinga* and dry thicket forest vegetation, wetland and mangrove (Ururahy *et al.*, 1983). This heterogeneity reflects the large annual rainfall range (800-2500mm), the geology and soils, and the local relief, with altitude varying from sea level up to 2000m asl.

An unsupervised classification was performed in the full scene of the Landsat TM image (bands 4,5,2), using 10 spectral classes. The resulting maps (Fig.8.12 and 8.13) show areas with dense vegetation in light and dark blue. The green, yellow and red colours refer to open areas, including coastal areas with sand dunes. White areas are either water bodies or misclassified pixels. The result reveals the difficulty of classifying the vegetation cover accurately by unsupervised methods. Although it did allow the separation of forest from non-forest areas, it included in the two forest classes several different forest types, including the coastal *restinga* and thicket forests. The differences between dark and light blue might be related to both density and relief.

Further processing of the image, including masking the water body areas and increasing the range of pixel values within the land areas through re-sampling could improve considerably the contrast between different cover types. A supervised classification, based on a training set target areas representing well known cover types could then be applied. This stage requires good ground control, which is not available consistently over the area at present.

The classified image helps to show the spatial distribution of the remaining forest areas. It shows that, apart from Poço das Antas Reserve and the southern upper slopes of Serra dos Órgãos mountain ridge, including Macaé de Cima, only a few scattered forest fragments areas remain in the region.

Colour composite (bands 3,4,5, or 4,5,2) or classified images can be overlaid with digital thematic data in a GIS, to check for possible spatial correlation between patterns in the image and environmental variables. This was done using both Erdas IMAGINE and ArcView softwares, combining thematic (soils, vegetation, relief, drainage and built environment) data at 1:250,000 scale with the full scene image (see Figs. 8.11 and 8.12). New human-made features (canals, roads) were clearly visible in the image. Differences in the boundaries of some vegetation, soil and relief mapping units and patterns on the image were also apparent. This indicates a potential for directing new field-checks, in order to confirm if these patterns are related to real differences on the ground.

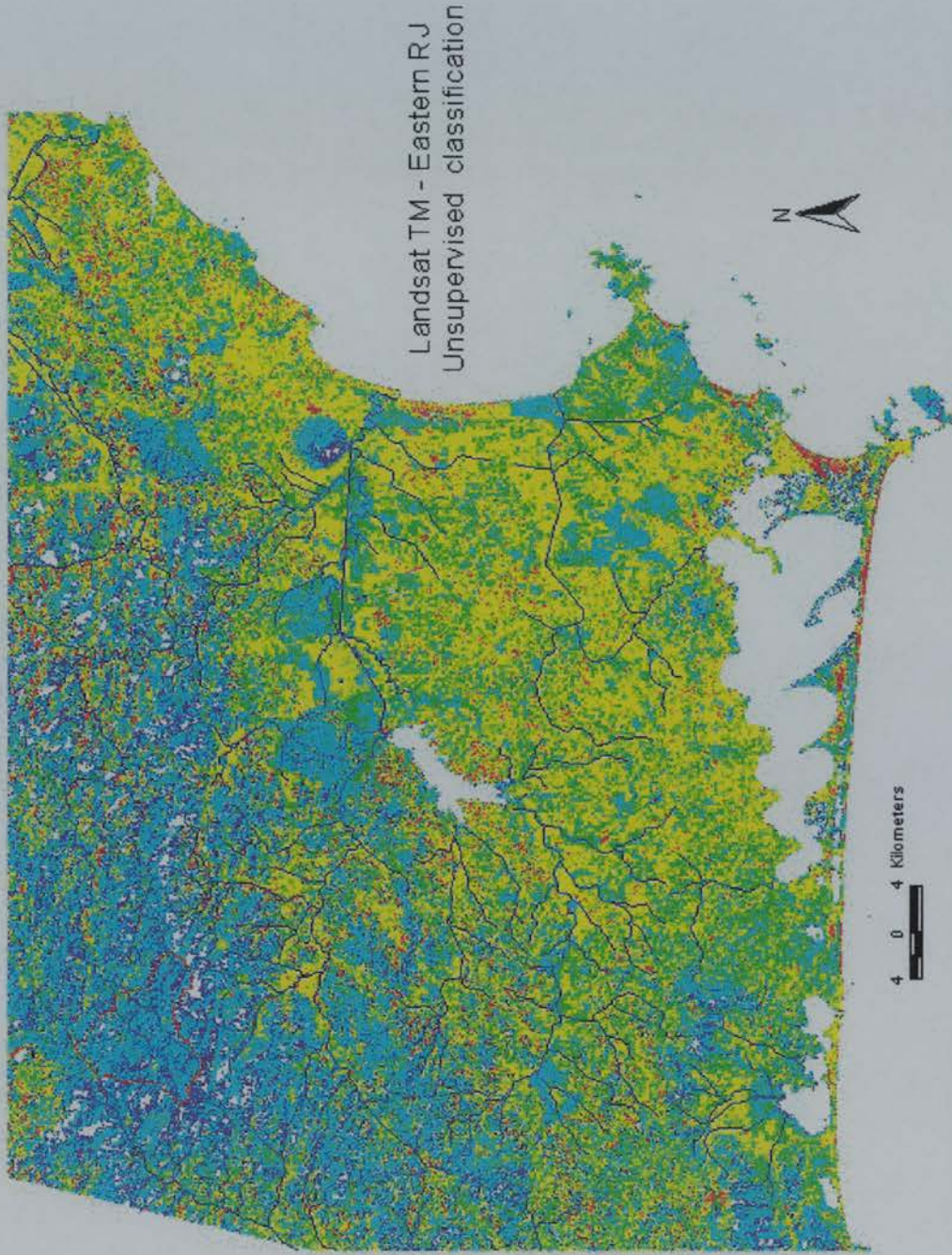


Figure 8.12 Unsupervised classification of the Landsat TM scene covering the eastern region of Rio de Janeiro (Macaé de Cima Reserve on the upper left). Dark and light blue are dense, woody cover, green and yellow are open vegetation (agriculture, pasture) and urban areas, red is bare soils, including sand dunes. White areas are water bodies or misclassified pixels.

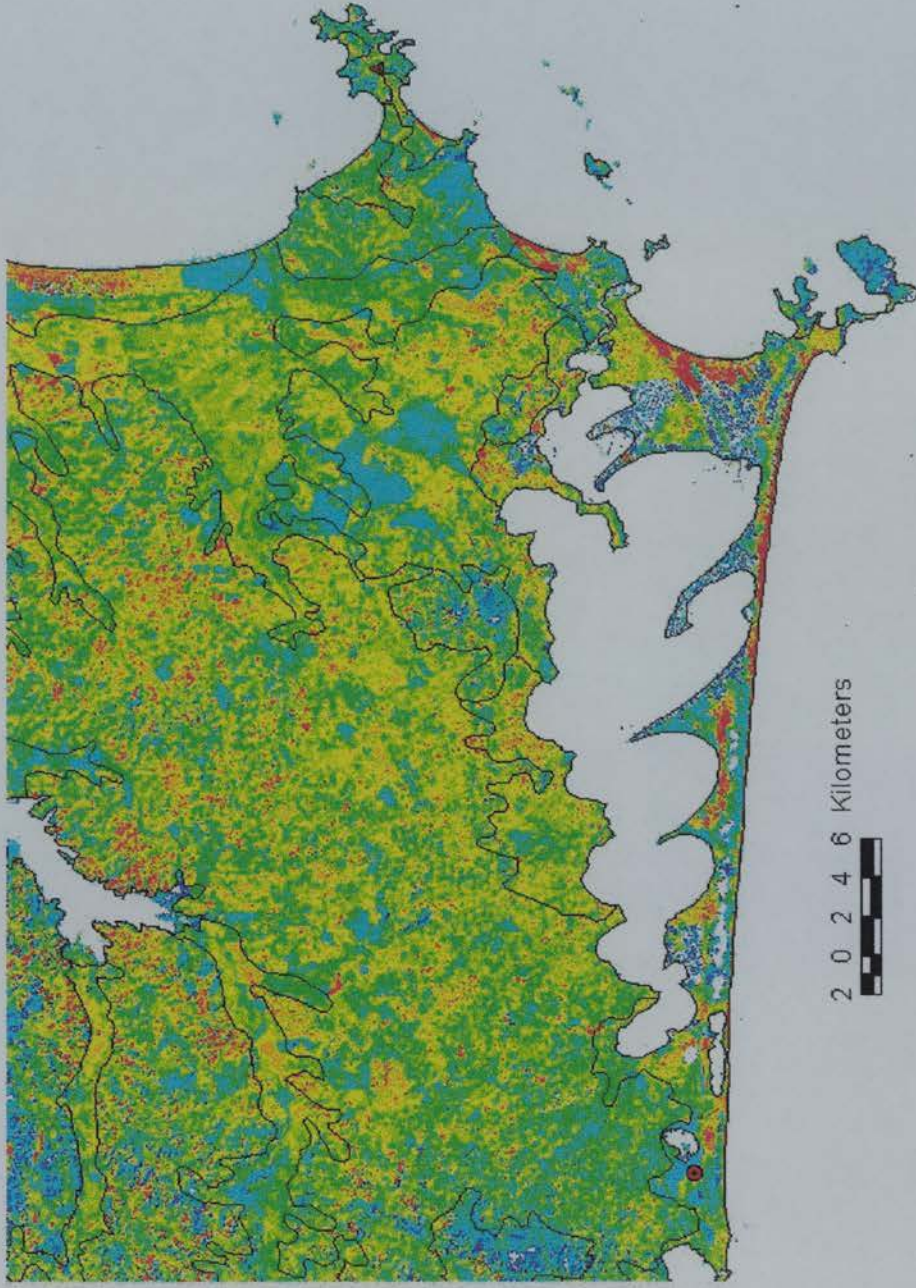


Figure 8.13 Classified TM image showing in more detail the coastal dry areas with *restinga* and forest vegetation (blue), with high moisture (dark blue), open vegetation and urban areas (green and yellow) exposed soils and sand dunes (red). It includes the Jacarepiá reserve on the left and Búzios on the right. Black lines represent potential vegetation boundaries (see Chapter 9).

The analysis of the image, in combination with the other spatial data, including the results from predictive vegetation modelling (see Chapter 9) can contribute directly to the selection of areas for both conservation and management purposes. One possible application is in the selection of areas for the establishment of forest corridors, connecting conservation units. These corridors could include a combination of fragments of primary and old-secondary forests, as well as replanted areas. Results from both species and plant community ordination (see Chapters 6 and 7) could be used in the selection of species adapted to particular sites.

A similar exercise to the one in Section 8.5 was carried out to illustrate a spatial analysis application for conservation planning at the regional level. The aim is to find the best option for the establishment of a forest corridor connecting the Macaé de Cima and Poço das Antas Reserves. The solution adopted was to overlay the classified image with layers containing the Reserves boundaries and 100 m buffers zones along the river courses (see Figs. 8.14-8.16). The best solution should be the route that combines the shortest distances between the forest fragments or patches along the river corridors. The final solution however, should take other environmental factors such as relief and soils (see Chapter 9), as well as socio-economic constraints into account.

8.7. Spatial Analysis for Ecological Research, Forest Management and Conservation of the Atlantic Forest

In summary, in this chapter an attempt was made to utilise existing methods and tools in the analysis of the spatial patterns of the forest vegetation of the Macaé de Cima Reserve. The analysis can only go so far because, at this stage, there is insufficient ground data, but the approach offers a promising route for future planning. The combination of techniques adopted tries to integrate the scientific analysis of the spatial variability of the forest and its links with the physical environment with the application of the ecological and environmental information for conservation and management purposes. Thus, the objective has been only partially achieved in the present research, mainly because of the lack of additional environmental data, particularly on soils and geomorphology, at spatial scales compatible with the both the vegetation data and the management needs

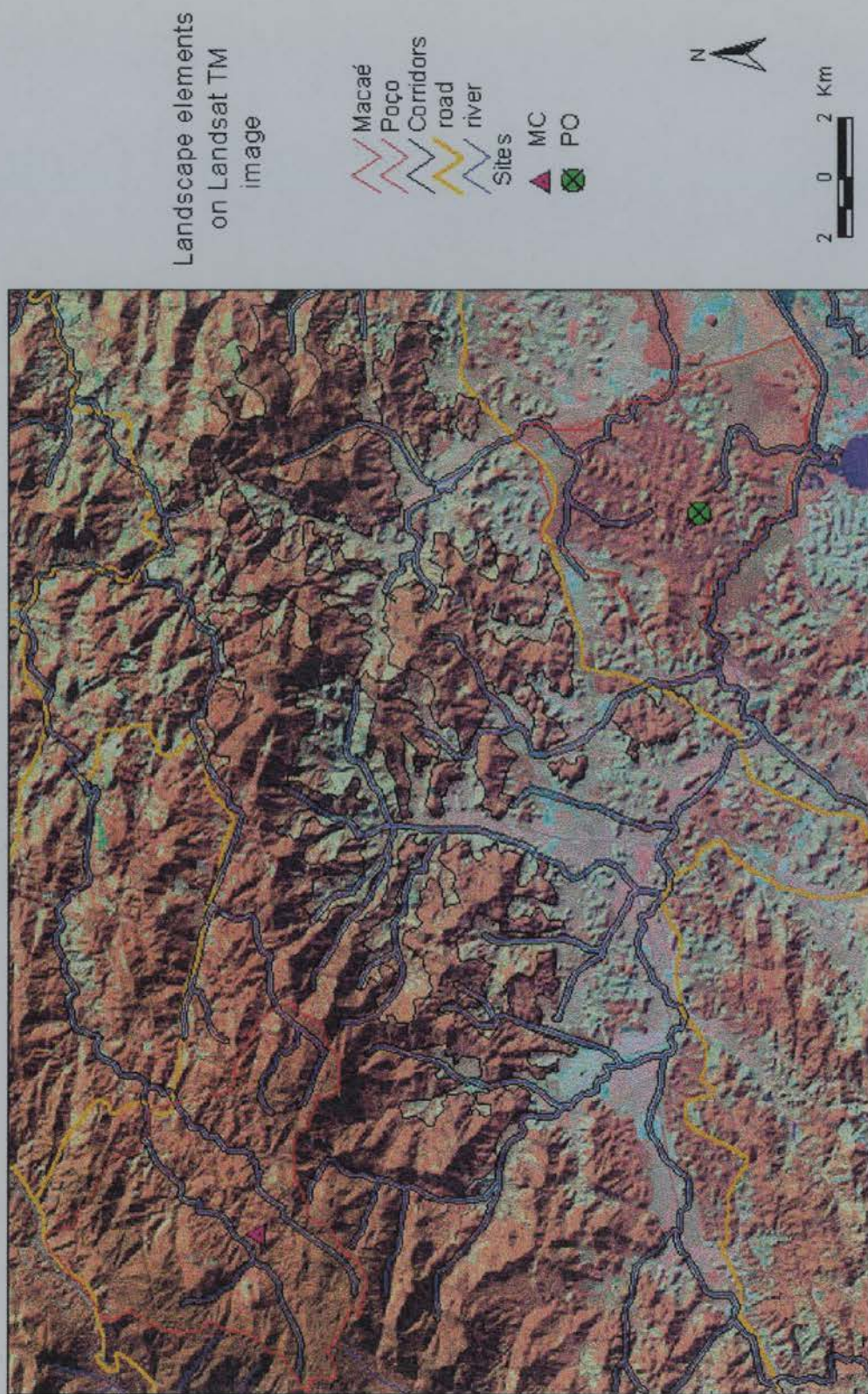


Figure 8.14 Landsat TM colour composite (bands 452) showing the region between Macaé de Cima and Poco das Antas reserves, the forests remnants on the southern slopes of the Serra dos Órgãos (red-brown), and strip corridors along the rivers courses.

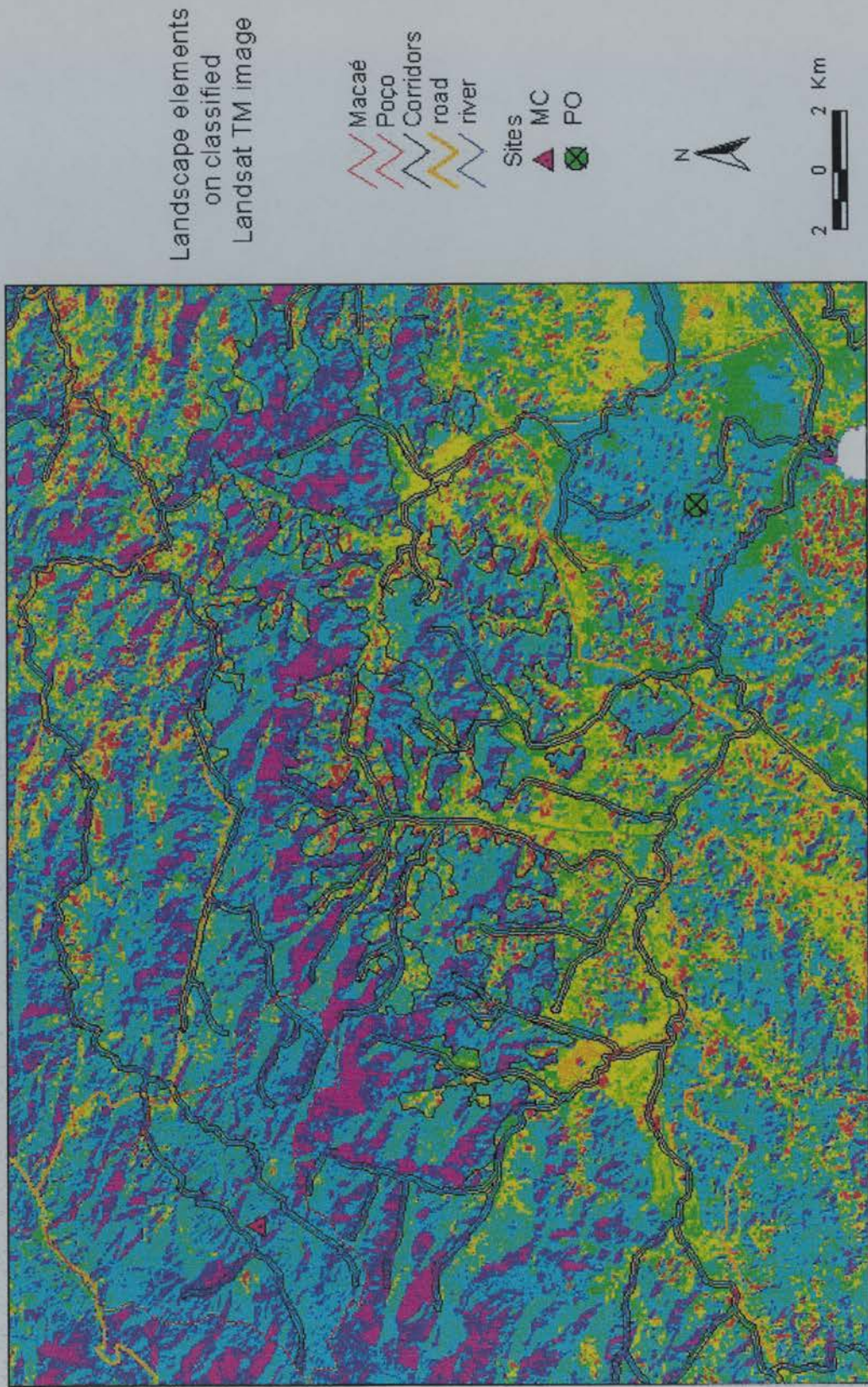


Figure 8.15 Classified TM image, showing the region between Macaé de Cima and Poco das Antas reserves, the forests remnants (purple, dark and light blue), the cleared areas (green, yellow and red), and the strip corridors along the rivers courses

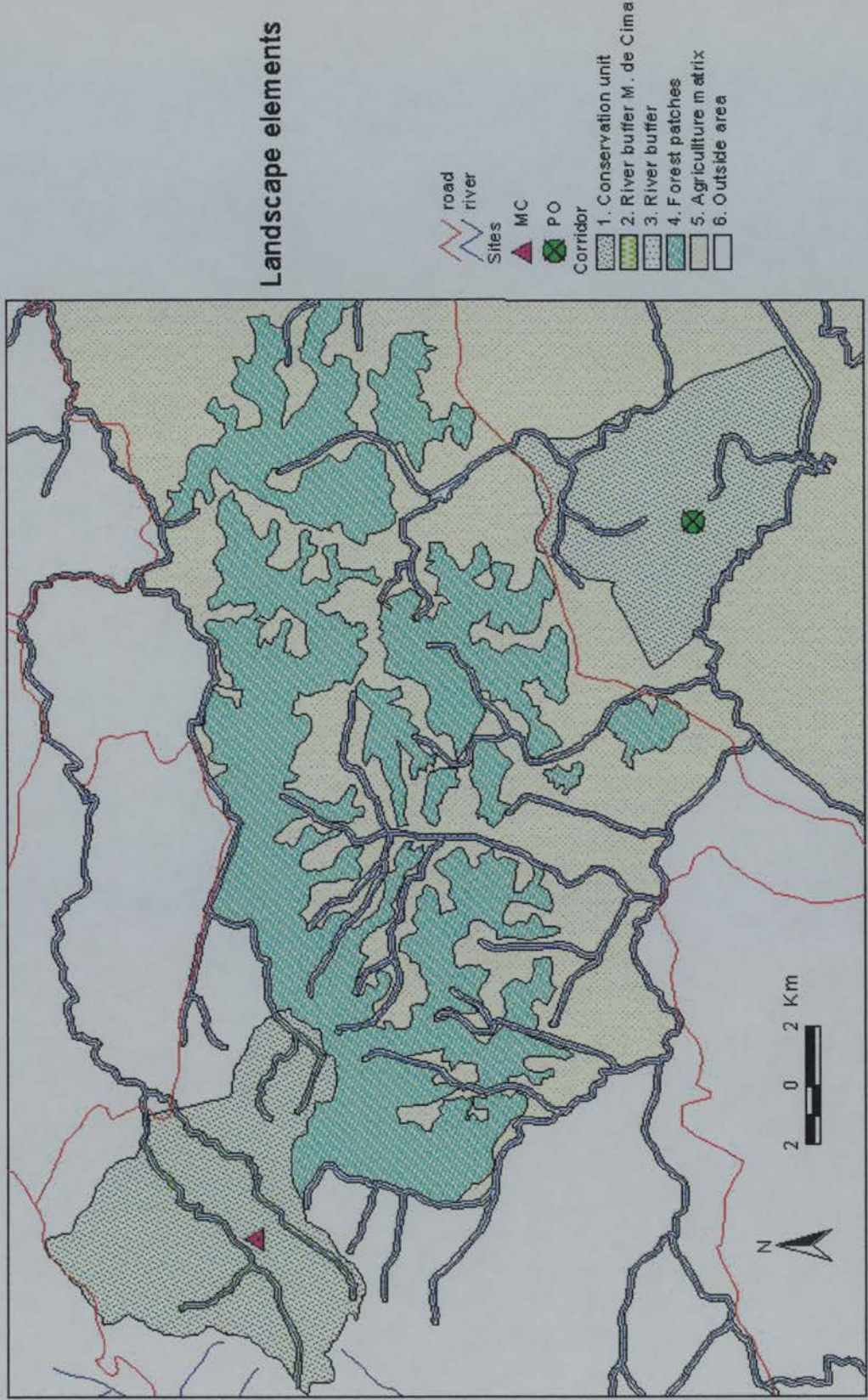


Figure 8.14 Map of the region between Macaé de Cima and Poço das Antas reserves, showing forest remnants (patches) and strip corridors along the rivers courses (100 m buffers) which could connect both reserves and the forest patches.

Although soil and relief data were collected on all sampling plots, which allowed the analysis of the relationships with vegetation (Chapter 6), they do not permit the establishment of soil or relief mapping units at a more detailed scale. The terrain information provided by the DTM, the more detailed geological maps, the aerial photographs and the Landsat TM images can help in part to overcome this deficiency. However, additional local or site data, including soil profiles and the characterisation of landforms are needed, in order to establish with much greater accuracy the characteristics and the spatial distribution of the landscape units.

The vegetation data provided a good basis for the analysis of the forest structure, including the characterisation of forest types, related to the physical environment (see Chapters 5 and 6). However once again, for detailed characterisation of the landscape units, more data would be needed, including quantitative data from secondary forests in different types on environment and levels of disturbance, as well as on the non-forest vegetation that occur in areas such as rock outcrops.

Despite these constraints, the spatial analyses did show the utility and the potential of tools such as GIS and digital image processing. The land cover map (1970), apart from giving a relatively accurate view of the spatial distribution of the vegetation cover, can be used as a baseline for further landscape analyses and monitoring. The combination of all the spatial information already available in a common spatial database will increase the accuracy of additional ecological and environmental studies. New data and information can be introduced and analysed in a much faster way, producing immediate results that can be applied to planning. This approach has the merit of highlighting the gaps in the available information.

The possibility of using a similar approach over different spatial scales was also explored. It was shown how the digital processing and classification of satellite imagery can be combined with additional spatial data to analyse the variability of the vegetation cover, using the eastern region of Rio de Janeiro as an example. The integrated analysis of point and spatial data in the study of the Atlantic Forest relationships with the physical environment at different spatial scales, and its potential for biogeographical analyses and conservation planning will be discussed in more detail in Chapter 9.

CHAPTER 9 Spatial Analysis and Modelling: a Vegetation Model for the Atlantic Forest

9.1. Introduction

Predictive vegetation models have been developed for a number of purposes, including testing scientific hypotheses about plant species or community distributions, potential vegetation mapping, vegetation management, wildlife distributions, environmental and land use planning, and studies on effects of climatic changes (Franklin, 1995; Kalkhoven & van der Werf, 1988). There is an increasing availability of spatial data on several environmental factors known to influence vegetation, including remote sensing data from which actual vegetation distribution can be mapped. The GIS technology, a useful tool for combining different sources and types of environmental spatial data, has also developed fast, with an increasing number of analytical features being incorporated into increasingly user-friendly software packages. With the increase of both data storage and processing power, combined with the popularisation and decreasing cost of computers, it is now much easier to combine larger data sets in order to test spatial models.

In this chapter, the theoretical basis for the development of a predictive vegetation model for the Atlantic forest in SE Brazil will be discussed. A conceptual spatial model is proposed, based on known relationships between the forest vegetation and the physical environment. An example will be given on how the model could be implemented, by using GIS technology.

9.2. Spatial Aspects of the Atlantic Forest Vegetation

The vegetation mapping of Brazil by the Radambrasil Project began in the northern portion of the country, focusing on the Amazon region, where a great proportion of land was still covered by natural vegetation. When the Project moved southwards, it faced a difficult task, as most of the natural vegetation had been altered or totally substituted by agricultural crops, pastures with exotic grasses, or monocultural forest plantations, or affected by a high incidence of burning (Urrahy *et al.*, 1983). Even areas covered with secondary forests are subject to intensive use,

so that the floristic composition is probably very different from the natural composition and structure (Por, 1992). The solution has been to develop a conceptual model of the original or *potential* vegetation (Franklin, 1995; Kalkhoven & van der Werf, 1988), based on the environmental factors considered to be most important in controlling vegetation distribution.

This approach was adopted in the vegetation mapping at 1:1,000,000 scale of sheet SF 23, which covers all Rio de Janeiro and parts of Espírito Santo, Minas Gerais and São Paulo states, in SE Brazil (Collares *et al.*, 1982). The model considered climate, expressed by the ombrothermic relationship $P \geq 2T$ (Bagnouls & Gaussen, 1957), as the primary controlling factor. Then, it considered geology as the second controlling factor. Finally, the model used the relief, based on altitudinal classes adopted in the Radambrasil classification system (Veloso & Goes-Filho, 1982), as well as the degree of human disturbance, to define the resulting *potential* vegetation (Ururahy *et al.*, 1983).

This conceptual model, further enlarged for all the Brazilian vegetation mapping, was adopted in the design of the vegetation map of Brazil at 1:5,000,000 scale (IBGE, 1993a). The resulting maps have been shown to be remarkably accurate, considering the level of detail allowed by the small scales (Oliveira Filho & Ratter, 1995).

A different classification system had been adopted in the vegetation mapping of Rio de Janeiro, resulting in different boundaries between the vegetation types (Golfari & Moosmayer, 1980). The differences can probably be explained by the use of different altitudinal classes and a different climatic classification. However, the vegetation classes in both maps are on the whole quite similar, and can be easily related to each other.

There is also some difficulty in relating vegetation map classes to local or site vegetation studies, due to the lack of a general agreement on a common classification system. However, since the publication of the IBGE vegetation map, and the related classification system (Veloso *et al.*, 1991), this situation has improved. In most recently published papers, researchers have attempted to relate the described vegetation to the IBGE classification, which makes comparison between different areas much easier. It also helps to fit previous work describing similar vegetation

into a common system.

It can be argued that the assumptions of the RadamBrasil model can only be put to trial with the availability of more floristic and related environmental data. Recent analyses based on extensive floristic data covering most of SE Brazil (Fontes, 1997; Oliveira Filho & Ratter, 1995; Salis *et al.* 1995; Torres *et al.* 1997), have shown that, in general terms, the assumptions of the model and the resulting maps, are sound. The boundaries between the ombrophilous (rainforest) and seasonal forest areas have been shown to be accurate. Differences related to altitude have also been confirmed, although leaving some questions concerning the values adopted to define the altitudinal ranges of the formations (see Chapter 7).

Although these analyses cover most of SE Brazil, a close examination of the dataset shows several geographical gaps. Most data come from Minas Gerais and São Paulo states, while both Rio de Janeiro and Espírito Santo have only one area each (M. de Cima-RJ and Linhares-ES) included in the analyses. Considering that these states both have a highly heterogeneous physiography, climate and geology, more data are necessary to give a better and more accurate picture. The availability of extensive new floristic data covering several areas from Rio de Janeiro (Chapter 7) could overcome this deficiency, at least in part.

Another important point is related to the validity of the relationships between the vegetation and the physical environment assumed in the model. One possible approach is to use multivariate methods to analyse such relationships. The reasoning is that those relationships found to be strong in the analysis can then be adopted in a vegetation model, calibrated and validated as new data become available (Jongman *et al.*, 1995).

The primary controlling factor of vegetation is assumed to be climate, expressed by the Bagnouls & Gaussen index. This model has been widely adopted elsewhere (Walter, 1985), and is considered to represent fairly well the influence of climate on plant formations. One option is to adopt an alternative climatic classification, such as Köppen, which is also widely applied. Another option, adopted in several zoning exercises for both agriculture and forestry, is to use the Thornthwaite relationship (Golfari *et al.*, 1978; Golfari & Moosmayer, 1980). All

systems try to compartmentalise the continuous climatic gradient into discrete sections, with consequent difficulties occurring in the transition zones.

Oliveira Filho & Ratter (1995) and Fontes (1997), by using multivariate analysis, found that the Köppen classes show a good degree of correlation with both forest floristic composition and physiognomy. They also found significant relationships between floristic composition and altitude. Altitude appears to be a mitigating factor in relation to lower rainfall and longer dry seasons, with those areas located on higher (>750m) altitudes in the seasonal forest region showing a greater similarity with the moist coastal forests. This can be related to the effect of lower temperatures decreasing the evapo-transpiration, and consequently, the stress related to lower availability of water during the dry season.

There was also correlation between floristic similarities and latitude. However, in this case, the patterns are not so clear, which may in part be related to the geographical gaps mentioned earlier. The clustering of areas along an N-S axis could be related to a climatic gradient, a geographical (distance) gradient, or both. It has been suggested that the Atlantic forests located north of the river Doce have greater floristic affinities with the Amazonian forests, based on the presence of several Amazonian species. Although this can be related to possible connections that go as far as the late Tertiary (Bigarella & Andrade-Lima, 1975), they also show some remarkable similarities in physiognomy and floristic diversity (Mori, 1989; Peixoto & Gentry, 1992). The region located between the Rio Doce and the Rio Paraíba could have functioned as an ecological barrier to several taxa (Prance, 1979). According to the vegetation map of Brazil (see Figs. 3.1 and 3.2), semideciduous forests originally covered most of the area, *i.e.*, it has a drier climate compared with other coastal areas. Currently, there are still only a few available floristic data from this area that could be used to analyse its affinities with the forests located in both northern and southern portions of the Atlantic forest (see Chapter 7).

Differences related to geology, and consequently soil and relief have not yet being adequately tested, probably due to difficulties in obtaining adequate and standardised environmental data for all the areas used in the analyses. An attempt was made to relate vegetation to geology and soils, covering most of the environmental variation in São Paulo (Torres *et al.*, 1997). Although the results did

reveal some relationships, the small number of areas used in the analysis makes it difficult to assess the degree of the relationships.

9.3. Rationale of Modelling

A hierarchy related to different spatial scales (see Fig. 9.1) can be established in the design of a conceptual Atlantic forest vegetation/landscape model, according to the relationships found in the multivariate analyses (Chapters 6 and 7). The model proposed in this study attains to the first or higher level of the hierarchy (regional vegetation), based on both the Radambrasil model and the results from the multivariate analysis (Table 9.1). The second level can be applied specifically for the Macaé de Cima/Serra dos Órgãos region, based on the analysis at local level (Chapters 5 and 6) as well as other works done in the region (Davis, 1945; Lima & Guedes-Bruni, 1997; Kurtz, 1995; PMA, 1993; Rodrigues, 1996; Veloso, 1945).

Table 9.1 Hierarchy of spatial scales considered in the present analysis

-
1. Regional Landscape/Reserve – vegetation structure determined by altitudinal range, geology, and regional climate - main physiognomic forest types or formations (primary/old-secondary lower montane/upper montane moist forest).
 2. Topography/watershed – vegetation-environment relationships controlled by on slope/catenary position (top, mid, low), orientation (N-S or coastal/interior), large disturbance events (landslide, logging, clearing, and fire) - forest stand/community level.
 3. Local site/gap – vegetation structure controlled by species autoecology (tolerance to light, moisture, nutrients, dispersion), biotic (pollination, dispersion, herbivory, symbiosis), and disturbance (natural/human) factors.
-

9.3.1. Environmental Parameters

Climate

The influence of climate on vegetation can be expressed by use of both the Köppen classification and the ombrothermic relationship $P \geq 2T$. According to relationships found in both classification and ordination analyses (Chapter 7), the main distinction between the areas relates to the climate types A and C. The A climate is related to lowland and lower slope (submontane) forests and the coastal *restinga* forests, while the C climate can be related to the subtropical submontane and montane forests.

Biogeography (ecology/geological history)
(Southeastern Province of Atlantic Forest)

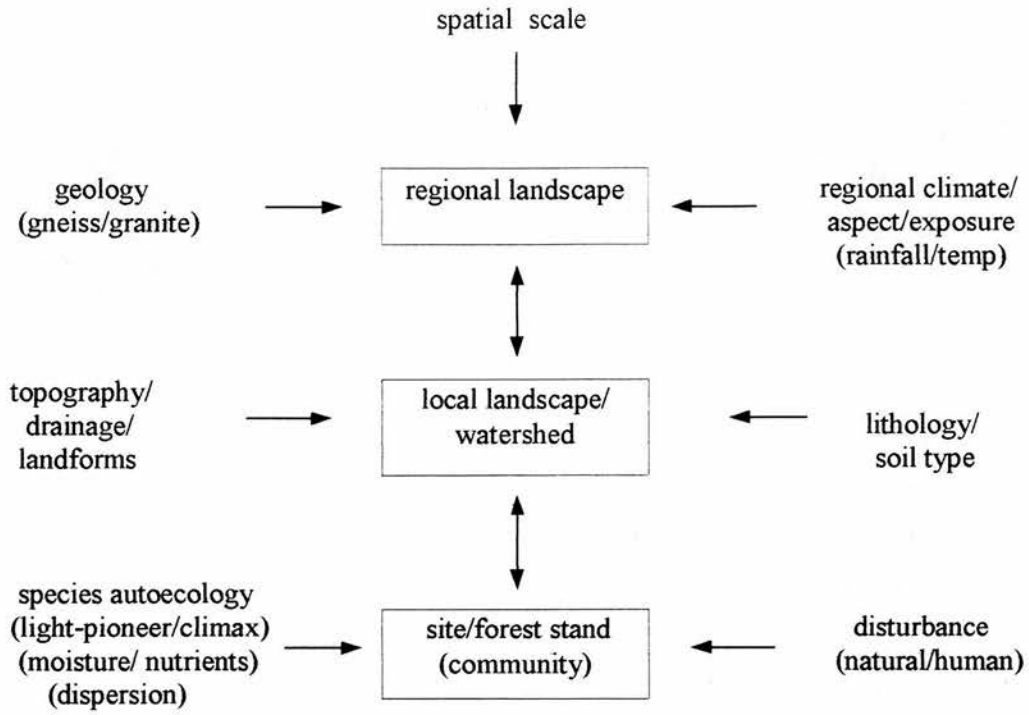


Figure 9.1 Hierarchy related to spatial scales for an Atlantic Forest Vegetation Model

The subtypes f, m and w refer to the rainfall distribution throughout the year which, in combination with temperature, strongly affects the amount of moisture available to vegetation. The relationships between climate and vegetation are summarised on Table 9.2.

The characterisation of the vegetation based on the Bagnouls & Gaussen relationship follows a similar reasoning to the Radambrasil model, i.e., it divides the region into two main climatic types. Areas with less than 60 dry days are covered by evergreen moist/wet forest (D), mixed *Araucaria* forest (M) and *restinga* forest (Pa). Coastal areas where more than 60 dry days occur are covered by seasonal semideciduous (F) forest and *restinga* (Pa) forest (northeastern RJ and southern ES).

Table 9.2 Correspondence between climate types (Köppen) and forest formations

Am	- Lower slope (submontane) tropical evergreen wet forests (Db, Ds)
Af	- Lowland and lower-slope (submontane) tropical evergreen moist forests (Db, Ds) and coastal <i>restinga</i> forest (Pa)
Aw	- Lowland and lower-slope (submontane) tropical evergreen moist forest (Db, Ds), and coastal seasonal semideciduous (Fb,) and <i>restinga</i> forests (Pa)
Cf	- Montane and high montane evergreen moist forest (Dm, DI), montane ecotone evergreen/seasonal semideciduous forest (D/Fm) and mixed <i>Araucaria</i> montane and high montane forest (Mm)
Cw	- Submontane and montane subtropical semideciduous forests (Fs, Fm)

Geology

The geology can be used to distinguish the coastal *restinga* forests, the alluvial forests and rock outcrop vegetation (*campo rupestre*). Floristic similarities among areas within the same formation are also closely related to geology.

Table 9.3 Correspondence between geology and forest formations

1. Quaternary	Marine sand deposits - <i>restinga</i> (low thicket) forest (Pa). Alluvial plains, on both coastal lowland and river valleys on mountain regions - alluvial evergreen moist forest (Da).
2. Tertiary	Barreiras sedimentary formation, northern coastal RJ, coastal ES - lowland evergreen moist (Db) and seasonal semideciduous (Fb) forest, related to the southern BA forests.
3. Precambrian	Gneiss and granite rocks, covered by regolith of variable thickness – lower slope (submontane) and upper slope (montane, high-montane) evergreen moist (Ds, Dm, DI) and seasonal semideciduous (Fs, Fm) forests. Gneiss and granite rock outcrop – shrub and grassy vegetation (<i>campo rupestre</i>).

Relief

The relationships between relief and vegetation combine both landforms, expressed by the relief classes (IBGE, 1993b) and the altitudinal range (Table 9.4)

Table 9.4 Correspondence between relief classes and forest formations

1. Coastal plain, up to 100-200 m altitude – lowland evergreen moist (Da, Db) and seasonal semideciduous forest (Fb).
2. Coastal slopes (E-SE facing) of the Serra do Mar and Caparaó mountain ridge, 200-700 m a.s.l. – lower montane (submontane) evergreen moist/wet forest (Ds).
3. Slopes (W facing) of the Mantiqueira and Caparaó mountain ridge, 200-700 m a.s.l. – lower montane (submontane) seasonal semideciduous forest (Fs).
4. Coastal slopes (E-SE facing) of the Serra do Mar, Mantiqueira and Caparaó mountain ridges, 700-1300 m a.s.l. – upper montane evergreen moist forest (Dm).
5. Slopes (W facing) of the Serra do Mar, Mantiqueira and Caparaó mountain ridges, 700-1300 m a.s.l. – upper montane seasonal semideciduous/transition forest.
6. Top slopes of the Serra do Mar, Mantiqueira and Caparaó mountain ridges, 1200-1300 to 1700 m a.s.l. – high montane moist (cloud) evergreen forest (DI).
7. Top slopes of the Serra do Mar and Mantiqueira mountain ridges, above 1600-1700 m a.s.l. – high montane mixed <i>Araucaria</i> forest (MI), rock outcrop shrub and herbaceous (<i>campo rupestre</i>) vegetation (rm, rl).
8. Plateaus and smooth hills, Paraná river Basin 300-700 m a.s.l. – Seasonal semideciduous lower montane (submontane) forest (Fs).
9. Plateaus and smooth hills, Paraná river Basin 700-1200 m a.s.l. – Seasonal semideciduous upper montane forest (Fm).

9.3.2. Vegetation Legend

The final legend of the Predictive Vegetation Model for the Atlantic Forest (or PVMAF) is shown on Table 9.5. It summarises the relationships between the forest, the physical environment, and also the geographical regions. It includes only the natural or potential vegetation, according to a combination of environmental and geographical variables. Therefore, it does not at this stage take into account the effects of different types and intensities of anthropogenic actions on vegetation.

Although the proposed legend was designed to take into account the relationships between the environmental and geographical variables and the floristic similarities between different areas within the Atlantic forest (See Chapter 7), it refers mainly to the forest physiognomic classes of the IBGE classification system. The reasons for this are both the good degree of correspondence between the IBGE classes and the floristic similarities among the areas, and the need for a system that could be easily related to existing information and data. The IBGE classification is an open system (*Veloso et al.*, 1991) i.e. it allows the subdivision of the formation

and sub-formation into more detailed classes, which could be related either to floristic types or to specific environmental characteristics such as soil or landforms.

Table 9.5 Final Legend for the Atlantic Forest Vegetation

1. Dense evergreen (rain) forests (D)

- 1.1. Alluvial forest - Quaternary alluvial plains, poorly drained soils with medium diversity forest communities, composed by pioneer, wide range species and tolerant species. Permanently waterlogged soils with low diversity forest communities, composed basically by tolerant species - **Da**
- 1.2. Lowland forest - medium to high rainfall, coastal plains and lower slopes (up to 200m a.s.l.), medium to well drained soils, medium to high diversity (northern ES) forest communities - **Db**
 - 1.2.1. Moist forest - high rainfall (Afm climate), coastal plains and lower slopes of the Serra do Mar (SP, RJ) and Caparaó (ES), and Tertiary plains (northern ES) - **Dbf**
 - 1.2.2. Seasonal evergreen forest - medium rainfall with small dry season in winter (Aw climate), coastal plains and lower slopes of central and NE R. de Janeiro, and southern E. Santo **Dbw**
- 1.3. Submontane (lower montane) forest - coastal medium slopes (200-700 m a.s.l). Af climate, high biomass, medium to high diversity (RJ, northern SP) - **Ds**
 - 1.3.1. Wet forest - high rainfall (Af climate), slopes of the Serra do Mar, central RJ - **Dsf**
 - 1.3.2. Moist forest - high rainfall (Afm climate), slopes of the Serra do Mar and Mantiqueira (SP, RJ, MG), Caparaó (ES) - **Ds**
- 1.4. Montane (upper montane) forest - upper slopes (700-1300 m) of the Serra do Mar, E-NE Mantiqueira and Caparaó (SP, RJ, MG and ES). Cf climate, high biomass, medium to high diversity (RJ, northern SP) - **Dm**
- 1.5. High montane (cloud) forest - top slopes (1200-1700 m) of the Serra do Mar, E-NE Mantiqueira (SP, RJ, MG) and Caparaó (ES). Cf climate, high biomass, medium to high diversity - **DI**

2. Seasonal semideciduous forest (F)

- 2.1. Lowland forest - coastal plains and lower slopes (up to 200m a.s.l.) of NE R. de Janeiro and southern ES, Aw climate, medium to well drained soils, medium diversity - **Fb**
- 2.2. Submontane forest - plains and lower plateaus and slopes of the Doce, Paraíba and Paraná watersheds. Cw climate, well drained soils with medium to high fertility - **Fs**
- 2.3. Montane forest - upper plateaus and slopes (W) of the Doce, Paraíba and Paraná watersheds. Cw climate, well drained soils with medium to high fertility - **Fm**
- 2.4. Transition (ON) montane forest - upper plateaus and slopes (700-1300 m) of the Mantiqueira Paraíba and Paraná watersheds (SP, MG), with Cf climate - **FDm**

3. High montane mixed *Araucaria* forest (MI) - restricted areas on upper plateaus and slopes (above 1500 m) of Serra do Mar and Mantiqueira (SP, RJ, and MG), and Paraná watershed - **MI**

4. Coastal thicket (*restinga*) forest - coastal marine sands or spodosols. Thorn shrubs and small trees, with medium diversity - **Pa**

5. Rock outcrop (*campo rupestre*) vegetation - shrub and herbaceous succulent plants - **Rm**

9.5. The Potential Vegetation of Eastern Rio de Janeiro

In order to test and illustrate how the model could be applied, a simulation was carried out using spatial environmental data for the eastern region of Rio de Janeiro State. (see section 8.6). The main parameters of the physical environment

were climate, soils (EMBRAPA, 1992), relief and geology (DRN, 1979; Radambrasil, 1983). The boundaries between the ombrophilous and seasonal forest ecological regions of the Radambrasil vegetation map (Ururahy *et al.*, 1983) were used as surrogate information for climate.

The map shows which main vegetation types should cover the different types of environment under the current climate, without human disturbance. The use of additional environmental data such as a climate layer based on interpolation of rainfall and temperature data from meteorological stations, as well as a DTM at the same scale (1:250,000) would considerably improve the model simulation. However, the present output can be considered as a fairly accurate picture of the potential vegetation, based on the available environmental data for the area.

The model output layer was overlaid with a colour composite Landsat TM image (bands 452, Fig. 9.3) and the classified image (Fig 9.4, see also Section 8.6) to show the current spatial extent of the proposed potential vegetation classes. The combination of both datasets can be used to check to which degree the spatial environmental data is correlated with the vegetation. It could be used also to improve the spatial delimitation of the environmental data, such as soil types.

Existing vegetation maps of these areas (IBGE, 1993; Ururahy *et al.*, 1983) show at least six different vegetation types, including the montane and high montane forests of Macaé de Cima, included in the model as a single, upper montane forest class. The overlay reveals different forest types (moist/seasonal) with similar reflectance levels (represented by colours) on the TM image, which helps to illustrate the need to use surrogate information on the image classification. On the other hand, the image shows areas with different reflectance values within the same potential vegetation unit. This is clearest in the alluvial and coastal (*restinga*) areas. This illustrates the utility of the TM image to reveal differences in vegetation that are not reflected in the previous vegetation mapping and in the proposed model. One of the probable reasons is the difficulty in representing small variations in vegetation at broad scales. The role of factors such as drainage, soil texture or fertility, that might affect such variation in apparently homogeneous environments, should be further investigated.

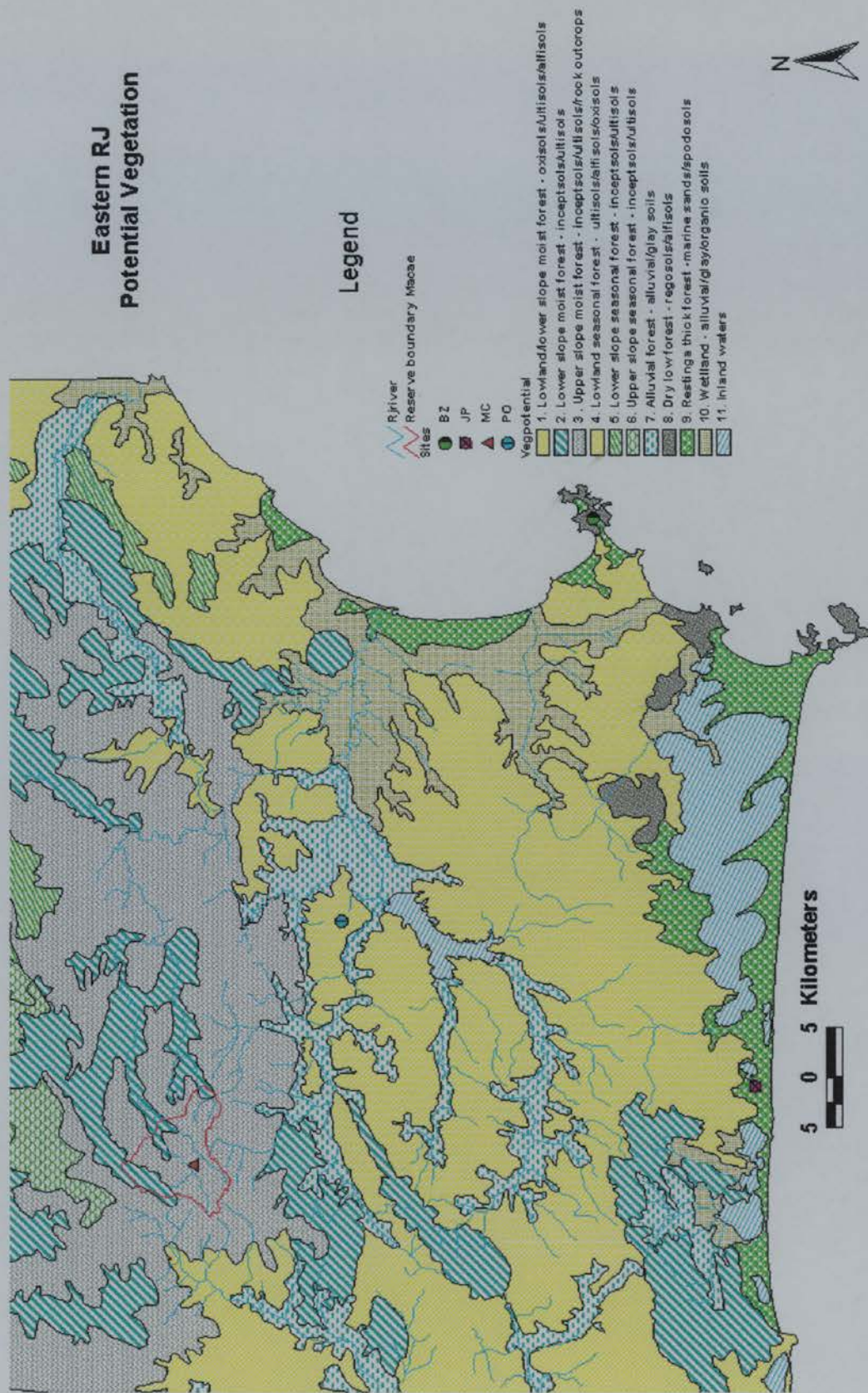


Figure 9.2 Map of the potential vegetation of the eastern region of the Rio de Janeiro State, showing also the location of the Macaé de Cima reserve and of three other areas (Poço das Antas, Búzios and Jacarepiá) whose floristic data were used in the biogeographical analysis (Chapter 7).



Figure 9.3 Overlay of the potential vegetation map and drainage with colour Landsat TM colour composite (bands 452). Different types of forests or woody vegetation show similar reflectance values (red-brown). Different reflectance values also occur within vegetation units, which might reflect environmental differences or human disturbance.

The potential vegetation map also shows the location of Macaé de Cima and three other areas used in the biogeographical analyses (Chapter 7). This can help to illustrate the position of the areas in relation to the regional environmental gradient, as well as the spatial relationships between them. Furthermore, GIS permits the targeting of specific locations for detailed analysis or problem solving.

Búzios and Jacarepiá were clustered together in some of the analyses, which might reflect both their proximity and a similar dry climate in both areas. Although the Búzios dataset include plants from *restinga* areas, it refers more to the low dry forest that cover the coastal hills, characterised by regosols and alfisols. These areas have been classified as *caatinga* (steppe-savanna in the IBGE map) as a result of their physiognomy, with abundance of Cactaceae and other thorny species, resembling the dry woody vegetation characteristic of NE Brazil (Ururahy *et al.*, 1983).

Poço das Antas is perhaps the last large area of lowland forest in the State, which reinforces its importance as a conservation unit (IEF, 1994). The floristic dataset also include trees from the alluvial forests, a vegetation type that is often neglected in terms of its ecological importance (Scarano *et al.*, 1998). These alluvial forests are very similar in both physiognomy and floristic composition to *restinga* forests that occur in poorly drained soils, and could perhaps be classified as a single forest type.

The availability of quantitative vegetation data from these four areas, as well as other areas of the State would greatly improve the value of the model. The use of both classification and ordination of these data, in combination with more detailed or site specific environmental data could result in a much better picture of the relationships between both species and plant communities with the physical environment. This could lead to a much more detailed prediction in terms of communities and even species distribution across the State's landscape. This approach could also be adopted for other regions of the Atlantic forest, whenever there are sufficient ecological and environmental data to support both the multivariate analyses and the model simulations.

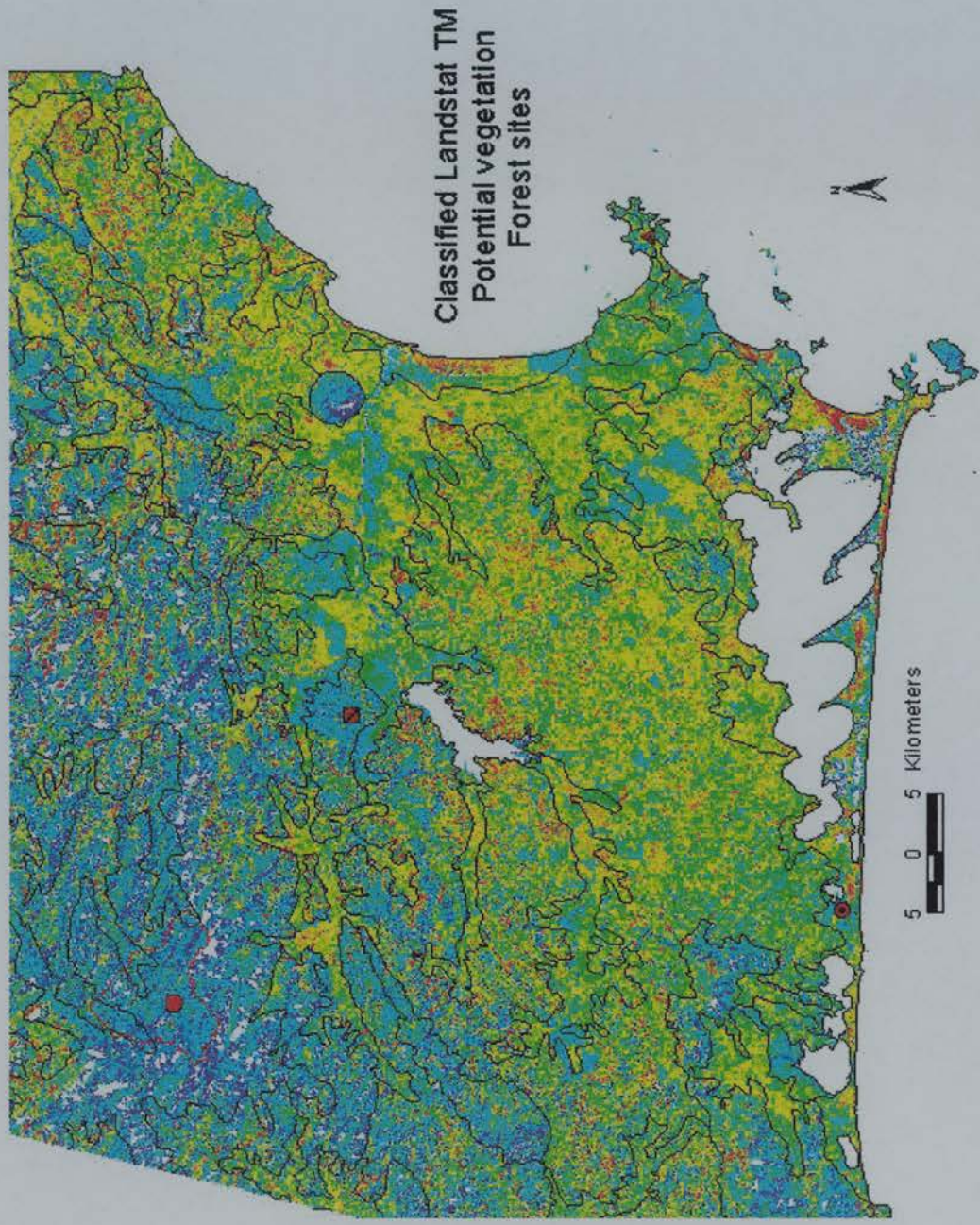


Figure 9.4 Overlay of the classified TM image (see Figs. 8.10 and 9.2 for key) with the potential vegetation map and the four forest sites. It shows a good agreement between agricultural land use (yellow, green) and the remaining forests (blue) with soils and relief (slopes, alluvial plains).

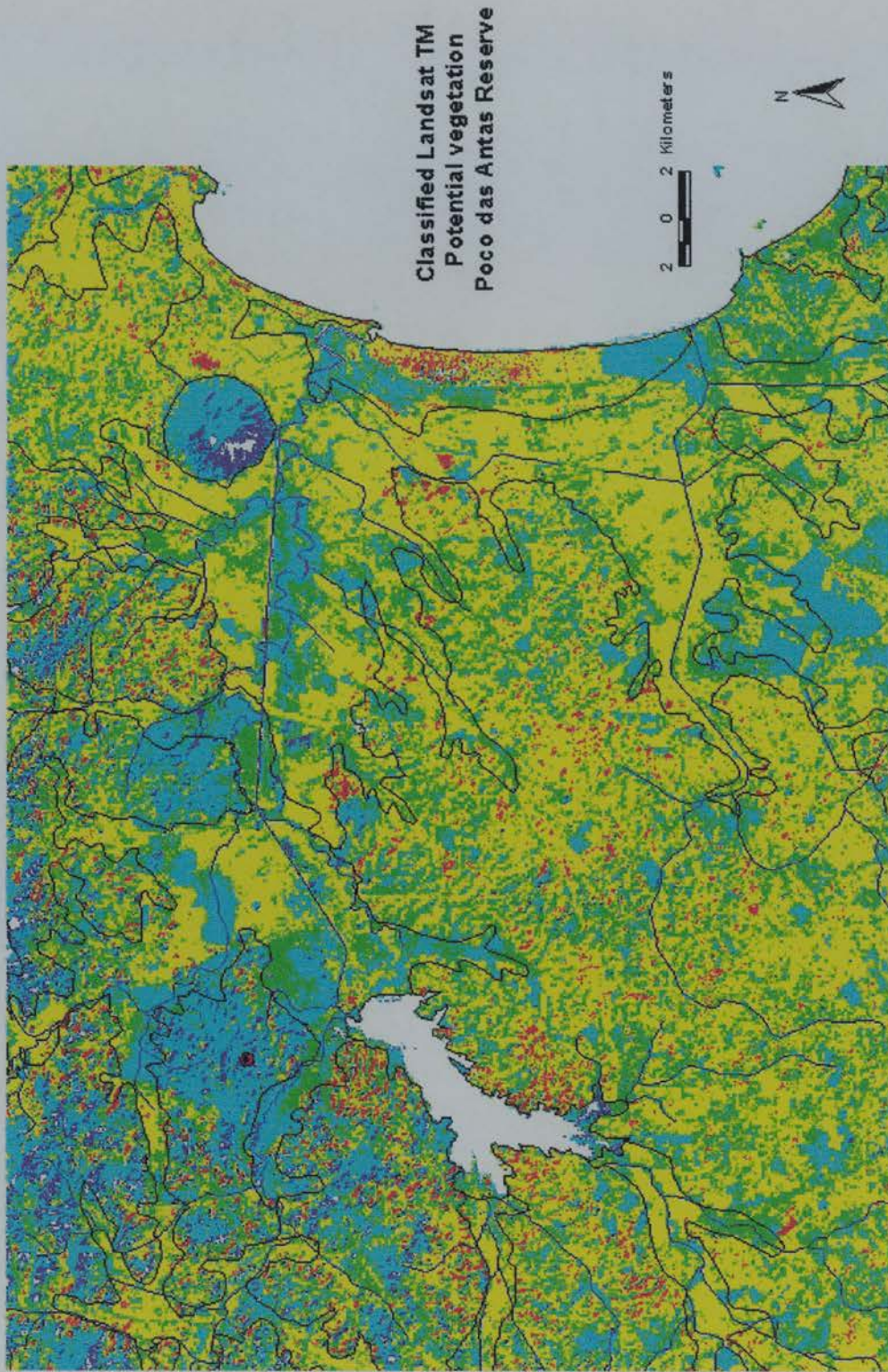


Figure 9.5 Overlay of the classified TM image with the potential vegetation map, showing in more detail the eastern coastal zone, including the Poço das Antas reserves (left), above the Juturnaiba reservoir (white). It emphasises agricultural land (yellow, green) on lowlands and alluvial plains, with few forest or woody vegetation areas, including *restinga* (on coastal sandy soils)

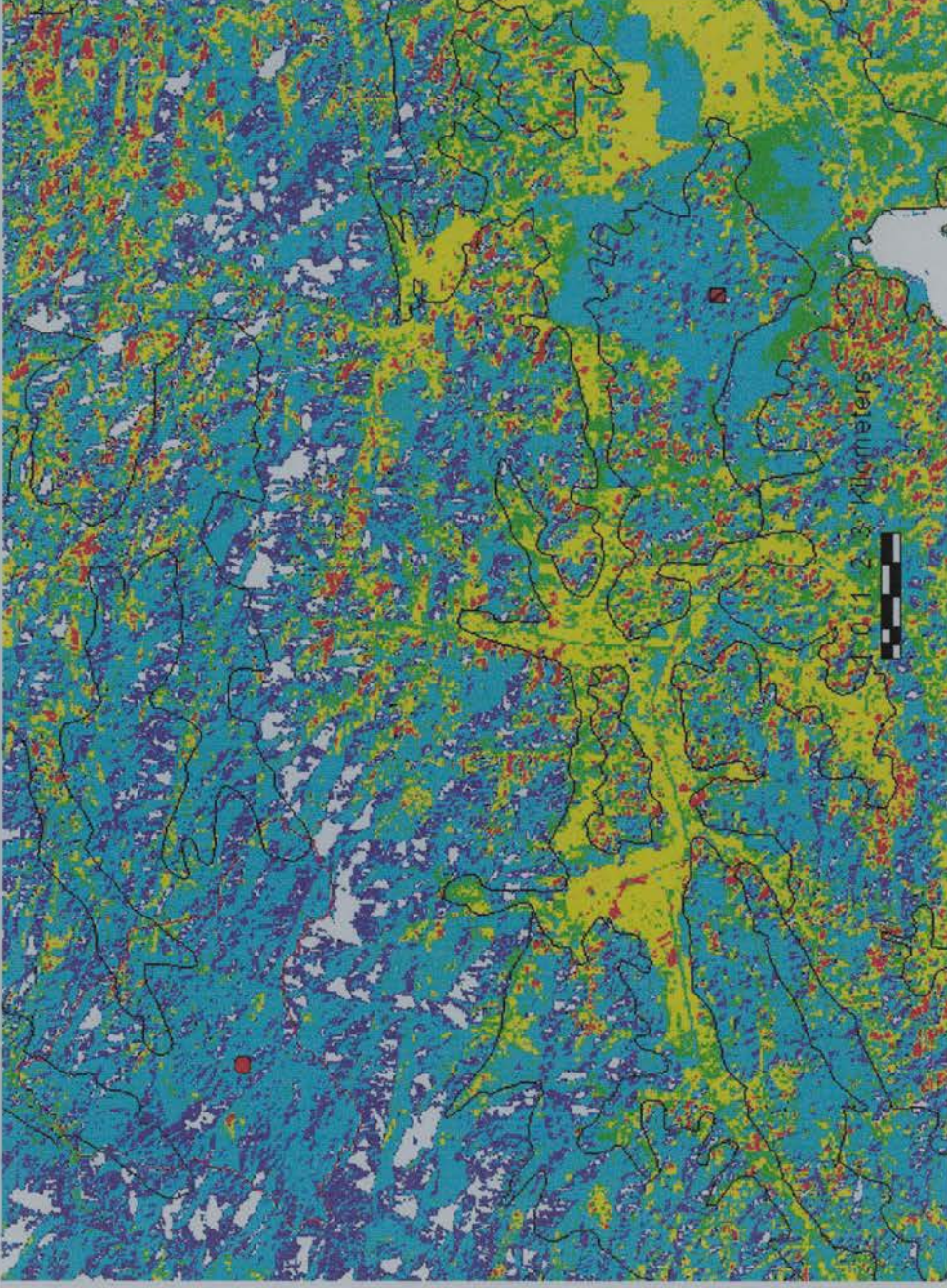


Figure 9.6 Overlay of the classified TM image with the potential vegetation map, showing in more detail forests (blue), open vegetation (green, mainly pasture), and exposed soils (red). It includes Macaé de Cima (upper left) and Poço das Antas reserves (right). It shows agricultural areas concentrated on alluvial plains and lower slopes, with the remaining forests on steeper relief (mostly cambisols).

In summary the proposed model of *potential* vegetation offer several practical advantages for researchers and planners. Firstly it gives an overview related to the latest or more accurate present day surveys of vegetation. Secondly it permits targeting on specific problems or areas of conservation interest, and thirdly it sets up a framework for more advanced quantitative analysis of vegetation and the relationships between plant communities and their environment. Above all it can be a valuable planning tool.

CHAPTER 10. Conclusions

10.1. The Study of the Atlantic Forest

The Atlantic Forest is arguably the most endangered forest region of Brazil. It contains a high floristic diversity, with more than 2000 species of trees and shrubs. It has floristic links with the central Brazilian gallery forests and with the Amazonian forests, as well with the subtropical forests of the Paraná river basin, which extend to Paraguay and Argentina. The proximity of several of the remnants with many of the largest urban centres of Brazil, which provide the only natural areas for a large percentage of the Brazilian population, also makes any effort to study and protect these forests a matter of high priority.

The management and conservation of the Atlantic forest has been undermined by the relative lack of knowledge of the forest ecosystem as a whole. An ecological classification of the Atlantic forest into relatively homogeneous areas could provide a valuable baseline and a framework for more detailed studies in each of these ecological/land units. So far, the attempts to characterise the floristic patterns and their relationships with environmental and geographical variables have suffered from a lack of sufficient floristic and ecological data and an uneven geographical distribution of the whatever data is available. The species richness of the forests and its extensive longitudinal range has been a serious constraint for any overall ecological analysis, due to difficulties in handling the large amounts of data. Only recently, with the availability of powerful computer systems, combined with the development of multivariate analysis, digital image processing and geographical information systems software has the analysis for large datasets of both point and spatial data become a more feasible undertaking.

In this research an attempt has been made to develop a logical procedure demonstrating how such methods could be used in an integrated way to characterise the Atlantic forest ecosystem, at different levels or scales of detail. A case-study strategy was adopted as a way to test the strengths and constraints of such approach. The selected study area, the Municipal Ecological Reserve of Macaé de Cima, offered a good choice in terms of both biogeographical and ecological importance.

The Reserve is covered by two main forest formations, the montane and high montane moist forests. The role of the physical environment on the structure and composition of these forests is still poorly known. The local physical landscape offered a challenge in itself, on account of its difficulties of access and also because of problems of analysis of spatial data from aerial photographs and satellite imagery.

The availability of a recent floristic botanical survey of the Reserve offered the opportunity to reduce the uncertainty in the identification of the tree species measured in the field. The fact that Macaé de Cima is a municipal Reserve that belongs to a medium sized town, with the land owned by private landowners, offered an additional challenge. The local government has very limited resources to promote investigations or to enforce legislation on such a large area. Research projects carried out by independent organisations such as universities or botanic gardens, with cooperation and participation of the local farmers, has helped to reduce suspicions and increase their awareness of the ecological importance of the area. Their local knowledge can be a valuable input to any research, not only in terms of logistics, but also in terms of information on local plants, animals and land use history. Finally, applied research of this sort should produce results that could help to increase understanding of the local ecosystems, resulting in better land management and reducing the negative impacts on the local fauna and flora.

10.2. The Research Results

The study of the forest structure and composition based on several forest plots helped to characterise the forest as a whole and its variation across the local landscape (research question 1). The results confirmed the high diversity of species of the forest (164 species of trees > 10 cm dbh in 4000 m²) and its relatively high average biomass (43 m²/ha of basal area). They also confirmed that both the forest structure and composition vary considerable along a local gradient related mainly to both altitude and location along the relief. Montane forests cover all the areas below 1100 meters. From 1150 to 1300 m, the forests are either of a transitional nature or with characteristics that resembles more the high montane forest formation, depending to their location on the slope. Above 1300 metres, the forest can be classified as high montane forest, with canopy height and cover varying according

the site conditions, especially soil depth. Additional parameters that influence the forest structure and composition were aluminium and slope.

The survey has shown the similarity of the high montane forest of Macaé de Cima with other Neotropical upper montane forests, located in the Andes, Central America and Caribbean, both in terms of physiognomy and at the generic level. The biogeographical analysis, carried out by comparison of the Macaé de Cima floristic composition with 50 other areas within the Atlantic forest domain, has shown that the area has strong floristic links with other coastal moist forests of SE Brazil as well as the more southern, subtropical mixed *Araucaria* forest. The analyses have confirmed the occurrence of a strong gradient related to both geography and climate in the SE portion of the Atlantic forest (research question 2). Although latitude and longitude can also be related to a climatic gradient, a good degree of correlation with the relief reinforces the importance of locality on the general composition of the forest. It also emphasises the role of geology on the similarity patterns among the areas, as most relief units share a common geological background.

The research has shown how the investigation of the relationships between the forest vegetation and the physical environment could be used to develop a conceptual spatial model of the Atlantic forest vegetation (research question 4). The model proposed is hierarchical, with the input parameters ordered according to their importance for the overall patterns, revealed by the multivariate analyses. The proposed model aims to show to at which extent the available information can be used to predict the probable or potential composition in any given area of the Atlantic forest in SE Brazil.

Any model must be seen as a simplification of the reality. It is impossible to summarise all the current knowledge about the Atlantic forest environment and all its interrelationships in a set of rules or equations, and the utility of such a complex model is also questionable. The proposed model should be seen just as an attempt to summarise, in a simple set of rules, the spatial relationships between the Atlantic forest vegetation and general aspects of the physical environment. The model helps to reveal the main limitations of the existing data and knowledge, which could direct future research efforts. The general reasoning behind the model could be tested with new data, especially from the gaps revealed by the geographical coverage of the

existing data. The availability of more and better data, as well as the knowledge from research on other important aspects of the Atlantic forest ecosystems, especially on the dynamic processes, could lead to the development of more detailed and precise forest models. It is hoped that the proposed conceptual model could serve as a starting point to such developments.

The collection and organisation of both floristic and environmental data used in the analyses has suggested several improvements that could be made in the proposed analytical approach. The results of the local scale analyses have emphasised the advantage of using quantitative (density or IVI) floristic data instead of purely floristic (presence/absence) data in both classification and ordination analyses. Even at a more detailed scale (state or regions within the states), the existing data are characterised by different sampling methods (area x point), intensities, and inclusion criteria. However, the increasing availability of published phytosociological data makes any effort to use such data invaluable. One possible approach is to reduce the effect of uneven sampling by means of data standardisation, using logarithmic transformations or cover scales.

The lack of a standard in the collection of the additional environmental data, in terms of both the data type and sampling, is another serious limitation. Several published works do not include soil data, and the soil parameters used in the analyses also differ. In many publications there is an absence or incomplete environmental data such as rainfall and average temperature, geology, relief or altitude of the sites. Although in some cases such information can be obtained from maps or other sources, there is a margin of error associated to the use of such data, and they are not always easily accessible. In many cases the climatic data refers to stations that do not characterise properly the climate in the study area. This can be illustrated by the use of the Nova Friburgo meteorological station data to characterise the climate of Macaé de Cima. The station is located only a few kilometres from the reserve, but it has a lower altitude and is located in a transition area in terms of rainfall. As a consequence, it registers a higher average temperature and lower rainfall than occurs in the reserve.

10.3. Contribution of the Research Project for the Management of the REM Macaé de Cima

One of the main objectives of the research project was that the results would contribute to the management of the Municipal Ecological Reserve of Macaé de Cima. Perhaps the main benefit of the research is to provide information through spatial data on the variation of the forest across the local landscape (research question 3). The analysis of both plot and spatial environmental data has allowed the design of an ecological landscape classification of the Macaé de Cima Reserve. The results provided an estimate of the spatial extent of human impact, as well as its trend in the period from 1970 to 1996. This information provides a sound basis for the establishment of a management plan for the reserve. The ecological landscape classes also serve as a basis for the reserve zoning, with different management proposals according to the environmental characteristics of each landscape unit.

The lack of spatial data on important parameters such as soils and landforms has allowed only a first approximation in the establishment and characterisation of landscape classes. The existing maps show only generalised classes, which incorporate into one mapping unit two or more types of both soil and landforms. It was not possible to collect all the information during the fieldwork due to the lack of both resources and time. However, the analyses of the limited soil and relief data available, combined with the spatial information provided by the aerial photographs and the digital terrain model, have helped to overcome this difficulty, at least partially. However, it is acknowledged that a soil and geomorphological survey of the reserve would lead to greater improvements in the characterisation of the proposed landscape units, including both the establishment of new units or the merging of two or more units. The same can be said in reference to wildlife. Data on the spatial distribution of animal groups and their use of the forest resources could also lead to improvements in the characterisation of the landscape units as well as in the reserve zoning and management.

Finally, all the information produced by this project, including all the spatial digital data, will be made available to the Macaé de Cima Reserve managers, where it can be used for planning (research question 5). The project results should reinforce awareness of both managers and landowners about the importance of using adequate

scientific information in the solution of environmental problems. It can be also a starting point for the establishment of a Geographical Information System on the municipal environmental resources, which could be used in the local land use planning.

The study of the Macaé de Cima forest contributes to our knowledge about the forests of the Rio de Janeiro State as a whole. The forests contain a large number of endemic species, and recent quantitative surveys have shown that they also have a high diversity of woody species. Almost the entire state is located in one of the three putative Pleistocene refuges for the Atlantic forest region. A better understanding of the floristic patterns within the state and their relationships with climate and other aspects of the physical environment could increase our understanding as to how the vegetation changed during recent climatic change events. It could also help to clarify the current floristic links between the SE coastal forests with other forest regions of the Atlantic forests, such as southern Bahia, the semideciduous forest of central Brazil and the Paraná river basin, and the southern *Araucaria* forests.

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Appendix 1. List of Acronyms used in the Text

CNPC-EMBRAPA - National Centre for Soil Research – Brazilian Agricultural Research Organization

CNPq – National Research Council

CPAC-CEPLAC – Research Agricultural Centre for Cocoa – Executive Commission for the Cocoa Crop

CPRM – Company of Mineral Resources Research

DIP – Digital Image Processing

DNAEE – National Department of Water and Electric Energy

DNPM - National Department of Mineral Resources

DRM – Department of Mineral Resources – Rio de Janeiro

DTM – Digital Terrain Model

FIDERJ – Foundation Institute of Economic and Social Development of Rio de Janeiro

IBAMA – Brazilian Institute for the Environment and Renewable Natural Resources

IBDF - Brazilian Institute for Forest Development (replaced by IBAMA in 1989)

IBGE – Brazilian Institute of Geography and Statistics

IEF-RJ – State Institute of Forest – Rio de Janeiro

IF-SP – Forest Institute – São Paulo

INPE – National Institute for Space Research

IUCN – The World Conservation Union

JBRJ –Botanic Garden of Rio de Janeiro

RBGE - Royal Botanic Garden Edinburgh

TM - Thematic Mapper

TIN - Triangulate Irregular Network

UFF – Universidade Federal Fluminense

UFRJ – Universidade Federal do Rio de Janeiro

UFRRJ - Universidade Federal Rural do Rio de Janeiro

USP – Universidade de São Paulo

WRI – World Resource Institute

WWF – The World Wide Fund for Nature

Appendix 2. Soil Analysis Methods

The soil samples collected in the Macaé de Cima forest plots were analysed in the laboratories of the National Centre for Soil Research (CNPQ-EMBRAPA) according to the following methods (EMBRAPA, 1979; Landon, 1991):

1. For silt and sand particles, 20 grams of air-dried fine soil were dispersed by NaOH 1N in 100ml of distilled water. For the clay fraction the sample was dispersed in distilled water. The textural fractions were analysed by the international pipette method.
2. The pH was determined in water (2:1 water soil ratio).
3. Ca + Mg and Al levels were determined by extraction with 1N. KCL. Ca + Mg was measured by titration with EDTA, and Al level by titration with NaOH, using a bromothymol indicator.
4. P, K, and Na were extracted with 0.05N HCL, plus 0.025N H₂SO₄ (Mehlich or North Carolina extractant). The measurement of K and Na was carried out by flame photometry. The determination of P was made by colorimetry in a phosphomolybdate complex, using ascorbic acid as reducer.
5. Total acidity (H + Al) was obtained using a 1N calcium acetate extractant solution at pH 7.0. It was determined by titration with NaOH, in the presence of phenolphthalein.
6. The C content was analysed by the Walkley-Black method. The total organic matter was estimated according to the formula $O.M \% = C \% \times 1.724$.
7. Cation Exchange Capacity (CEC) was calculated according to the formula
$$CEC = Ca + Mg + K + Na + H + Al$$

Appendix 3. Physical Environmental Data from the Macaé de Cima Region

1. Soil Types (Symbols refers to the mapped legend for soil units)

Red-Yellow Latosol (Latossolo Vermelho-Amarelo) - LV, LVH

The group includes soils classified as Oxisols (Ustox or Udox) by the U.S. Soil Taxonomy, or Orthic or Acric Ferrasols by FAO-UNESCO. They are highly weathered mineral soils, with a latosolic horizon B, low Ki molecular reaction (less than 1.9), colour varying from red to yellow. Predominantly clay soils with Fe_2O_3 levels in the horizon B below 9%. They are generally deep and well drained, with a sequence of horizons A, B and C, and gradual and diffuse transition between sub-horizons. They are allic, e.g., with more than 50% of Aluminium saturation (V), reaching up to 95%. Soils with a moderate A horizon have levels of organic C between 0.55 to 2.15% (LVa6). Soils with a humic A horizon have levels of organic C between 1.67 to 3.82% (LVH1). There is a predominance of 1:1 clays, low primary mineral levels and low reserves of nutrients. The silt/clay relationship is less than 0.70. The degree of flocculation is near to 100%, which reflects the high degree of colloid aggregation, leading to porous and erosion resistant soils. They occur on steep and mountain relief in the Macaé de Cima region.

Red-Yellow Podzol (Podzólico Vermelho-Amarelo) - PV

The group includes soils classified as Ultisols (Udults, Ustults, Humults) by the U.S. Soil Taxonomy, or Acrisols and Dystric Nitisols by FAO-UNESCO. They are mineral soils with a textural B horizon with low activity clay (Tb), usually deep, with sequence of horizons A, B, and C, moderately to well drained. They show a moderate A horizon (PVa3), with the texture varying from medium/clay to high clay. They can be allic (V>50%) or dystrophic (V<50%). The horizon B has a yellow-red colour, with levels of Fe_2O_3 below 5% when the horizon has 20% of clay, below 10%, when the horizon has 10% of clay, or with equivalent proportions of Fe_2O_3 in relation to the variation in the levels of clay. They occur on steep to mountain relief in the Macaé de Cima region.

Cambisols (Cambissolo) - C, CH

Also known as Cambisols (Dystric and Humic) in the FAO-UNESCO System, the group includes soils classified as Inceptisols (Udepts) by the U.S. Soil Taxonomy. They are mineral soils with a cambic or incipient B horizon, with small textural differentiation among horizons A and B. The degree of evolution has not been sufficient to weather primary

minerals completely such as feldspar or mica. There is no significant accumulation of iron oxides, humus and clay, which could identify them as textural or podzolic (B horizon) soils. In comparison with soils with a latossolic B horizon (Oxisols), they are less evolved, with less soil depth. The presence of easily weathered primary minerals, either by clay activity, by the presence of amorphous minerals on the clay fraction or by the higher levels of silt and silt/clay ratios is another distinguishing characteristic. They show low activity clay (Tb), often higher than 13 mE/100 g, molecular relationship K_i generally around 2, and high silt/clay relationship (> 0.7). They show a sequence of horizons A, (B) and C; with A being either moderate (Ca17), prominent (Ca2) or humic (CHa1, CHa2). Texture varies from medium to clay. Drainage is moderate to good, with varying depth. They can be either allic ($V > 50\%$) or dystrophic ($V < 50\%$). Cambisols are the most widespread group of soils in the Macaé de Cima region.

Lithosols (Solos Litólicos) - R

Also known as Lithosols by FAO-UNESCO, the group includes soils belonging to the Lithic subgroups (Orthents) in the U.S. Soil Taxonomy. They are mineral soils, barely developed, 20 to 40 cm deep, over consolidated rocks, with little or no weathering. They include soils with A horizon directly over a rocky layer or with relatively developed but narrow B horizon. They also include soils where the proportion of pebbles and debris is greater compared to fine earth. They have moderate A horizons with low activity clay (Tb) and a medium to clay texture. They are allic ($V > 50\%$), being developed from the weathering of quartz and migmatites, occurring mainly on the higher and steeper parts of the relief.

Rock outcrop (Afloramento Rochoso) - AR

Considered as a type of terrain, representing areas with bare rocks exposed or terrain with reduced portions of coarse material., constituted by large portions of debris originated from the desegregation of rocks with some earth material., they are not specifically classified as soils.

Table 1 Key for other soil types included in the biogeographical analyses (Chapter 7) according to the Brazilian soil classification system and their US Soil Taxonomy and FAO-UNESCO equivalents (EMBRAPA, 1981; Sanchez, 1976).

LE , - Dark-Red Latosol, Usthox or Orthox (US), Orthic or Acric Ferrasol (FAO-UNESCO)
LR , - Dusky-Purple Latosol, Ustrutox or Eutrorthox (US), Rhodic Ferrasol (FAO-UNESCO)
TR - Dusky Red Earth, Alfisol (US), Luvisol or Eutric Nitosol (FAO-UNESCO)
A - Alluvial soils, Entisols (US), Fluvisols (FAO-UNESCO)
PA - Yellow Podzolic, Ultisol (US), Acrisol or Dystric Nitosol (FAO-UNESCO)
HG, HP - Gley Hydromorphic, Tropaquepts or Humaquepts (US), Gleysols (FAO-UNESCO)
AQ - Quartzite Sands, Psamments (US), Ferralic Arenosols (FAO-UNESCO)

2. Geology

Table 2 Geological mapping units in the Macaé de Cima region

-
- . **peγ1δo** - **(Pre-Cambrian - granite) - S1** - Serra dos Órgãos (Superior Proterozoic), Juiz de Fora/Paraíba do Sul Complex (intrusive suite) - post-tectonic granite, generally clear-grey, medium to fine grain, granites and granodiorites, rough (*grosseiro*), partially recrystallised, and with restricted migmatites domains, and para-type variations (fluorite).
 - . **peps** - **Paraíba do Sul Complex (Archean)** - bonded gneiss dominantly tonalitics, migmatites, with cataclasis and recrystallisation, with foliation of axial plane at strong angles, and evidence of transpositioning; quartzite lens; gneiss of granite and tonalitic composition
 - . **pepδκz** - **Paraíba do Sul Complex (Archean)** - gneiss and migmatites, bonded and cataclastics, basement of the Moving Atlantic Belt.
 - . **Granite Nova Friburgo** - granite rocks of fluid structure, quartz-dioritic to granite composition, constituting circumscribed masses.
 - . **peIIIde** - **Unity Desengano** - gneiss lenticular, porphyroblastic and mylonitic, without banding; gneiss of medium to gross granulation, lenticular structure, of cataclastic origin, passing to a mylonitic-porphyroblastic gneiss.
 - . **peIIsf** - **Unity São Fidelis** - mylonite gneiss and biotite gneiss, normally banded, porphyroclastics and porphyroblastics, with intercalation of varied lithology and of calc-silicate.
 - . **peIIse** - **Unity Santo Eduardo** - predominantly mylonite gneiss and blastomylonite, normally banded, porphyroclastics and porphyroblastics, with intercalation of varied lithology, and of amphiboles (biotite), migmatized gneiss, of calc-silicate rock and quartzite inter-stratified with quartz schist.
 - . **peIIrbl** - **Unity Rio Bonito-Lumiar** - Series Serra dos Órgãos; heterogeneous migmatites predominant, besides migmatized dioritic bodies and porphyroblastic migmatites
 - . **peIIIim** - **Unity Imbe** - grey migmatites predominant, with feldspars, porphyroblasts of round shape
 - . **γsp** - granitic masses
 - . **Qa/Qhc** - **Holocene** - Alluvial (colluvial) deposits, with sandy, sandy-clay and clay-silt-sandy texture, in small areas along the Macaé, Bonito and das Flores rivers.
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Source: DRM/CPRM, 1980; Radambrasil, 1983

3. Relief

Table 3 Relief classes of the Macaé de Cima region (extracts for the region)

-
- . **EFo5** - Relief (landform) system - denudation in interfluves and slopes, dissection extremely strong; strong structural control with fractured scarps (crests, spurs and cornices). Drainage incision between 344-466m, and slopes $> 37^\circ$. Landforms covered by shallow clay and sandy-clay surface formations. Morphogenetic processes on unprotected slopes (mechanic desegregation, strong action of chemical weathering), area of unstable dynamics (intense morphogenetic processes action), with fine to very fine drainage density ($P= 1200-2500$ mm). Constraints to land use linked to constant mass movement, with landslides and rock falls, even with vegetation cover.
 - . **Mfo4** - Structured landforms represented by crests of sharp tops, sugarloaves, hills, peaks, nearly parallel scarps, and leaf surfaces. Drainage incisions of 212-312m, slope with $24-37^\circ$, clay formations on surface ($P = 800-1750$ mm). Dominance of diffuse and concentrated runoff processes, favouring formation of gullies and ravines, and several types of mass movement. Dominance of concentrated erosion processes (area of unstable dynamics). Drainage density fine to very fine. Constraints to occupation linked to frequent occurrence of rock falls and landslides, especially during the summer rainy season.
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Source: Radambrasil, 1983

4. Bioclimatic Zones

Table 4 Bioclimatic zones of the Macaé de Cima region (extracts for the region)

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- . **Region 1** - 800-2000m (2787) alt. Annual $T = 13-18^\circ$ C with frost over 1000m, $P = 1500-2400$ mm, annual deficit 0-10mm. Submontane (subtropical type) super-humid to humid climate. Perennial wet/moist forest vegetation.
 - . **Region 3** - 0-800m.alt. Annual $T = 18-23^\circ$ C., $P = 2000-2600$ mm, annual deficit 0-30mm. Super-humid subtropical to tropical climate. Atlantic slope perennial wet/moist forest vegetation.
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Source: Golfari & Moosmayer, 1980

5. Ecological Systems and Land Capacity Classes

Table 5 Ecological systems of the Macaé de Cima region (extracts for the region)

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- . **N. Friburgo System** - Perennial montane and high-montane forest. Regional level of human disturbance zero to medium. Submontane subtropical climate, with a sub-dry season. Mountain relief, altitude above 800m. Soils C, LVA (low fertility), plus R.
 - . **Estrela System** - Perennial submontane forest. Regional level of human disturbance zero to low. Tropical superhumid climate, with no dry season. Steep relief, 100-800m altitude. Soils C, LVA (low fertility, medium depth), plus R. Land with effective depth > 100 cm, low fertility, base saturation $< 35\%$, medium productivity for forest species climatically adapted.
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Source: Golfari & Moosmayer, 1980