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Spatio-temporal dynamics of Neotropical high-altitude mixed oak forests in western Mexico

Thesis submitted for the degree of Doctor of Philosophy at the University of Oxford, Oxford, UK

Michaelmas term, 2006

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THESIS

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Abstract

This thesis contributes to the understanding of two of the most intriguing questions that forest ecologists have faced over recent decades: 1) how high diversity is maintained in species-rich ecosystems; and 2) what is the role of spatio-temporal environmental variation in structuring forest communities. The aims of the research were to ascertain how species composition varies both spatially and temporally and how changes in the vegetation can be understood in the context of species coexistence theories (niche *versus* neutral). A group of 38 sympatric species, including 9 species of *Quercus*, on which little ecological research has been undertaken, were used in this study.

The data used in this project include eleven years of periodic remeasurements of permanent plots established in high-altitude oak forests in Mexico. Adult, sapling and seedling trees were studied as well as their environmental surrounding. Spatial and temporal variations in forest composition were analysed using multivariate statistical approaches.

The results show that there are discrete communities in these mixed oak forests that correspond to specific environments. At a broad scale the study area can be classified into two floristic zones, a mesic zone characterised by associations that include *Quercus candicans, Q. laurina* and *Q. castanea* and; a xeric zone dominated by *Q. crassipes*. However of a finer scale of analysis important variation in composition was associated with different life stages of the trees, with adult trees showing much stronger environmental associations than seedlings and saplings.

Successional pathways and rates vary at relatively fine scales. This may be as a result of dominance alternation between dominant canopy species.

Micro-niche zonation processes caused by a high degree of environmental heterogeneity combined with individual species traits explain the coexistence of phylogenetically similar sympatric *Quercus* species. A hierarchy of processes, each acting at a different spatial and temporal scale, determines species diversity and coexistence. The overall findings support the idea that niche differentiation rather than chance events such as dispersal limitation, are more important in permitting species coexistence.

I dedicate this work to Paula and her tireless will

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CHAPTER 1 - General introduction

1.1 Introduction

Tropical rain forests have been at the centre of attention from a wide-range of perspectives. Losses to agriculture and cattle frontier expansion, ecosystem fragmentation and global climate change have all received attention. Innumerable ecological investigations are frequently conducted across these woodlands as concerns for losses in biodiversity increase. The appeal of tropical rain forests is due to their extraordinary complexity and richness of both flora and fauna. Floristically, although there are large differences between regions (Phillips & Gentry, 1994) it has been shown that in 0.5 km^2 of some tropical forests there are more tree species than in all of North America and Europe (Burslem et al., 2001).

Questions related to floristic diversity are why it is high in some places and low in others, and how species coexist in such a large numbers within a similar area. Discovering how species diversity and coexistence arise will influence how conservation and management activities should be practiced. Across large geographical scales climatic, altitudinal and physiographic variations determine patterns of species composition and, therefore, relative species abundance (Debski et al., 2002). On small geographical scales, although it has been shown that micro-environmental heterogeneity explains patterns of floristic distribution and coexistence in many circumstances (Oswald & Neuenschwander, 1993; Svenning, 2001); there are local patterns of distribution that can not be explained by environmental gradients (Zobel et al., 2000). The common expectation is that each species is adapted to exploit a unique habitat in which it is the most effective competitor. This permits the coexistence of multiple species in heterogeneous environments. Furthermore, recent work (Loehle, 2000; Nakashizauka, 2001; Hofer et al., 2004; Liebhold et al., 2004; Svenning et al., 2004) has shown that separation in time or space, which often vary at small scales, can permit coexistence and promote species diversity. However, the question remains, what kind of temporal and spatial variation permits coexistence and promotes species diversity? (Guo, 1998). Numerous hypotheses have been put forward to explain species diversity and coexistence processes (Hill & Hill, 2001), however, up to now no convincing and

universally accepted one have yet emerged. Whitfield (2002) claims that traditionally, plant ecologists have found it difficult to explain the mechanisms that structure the distribution, abundance and coexistence of species-rich communities.

A possible reason for a lack of consensus amongst plant ecologists might be the fact that those who have studied how species diversity and coexistence is driven have spent most effort examining these processes in lowland tropical rain forests. In contrast, relatively fewer investigations have been conducted in species-rich sub-tropical, temperate or arid forest ecosystems. The lack of investigations over a wide range of systems, other than lowland tropical rain forests, has hampered the development of a general view about the possible factors that account for species diversity and coexistence.

A likely solution that might provide deeper insight into the processes would be to look for general processes in non-tropical lowland rain forests as well as involving large congeneric series of species. This approach would reveal whether the processes inferred from tropical rain forests also act over a wider range of floristic and environmental circumstances. In this context, with the aim of developing a better understanding of the mechanisms, this thesis explores which processes allow species coexistence of a group of congeneric *Quercus* and allied timber species growing sympatrically at high altitudes in the sub-tropical Cerro Grande, Sierra de Manantlan, western Mexico.

The Sierra de Manantlan is an area that contains an extraordinary species pool from both the Neotropical and Neartic phytogeographical realms (Vázquez-García et al., 1995; Cuevas-Guzmán et al., 1997). Particularly, the regions of Cerro Grande is unique in having the highest single-point diversity of *Quercus* reported in the scientific literature, with up to five species co-occurring in a single 500 m^2 plot, around eleven species of *Quercus* within the range of the study area (18,000 hectares) and around 31 species of *Quercus* across the entire Sierra (130,000 hectares). This represents an exceptional opportunity for discovering the contributing causes that promote species diversity and coexistence, for analysing patterns and processes of ecological similar species and for elucidating the mechanisms relevant to the maintenance of species-rich forest communities growing at high elevations in an ecosystem that has been relatively little studied.

1.1.1 Species diversity and coexistence

The simultaneous co-occurrence of ecologically similar species of plants with similar ecological roles and with the same apparent habitat requirements has engrossed the attention of plant ecologists for a long time (Forcier, 1975). A central tenet in community plant ecology maintains that competitive interactions between individuals are amongst the most important mechanisms structuring forest communities. If this is true, no two organisms with identical resource requirements can co-occur since the superior competitor will steadily surpass the inferior. This was the idea behind the *Principle of the Competitive Exclusion* (Gause, 1936), an influential model developed in the early 1900s. According to Wang et al. (2002) a substantial number of present-day ecological investigations have been grounded on Gause's assumptions. As a result in many ecological investigations it is often assumed that in forest ecosystems:

i. There is always competition between individuals for the same few resources (nutrients, moisture, light, growing-space);

ii. Competition is greater between ecologically similar individuals and;

iii. Competition is an essential component for determining which species can co-occur, and in what numbers.

Competitive exclusion processes, as an explanation for species coexistence, are particularly controversial when trying to explain patterns of species coexistence in species-rich communities, since *a priori* all plants require the same basic resources (Barot & Gignoux, 2004). The large number of *Quercus* species growing in sympatric associations together with a number of other broadleaved and coniferous species in Cerro Grande appears to contradict assumptions *i*, *ii*, and *iii* since it would be expected that phylogenetically closely related individuals competitively will exclude one another.

Research into the mechanisms that explain species richness and coexistence are quite variable. The ecological literature on this issue is vast. For example, 10 year ago Palmer (1994) listed around a hundred and twenty hypotheses. Factors commonly thought to account for species diversity and coexistence include: habitat disturbance (different regeneration requirements); natural enemies (different susceptibilities to pests, predators, and pathogens); limitations to seed dispersal; variations in nutrient

availability; niche differentiation (different requirements for limiting resources); competitive equivalence (inability of a species to outcompete a similar species); and fluctuating recruitment (which, together with juvenile persistence, may result in a species "storage effect") (Burslem et al., 2001). Since many of these factors involve an eventual species alternation in both time and space, successional processes, or patterns of vegetation replacement over time and space, are an implicit crucial component in most, if not all, species diversity and coexistence paradigms. The range over which the mechanisms operate, either alone or together, seems to vary however, no single theory or experimental has proved to be entirely persuasive.

Because recent attempts to explain species diversity and coexistence have mostly focussed on two schools of thought: *i*) niche differentiation (Grinnell, 1917a) and, *ii*) neutral theories (Hubbell, 2001), these will be reviewed briefly as theoretical bases for the development of this thesis. The niche differentiation and neutral theories are essentially centered on discovering whether species are sensitive to habitat divergence or to local processes (niche differentiation) from those that maintain that species are unaffected by habitat variations (neutral theories) but by seed dispersal limitation. Although these contrasting views have been tested over a wide range of environmental and experimental conditions (Ackerly, 2003; Fargione et al., 2003; Tilman, 2004) and on woody (Ashton, 1998) and non-woody (Higgins et al., 2000a) species, the results have been quite variable and no clear explanation has yet emerged. Furthermore, because both models could theoretically have contrasting implications, not only for explaining patterns of floristic variation and coexistence, but also for implementing forest management and conservation practices, this chapter seeks to clarify these influential hypotheses and at the same time to assess the evidence offered to date.

Burslem et al. (2001) argues that the historical polarization of this debate into camps favouring different theories of how species coexist may be an artefact of the limited data available and the tendency to work on a narrow range of tropical sites. Within this context, the data in this thesis overcomes the lack of data and narrow gradient constraints by looking at group of sub-tropical species on which very little information has been produced. Such data has been generated over a geographical range of ca. 10 km in a network of 105 permanent sample plots (500 m^2 each) that have been

periodically monitored since 1991 using the same standard protocol for data collection (*see* Chapter 2; section 2.2.3 for details).

1.1.2 The niche differentiation view

Traditionally, the niche differentiation (Grinnell, 1917a) school of thought has been a central paradigm to explain mechanisms promoting species diversity and coexistence in species-rich communities. The niche hypothesis predicts that the number of species that can coexist in a community cannot be greater than the number of limiting spatio-temporal resources (Whittaker et al., 1973). If these limits are exceeded, one or more species will be excluded by the competitive effects of others that draw upon the same limiting resources (Silvertown, 1983). Classical investigations based on the idea of resource partitioning interpret the observed patterns of plant distribution as the result of local control and highly adapted species distributed across heterogeneous environments in which each species has specialised in the use of different resources (Denslow, 1980a; Whitmore, 1989b; Levine, 2002) or different reproductive strategies which describe separate niches allowing species coexistence (Forcier, 1975).

Spatial heterogeneity in microenvironments may provide unique regeneration niches for trees and may promote forest diversity. One manifestation of niche differentiation consists of habitat specialisation, as explained above, such that different species are best suited to use the different micro-habitats in which they are competitively dominant and relatively more abundant (Bazzaz, 1996; Tilman, 1997). A classical issue in this context is how much does niche partitioning (specialization on different resources) versus chance events, such as seeds reaching a suitable site for germination, contribute to the diversity of trees regenerating in gaps? To demonstrate coexistence via niche partitioning, Brokaw & Busing (2000) argue that three premises must be confirmed:

i. There is a gradient in the availability of crucial resources in gaps;
ii. Tree species perform differently along this gradient and;
iii. These differences contribute to species coexistence.

Nonetheless, the idea of the niche, particularly the partitioning of limited resources as a prerequisite for species coexistence, has not found generalised acceptance amongst

plant ecologists. A commonly cited trouble in testing for evidence of niches with plants confined to a single habitat has been the quantitative delimitation of a plant's niche (Ashton, 1998). For example, opponents of a niche view argue that it is difficult to quantify how a species-rich community can sufficiently partition an area into different micro-sites (niches) and divide such a limited range of resources (*e.g.* light, water, CO_2, mineral nutrients, etc.) amongst its members (Silvertown & Law, 1987).

1.1.3 Empirical and experimental evidence for niche partitioning

An important number of studies (Lieberman et al., 1995; Lieffers et al., 1999; Légaré et al., 2001) have showed that tree seedlings growing in canopy gaps in the forest respond differently to light entering into the forest understory. Thus, in forest gaps light partitioning has been hypothesised to increase habitat heterogeneity (Denslow, 1980a; Brown, 1996) providing favourable conditions for the coexistence of large numbers of species in tropical lowland rain forests. This has been one of the most explored areas used to demonstrate the existence of niches and their effect on species diversity and coexistence. For example, Kobe (1999) working with a seedling transplanting experiment of four related species (*Trophis racemosa, Castilla elastica, Pourouma aspera,* and *Cecropia obtusifolia*) growing on alluvial soils at La Selva Biological Station, in Costa Rica, showed that there were significant differences in diameter growth as a function of light availability amongst the four species. The author observed that all species decreased in mortality with increases of light up to 20% of full sun; however, above 20% full sun, mortality of *Trophis racemosa* and *Castilla elastica* continued to decrease whilst that of *Pourouma aspera* and *Cecropia obtusifolia* remained constant. With less than 10% of full sun, there were up to fivefold difference in mortality with *C. obtusifolia* having the highest mortality. He concluded that light gradient partitioning provides a convincing explanation for successional dynamics and suggested that species coexistence and diversity in the study area is at least partly maintained through light niche differentiation.

An example of species coexistence in closely related taxa was provided by Hall et al. (2003) who found that partitioning of light by tree seedlings of three co-occurring species of *Entandrophragma* helps to maintain species diversity in tropical forests of Central Africa. The authors experimentally demonstrated that the best way to favour

recruitment of *Entandrophragma* seedlings was through a series of small to intermediate sized canopy gaps, which provided suitable environmental conditions for seedlings to grow. Likewise, compelling results supporting niche partitioning are reported by Debski et al. (2002), using data on species' spatial patterns of distribution and soil-derived information in two 50 ha permanent sample plots established in Malaysia. They found clumped species' distributions in both plots. The authors suggest that biotic and abiotic factors may be influencing the distribution of the species and eventually limiting their abundance and thus promoting coexistence. However, they pointed out that even though soil type was an important determinant of habitat preferences for the different species, the spatial separation of seedlings due to soil characteristics accounted for only a small portion of the high species richness, suggesting that other mechanisms must also be sought to account fully for the maintenance of tropical tree species richness. In *Quercus* forests, studies have shown (Collins & Good, 1987; Ashton & Berly, 1994; Ashton & Larson, 1996) that micro-environmental factors affect differently the dynamics of sympatric *Quercus* species that occur together within the same forest landscape. These studies have demonstrated that one of the most important factors affecting acorn germination, seedling growth and establishment and ultimately patterns species distribution in *Quercus*, appears to be the amount of light received at the ground story (Ashton & Larson, 1996), since light has a variable effect on species of *Quercus*, this may be cause random mortality of juvenile individuals across the landscape and thus producing variation in patterns of floristic distribution.

In addition, there are indications that the combined effects of shade and drought in many temperate and tropical forests can promote the existence of a wide range of niches and thus to differential dynamics of several species, producing complex patterns of coexistence. Sack (2004) experimentally showed that shade and drought tolerance of 13 European tree and shrub species varied when subjected to different levels of light and watering, suggesting that niche differentiation with combinations of irradiance and water supply may explain patterns in species diversity. Recently published work on niche differentiation considers how canopy-derived environmental conditions also explain coexistence of multiple species. Daws et al. (2002) found that the effect of four factors related to canopy gap formation (red: far-red light, soil nitrate concentrations, soil temperature fluctuations and soil water potential) had different impacts on seed

germination of four sympatric species of *Piper* (*P. dilatatum, P. hispidum, P. marginatum and P. peltatum*). The authors argue that seeds of the four species are affected differently by each of the factors evaluated and consequently this contributes to differences in germination levels allowing temporal species coexistence by reducing intraspecific competition.

It has been observed that plant species which coexist as adults within a community may express niche differentiation at a seedling stage (Latham, 1992). In this context, in Cerro Grande, previous studies (Figueroa-Rangel & Olvera Vargas, 2000a; Olvera Vargas & Figueroa-Rangel, 2000a) have shown that the upper canopy of some stands may be composed of 3-5 oak species. Therefore, in this thesis it is postulated that in the study area there should be consistent microhabitat variations in terms of micro-topographic, edaphic or micro-physiographic gradients. Microhabitat variations subdivide an ostensibly uniform habitat into several micro-niches each one representing differential environmental characteristics and thus allowing the co-occurrence of several *Quercus*, as well as other species. If this is so, a careful spatio-temporal analysis of the distribution of the vegetation across the physical environment of the study area might reveal evidence for existing habitat partitioning. Partitioning of habitats at the seedling stage may reduce competition between ecologically similar species and hence contribute to *Quercus* species persistence at these sites. If no differences in habitat heterogeneity are found, the findings in this thesis will contradict the 'Principle of Competitive Exclusion' (Gause, 1936), a school of thought that has dominated ecological thinking for at least the last 30 years.

1.1.4 The neutrality processes view

In recent years a number of forest ecologists have rejected the niche differentiation view, and as a result several attempts have been made to discover a convincing alternative for explaining the mechanisms that sustain species diversity and coexistence. Brown & Jennings (1998) pointed out that several authors have proposed that rather than species being highly specialised, most are generalists capable of adequate growth under a range of conditions. Therefore, a growing number of investigators have claimed that species interactions and the existence of habitat heterogeneity play a small part in influencing community structure. Hence, "neutral models" (Hubbell, 2001), which

emphasize independent species distributions across a landscape, have gained considerable support from a large number of plant ecologists.

Hubbell (2001) and Bell (2001) claim that niche differentiation does not explain patterns of tree species diversity in tropical rain forests and argue that dispersal limitation from a regional species pool to local communities is the main driving force for species coexistence. According to Hubbell (2001), in highly diverse forest ecosystems, all species are ecologically equal. This implies that there are neither superior competitors nor a wide range of complex scales of environmental gradients. As a result, no single species is excluded through competitive exclusion or favoured by particular environmental circumstances. Rather, their presence in the community is merely due to stochastic events such as seed dispersal. Thus, there is growing belief that local communities are governed by ecological drift, mediated by demographic stochasticity (Svenning et al., 2004). Therefore, one of the fundamental ideas behind the neutral paradigm is that it only takes into account dispersal capacity, ignoring the importance of environmental variations or unexpected modifying events such as disturbances (*e.g.* fire, grazing, tree fall, etc.). These last factors are highly important in the niche-partitioning model.

Thus, one of the most distinctive features of the neutral paradigm is that it stresses that because the abundance of a species is a result of a random dispersal effect, all species within a community follow a random distribution across the landscape. Therefore the entire vegetation describes a compositional drift in which no particular floristically clumped associations are distinguishable (Mazancourt de, 2001; Condit et al., 2002). As a result the compositional similarity between plant communities will decrease as the distance between two points increases (Gilbert & Lechowicz, 2004).

1.1.5 Empirical and experimental evidence for neutral processes

Whilst the role of niche differentiation has been theoretically and experimentally demonstrated to work in a wide range of woody and non-woody plants, there is less evidence supporting the importance of compositional drift. Nonetheless, it has been theoretically (Zhang & Lin, 1997; Ricklefs, 2003) and experimentally (Symstad & Tilman, 2001) demonstrated. The evidence supporting the existence of compositional

drift includes recent findings of (1) strong seed dispersal limitation and (2) nonenvironmental spatial dependency in species distribution, which are both predicted by neutral dispersal limitation (*cf.* Svenning et al., 2004).

In support of a regional (neutral) control, Bell et al. (2000) argue that there is little experimental proof to support the suggestion of niches as important mechanisms for species diversity and coexistence. They point out that if plants are closely matched to their local environments, they should perform poorly if transplanted. The rationale behind this belief is that if species are closely adapted to fit an ecological niche, they will perform poorly in unfavourable environments or even be unable to invade new spaces. In this context, in an experiment Bell et al. (2000) showed that sedges (Cyperaceae: *Carex*) growing in old-growth forest are quickly able to become adapt to a new habitats of different environmental characteristics, they observed that when individuals of Carex were transplanted far away from their origin and over contrasting environmental conditions, all transplanted individuals mostly experienced an exceptional local adaptation and sometimes, the rarest species to area was the most successful when compared to the local species. Based on these results the authors argue strongly that the effect of specific environmental variance was weak, concluding that the forest floor is not a simple mosaic of discrete habitats to which species become differently adapted. A mismatch has also been reported (Shmida & Ellner, 1984; Terborgh & Andresen, 1998) between environmental variations and species' distribution at the local and landscape levels as well which result in a compositional drift, or a random change in community species distribution. Terborgh & Andresen (1998) particularly found that compositional differences between permanent plots established in a wide geographical range of inundated forests, increase with distance, validating a neutral-based view.

The evidence in present-day literature strongly suggests that deterministic (niche-assembled) and stochastic (dispersal-assembled) processes are both at work in nature (Stevens et al., 2003), however their relative importance in explaining patterns observed in community ecology is still unresolved (Hardy & Sonké, 2004). Contemporary investigations have demonstrated that the lack of a general agreement is simply because spatio-temporal mechanisms have a direct involvement in both species diversity and coexistence. In this thesis it is argued that the lack of consensus emphasises the need to

incorporate hierarchical studies implemented at various spatio-temporal scales and over a wider range of ecosystems.

1.2 The niche and dispersal limitation involvement in forest management

Experience shows that failing to regenerate a stand after it is harvested may result in land that is more susceptible to conversion to pasture or cultivation (Ochoa-Gaona & González-Espinoza, 2000). This a common hazard to many forest ecosystems and one of the main reasons for designing sound silvicultural practices. In this context, two important challenges are involved in the design of sustainable forest management: the maintenance of ecologically dynamic processes, but considering only species of particular interest, and the creation of environmental conditions (niches) that favour the establishment of the desired species but at the same time, to avoid the establishment of undesirable species.

Despite the long dispute about whether niches or dispersal abilities are more important, neither theory has been particularly helpful to forest management. It is remarkably difficult to find a direct involvement of either process in supporting the design of forest management schemes in the scientific literature (but *see* Hall et al., 2003). From the perspective of forest management, whether species diversity and coexistence is mediated by niches or by dispersal limitation is of primary importance. The correct answer will offer fundamental information to assist decisions about how to undertake forest management. For example, if niche differentiation is responsible for species diversity and coexistence, determining the spatial scale at which this process operates would be helpful in considering the size of the canopy gaps so that particular environmental conditions can be created that would favour the establishment of desirable species.

In this context, the management of closely related species could be mediated through the manipulation of niche availability. In this case precise information about a species' specific habitat requirements may be needed in order to mimic natural processes and thus facilitate the establishment of the species of importance. In contrast, if species diversity and coexistence were mediated by dispersal limitation, the extent of canopy

openings for those species with big seeds and low dispersal ranges would be very important to ensure a successful re-establishment of the vegetation after harvesting. However, if neutral processes are at work to explain species diversity and coexistence and all species have identical behavioural (ecological) characteristics as Hubbell (2001) and Bell (2001) imply, no precise information on specific habitat requirements may be necessary for species to colonise a new area, due to the primary importance is seed dispersal rather than environmental adequacy.

One of the most serious questions that confront both forest researchers and practitioners when implementing silvicultural operations is the extent of canopy manipulation that is necessary. This allows control over gap size, frequency and the environment of the forest or of desired species, and thus species composition (*cf.* Simmone, 2000). In particular, if species coexistence is mediated by seed dispersal, it may also imply that the application of any particular silvicultural system for the establishment of a new stand after logging may be unimportant.

1.3 Outline of the thesis

This thesis, as a contribution to the long-standing debate on the mechanisms that explain species coexistence in species-rich forest ecosystems, examines the relationships between a group of 38 ecologically similar species, including 9 species of *Quercus*, growing at high altitude in sub-tropical *Quercus*-dominated forests. One of the main objectives is to elucidate whether this group of species exhibits non-random spatial distributions or whether a more haphazard pattern of cohabitation occurs.

The general objectives of this thesis, derived from these issues are:

- To describe local patterns of floristic variation of a group of ecologically similar timber species growing in a high-altitude sub-tropical mountainous forest.
- To determine the relative importance of the underlying environmental conditions in such floristic patterns.
- To investigate the dynamics of successional processes and their apparent causes.

- To investigate the composition, structure and dynamics of the juvenile vegetation and their contribution to the dynamics of the vegetation.

Chapter 2 gives a detailed description of the study area including its geographical location. It also provides an account of the fieldwork and methods used. Particular emphasis is devoted to describing the data collected over 11 years of periodic observations made on a network of 105 permanent sample plots. **Chapter 3** assesses the floristic patterns in the adult community. Of particular interest in this chapter was to determine whether environmental heterogeneity explains patterns of floristic association as well as to discern the ecological paradigm (niche *vs* neutral views) that best explains such patterns. **Chapter 4** investigates the dynamics of long-term successional trends using three different time scales (4, 8 and 11 years). The contributions of ingrowth and mortality on successional processes are also analysed. **Chapter 5** describes the dynamics of spatio-temporal patterns of variation in seedlings and saplings and relates these processes to the role of geographic separation and micro-environmental heterogeneity. Particular emphasis is devoted to the analysis of the dynamics of temporal species fluctuations as mechanisms by which this group of species coexist. **Chapter 6**, the final part of the thesis, focuses on three main areas: *i*) the general conclusions drawn from the research; *ii*) implications for the management of mixed-oak forests in Cerro Grande, and *iii*) the identification of research areas that need more attention.

CHAPTER 2 - The study area and research methods

2.1 Introduction

This chapter describes the study area located in the Sierra de Manantlan Biosphere Reserve in West-Central Mexico. Emphasis is concentrated upon its biological importance and its objectives of management. Vegetation history and the origin of the Holarctic flora, including the species migration that occurred during the Pleistocene is reviewed. The global diversity of *Quercus* and across the study area is also discussed. In addition, the chapter provides a detailed description of the fieldwork and sampling methodology carried out in this research. The methods followed in establishing, maintaining and re-measuring a network of 105 permanent sample plots, and handling the data gathered from them is described in detail. In the last section the general structure of the data set produced over 11 years of periodically collecting records from the sample plots is outlined.

2.2 Study area

2.2.1 The Sierra de Manantlán Biosphere Reserve

The Sierra de Manantlán Biosphere Reserve (SMBR) is a complex mountain system ranging from small outlying fragmented hills to vast and continuous forested areas at medium (450 m a.s.l.) to high (2860 m a.s.l.) elevations with a wide range of climates, physiographies and soils. The Reserve is internationally recognised as a floristic treasure house and officially recognised by the MAB-UNESCO programme due to its outstandingly high diversity of flora and fauna (SEMARNAP, 2000). The SMBR is a protected area declared as a Biosphere Reserve in 1987 in an attempt to integrate ecological conservation and regionally sustainable development goals. The SMBR extends almost unbroken over 130,000 hectares parallel to the Pacific coastline of México, approximately 50 km inland. Because of its proximity to the sea this region receives a significant amount of both direct and indirect precipitation through seasonal sub-tropical rains and mist. Geographically it is located between the Mexican states of

Jalisco and Colima (19° 26'47" - 19° 42'05" North latitude and 103° 51'12" - 104° 27'05" West longitude) (Figure 2.1).

The Reserve is located in West-Central Mexico between the Neotropic-Neartic realms and encompasses parts of the Sierra Madre del Sur in Tropical America. This mountain chain arose as a result of the upward folding of Cretaceous deposits, and resulted in a region of abrupt topography, with valleys and deep ravines that allow the persistence of a unique and diverse communities of plants and animals (Cuevas-Guzmán et al., 1997). The terrain is made up of innumerable intermountain valleys and plains, providing interesting niches where both temperate and sub-tropical floras and faunas converge. These have contributed to the outstanding diversity of the sierra. Another factor responsible for the biodiversity is its connection to the Sierra Madre Sur through the Trans-Mexican Volcanic Belt. Vázquez-García (1994) has proposed that this connection allowed an important spread and diversification of taxa of temperate environments into Mexico after they became separated from their other North American counterparts.

The SMBR is one of the richest Mexican regions and also one of the most important protected areas in North America. Recent botanical and wildlife explorations have recorded approximately 2,900 species of vascular plants; 110 species of mammals, 336 birds (representing 26% of all mammals and 33% of all bird species in Mexico), 85 reptiles and amphibians, 238 insect families, and 7 orders of arachnids and about 17 endemic plant species (SEMARNAP, 2000). One example of its valuable endemic species is the perennial "teosinte', *Zea diploperennis*, a wild relative of cultivated corn, rediscovered in 1977 (Iltis et al., 1979) and previously thought to have been extinct since 1921. Populations of the wild annual relative (*Mays* ssp. *parviglumis*) and the 'Tabloncillo' and 'Reventador' races of maize, traditional in this area, are further targets for conservation.

Based on Rzedowski's 1978, classification, thirteen vegetation types can be found within the Reserve, including relatively contrasting ones such as mountain cloud forest and tropical dry forest (SEMARNAP, 2000). Thus, SMBR is a unique area distinguished by its high floristic-diversity and enormous environmental heterogeneity in which temperate and sub-tropical elements converge. At higher elevations it has both tropical (*e.g. Davillia, Lonchocapus, Pseudobombax*) and temperate North American

(*e.g. Quercus, Tilia, Talauma, Carpinus, Magnolia, Cornus*) floristic elements; whilst at lower altitudes vast zones are covered by relatively floristically unexplored tropical dry forests. The biological diversity of the study area contains great potential for forestry, agriculture, medicinal and nutritional purposes (Benz et al., 1990; Benz et al., 1994). Several studies (Jardel Pelaez, 1991; Gerritsen, 1995; Rojas et al., 1996; Jardel Pelaez, 1996a) have indicated that the biological diversity of the present day in the SMBR is not just the result of tectonic, ecological and evolutionary processes but also because of the effects of human-related impacts such as gathering non-timber forest products, traditional agriculture and domestic grazing.

The geology and physiography of the SMBR is remarkably heterogeneous and rather discontinuous. Conventionally, this region can be divided into two main geo-physiographical regions. The biggest segment lies along the Trans-Mexican Volcanic Belt, the tallest mountain range in Mexico (Rzedowski, 1978) and one of the largest volcanic arcs on the North American plate dating from the late Miocene. It spans 1000 km and crosses central Mexico from the Pacific to the Atlantic coasts (Alva-Valdivia et al., 2000). A small part of the SMBR called 'Cerro Grande' is a plateau-like structure, which differs slightly from the main SMBR's physiographical alignment, and also differs in geology, soil and vegetation (Figure 2.1).

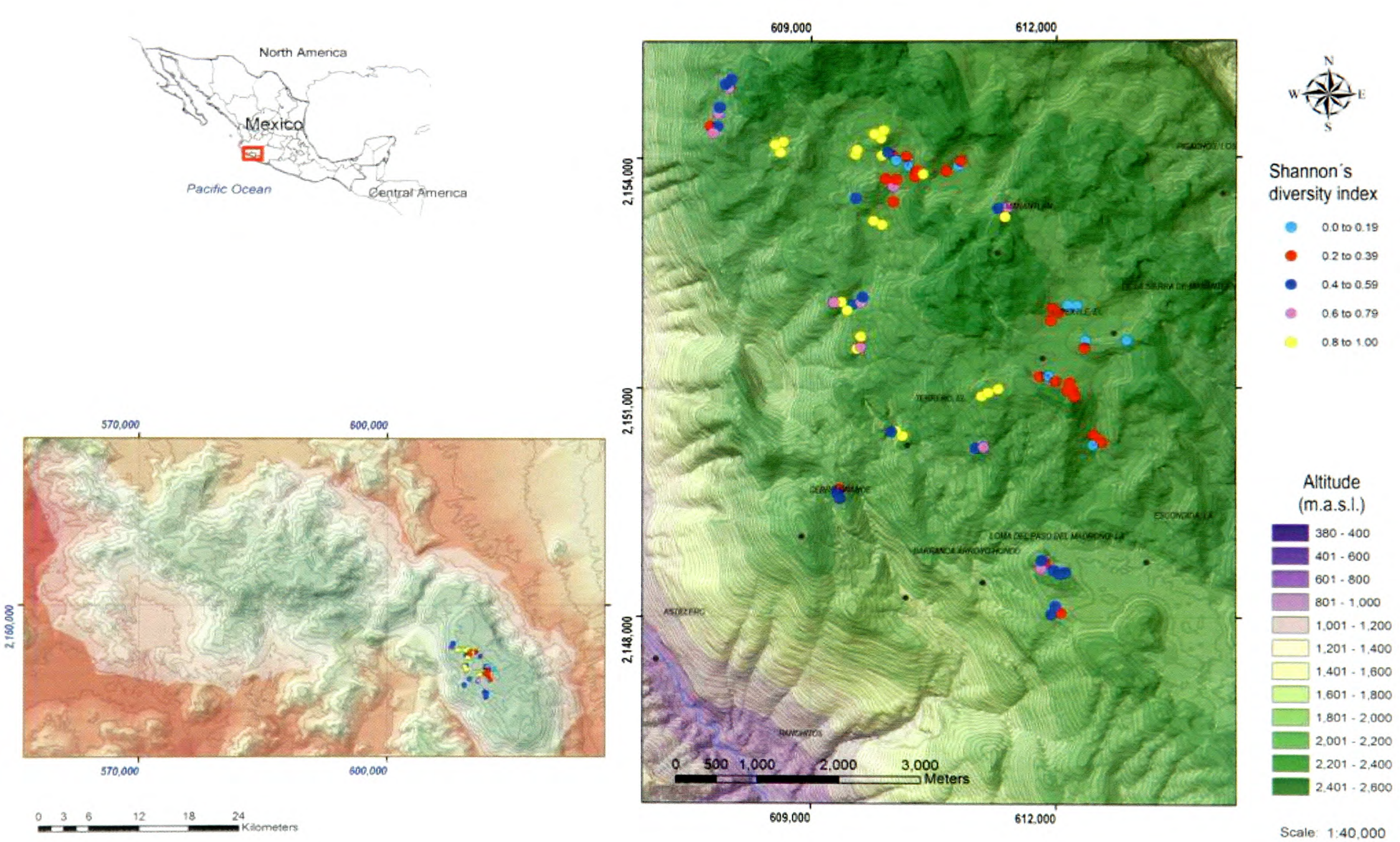


Figure 2.1 Map showing the Sierra de Manantlan, Biosphere Reserve, in western Mexico with the location and diversity of study plots in Cerro Grande represented by coloured circles.

2.2.2 The Region of Cerro Grande, Sierra de Manantlan

The research described in this thesis was carried out in Cerro Grande (CG). This is a calcareous plateau-like structure of Upper Cretaceous limestone (Lazcano, 1978) located on the extreme South-eastern side (19° 24′ 32" - 19° 31′ 02" North latitude; 103° 57′ 44" - 104° 01′ 09" West longitude) of the SMBR. Even though CG may appear as a different and separate biogeographical unit from the rest of the SMBR, mainly because of the differences in floristic composition and because of the contrasting physiognomic appearance between the two sections, CG comprises an important forested region of the SMBR. It is bounded to the East by an escarpment locally named 'Neverias', a steep cliff at more than 2000 m a.s.l. CG's area is about 18,000 ha of forested lands. Its physiography is exceptionally irregular, being characterised by a series of disconnected sandy ridges in which the underlying soil is generally exposed. The micro-relief varies over short distances; commonly it is made up of innumerable sinkholes and limestone karst of variable depths. The slopes vary in steepness from 10 to 60% although steep-sided ravines of more than 90% also occur. The altitudinal range extends from 430 m at El Llano de Toxín to 2 450 m at La Antena. Along this altitudinal gradient there is an outstanding floristic variation as well as a variety of habitats. The majority of potentially economic timber species (mainly oak, pine, fir) and mountain mesophytic forests grow on the top of the plateau (at approximately 1800 m a.s.l. and occupy roughly an altitudinal range of 500-600 m).

Topography

Two main topographic patterns can be readily differentiated on the CG plateau. The surrounding flanks constitute abrupt slopes and long rocky ravines. In these zones the bedrock, which is mainly calcareous material of sedimentary origin (Vázquez-López et al., 2000), is generally exposed. The dominant vegetation in these areas is mostly tropical dry forest, generally of low stature (< 6 m height). On the top of the plateau (above 1,900-2,000 m a.s.l.), the general topography that occurs around the flanks becomes less steep and craggy. Conventionally, over the top of CG three general micro-topographic patterns are distinguished: *i*) areas of undulating terrain of varying steepness and no consistent orientation with respect to solar radiation, *ii*) areas of gently rolling to flat terrain forming moderately long ravines and; *iii*) areas of steep slopes

and/or karstic dolines randomly distributed across the landscape. These topographical settings shape the environmental attributes of CG and create a multiplicity of micro-environmental gradients differing in solar radiation, humidity and soil moisture.

Soils

Martínez-Rivera & Ramírez (1998) describe the soils of CG as Andosols with scattered patches of Cambisols and Luvisols. By far the largest proportion is Andosols, which are a special type of mountain soil. They are characterised by having fluffy a consistency and dark colour, high porosity, high permeability and high aggregate stability. They generally have a high moisture storage capacity and are rich in nutrients (Nachtergaele, 2004). However, detailed soil descriptions based on field surveys and laboratory analyses are not yet available for CG. This makes it relatively difficult to set a clear demarcation between soil types and even more difficult to discern soil units at smaller scales, mainly due to the wide range of micro-topographic variation. A simple interpretation, based on laboratory analyses of soil samples collected during the fieldwork and complemented by personal observations, suggests that the soils in CG have a well-defined crumb structures with a sharp division between the upper organic layer and the A-horizon. These soils can be excessively well drained and easily eroded. In specific locations they may contain fine-textured loams, and also a high proportion of sand and fine gravel fragments giving a granular texture. Poor water-holding characteristics make them highly vulnerable to erosion, resulting in an upland-to-lowland humidity gradient.

Climate

Following Köppen's climatic classification adapted by García (1987) for application to Mexico, the climate in CG is Ca(W2)(w)(e)g. This corresponds to a Sub-humid temperate climate with warm summers and means annual temperatures fluctuating between 12° and 18°C. This is the wettest of the climates, classified as sub-humid with precipitation-temperature (P/T) relationship >55.0 (Martínez-Rivera et al., 1992). Meteorological records are rather limited for CG and not regularly collected. Data gathered at the nearby "El Terrero" meteorological station, situated approximately 5 km from most of the psps, show well-defined annual dry and wet seasons. Mean annual

rainfall is ~1660 mm with a unimodal distribution; with most falling between July and September; the rainy season may extend until October. Sporadic rainfall events may also occur during winter and occasionally extend to January and February. At higher altitudes, low temperatures occur which can fall to –3°C, depending on locality, and constant mists are important climatic factors that improve the water balance in the area. Heavy mists may be present, mainly during the peak of the rainy season, along with infrequent freezing in some places.

Hydrology

CG plays a key role in the local hydrology. It acts as a catchment and is undoubtedly an important water supplier to the nearby Marabasco and Armería rivers, flowing in the lowlands below the plateau. On the CG plateau, there are no permanent or temporary watercourses. Typically, when a rainfall event occurs the rain percolates quickly into the subsoil so that no standing water is found anywhere on the plateau. Rapid rainwater infiltration into the subsoil occurs even during the peak of the rainy season. This quick percolation frequently erodes the limestone bedrock and has created innumerable natural caves shaped by the collapse of the limestone, creating a distinctive landscape. Judged by the speed with which the water infiltrates the subsoil, supply is probably the principal limiting factor on these sites for vegetation establishment. For the local human inhabitants water is available from small reservoirs built of concrete or natural sinkholes.

The Zoning of the SMBR

The management of the SMBR is based on a scheme of territorial organization. For this the SMBR is divided into three zones; the *core zone* is an area where rigorous protection is practiced and where no logging, grazing, or gathering of non-timber forest products is permitted; the *buffer zone* encompasses peripheral areas around the core zone. Some forms of land-use (described later in this chapter) are permitted, and finally the *transition areas* also called the "influence zone" consist of all other areas surrounding the SMBR. The influence zone is not included in the legal decree of the Reserve (Jardel Pelaez, 1992). The Reserve has three separate core zones (El Tigre,

Manantlan-Las Joyas and Cerro Grande), which extend over ca 30% (41,898ha) of its area (Figure 2.2).

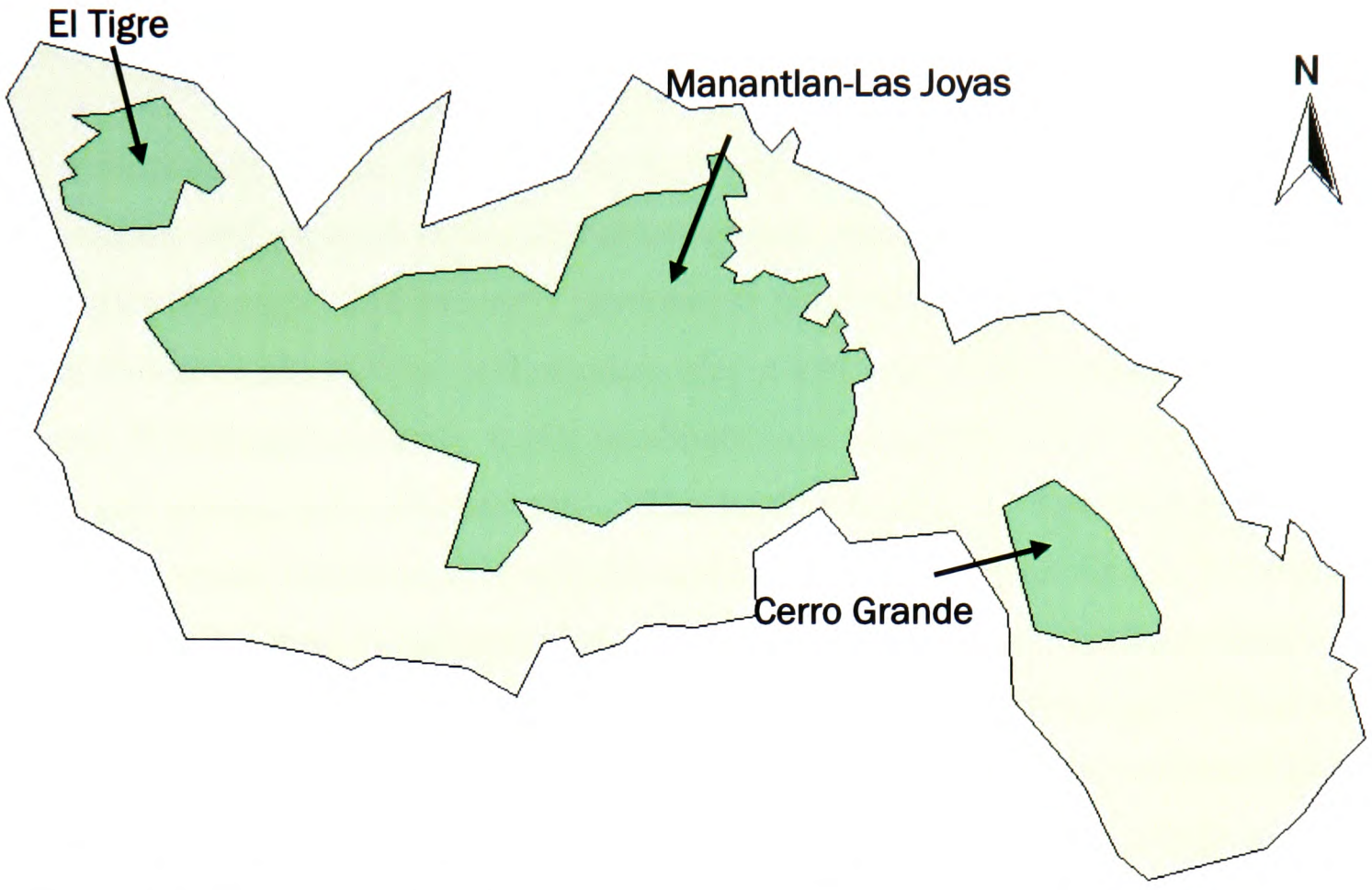


Figure 2.2. The core and buffer zones of the Sierra de Manantlan Biosphere Reserve. ■ Core zones (41,898ha); □ Buffer zone (97,672ha).

The core zones are aimed to protect watersheds and critical habitats for biodiversity conservation. Observational research (no manipulative experimentation), environmental education and visits by tourists are occasionally allowed in the core zones. Strict protection in strongly enforced in the core zones through several strategies negotiated with the landowners (Jardel Pelaez et al., 2003). The buffer zone surrounding the core extends over 70% (97,672ha). The main goals of management in this area are sustainable forestry, agriculture, cattle grazing, tourism and other forms of natural resource use including fishing.

The exclusion of most forms of grazing (including seasonal and permanent grazing by cattle, pigs, and sheep), logging and the construction of new human settlements from most of the core zones has been relatively successful, and so there have been very few negative impacts since it was declared protected area. Nevertheless, as with most relatively unused land in Mexico, the buffer zone faces pressures from deforestation.

grazing, constant fires, illegal logging, itinerant agriculture, and ever-increasing demands of a growing population.

Strategy of management of the SMBR

The management of the SMBR aims to integrate ecological conservation, social improvement and regional sustainable development, based on active participation and cooperation amongst stakeholders, government agencies and academic institutions (Jardel Pelaez et al., 1996b). Stakeholders play a key role in the management of the Reserve. It has approximately 8,860 inhabitants and roughly 21,533 live within the buffer and around the influence zones. The land is owned by three categories: the government owns one percent, 39 percent is privately owned, whilst the rest belongs to Ejidos (Ejido is a kind of land-based cooperative established under federal guidance in which the residents collectively own the land and work with pooled resources. Members of an ejido are called "Ejidatarios". Ejidos were instituted after the Mexican Revolution) and to comunidades indigenas (indigenous communities of the *Nahua* ethnic group). The decree that established the Reserve did not involve land expropriation so land tenure has remained relatively unchanged since prior the decree. Currently the Reserve falls within the territory of 32 agrarian communities and 80 private landowners all within the boundaries of seven municipalities in two states (Jalisco and Colima) (SEMARNAP, 2000; Gerritsen, 2002).

Residents of the Reserve are engaged mainly in subsistence agriculture (corn, beans, tomatoes, sugarcane, watermelon, mangoes), cattle grazing, timber production (mainly pine and oak lumber), and extraction of non-timber forest products. Since the decree and management program for the SMBR established restrictions over land use based on the administrative zoning already described, one of the most challenging tasks in the area has been to reconcile contrasting views over the objectives management of the area.

The basis of management of the SMBR involves cooperation between the federal authority (National Commission for Natural Areas, CONANP) represented by Reserve's Direction, the agrarian communities (Ejidos) and local organizations within the Reserve. These social organizations (committees) work together in the establishment

of institutional agreements and the execution of management programs directed towards sustainable use of natural resources, rural development and ecological conservation (SEMARNAP, 2000). Thus, the main task of the committees is to promote active local participation, generate inter-institutional mechanisms for managing the area and to address social, economic and environmental issues in an integrated way. In the SMBR, the Manantlan Institute for Ecology and Biodiversity Conservation (Instituto Manantlán de Ecologia y Conservación de la Biodiversidad: IMECBIO), a dependency of the University of Guadalajara, has also played a crucial role in promoting biodiversity conservation and sustainable development. Until 1993 it served as the Reserve's most important administrative and management agency, IMECBIO lead technical assistance and extension work in several communities (Gerritsen, 2002).

At present, applied research is mostly carried out by IMECBIO staff that provides the knowledge needed for formulating realistic management plans. Through environmental education the inhabitants of the region are made aware of the Reserve's existence and the need for biodiversity conservation (Jardel Pelaez et al., 1996b). Management activities thus incorporate a regional perspective which is community-based, and of participatory nature. Whenever possible, preliminary studies are carried out to gain insights into the local social organisation and the strategies of how they manage their natural resources, after which a participatory planning process is initiated. Thus, specific studies are developed in different communities in order to improve the quality of development activities (Gerritsen, 1995; Gerritsen, 2002).

This has allowed the development of management programmes in ways that have helped both the people and the environment, or at least have resulted in very few negative environmental effects due to land use (mainly forestry operations). An example of this kind of social organization is with a sawmill enterprise in the "El Terrero" ejido, located in Cerro Grande. Members of the Ejido collaborated with members of IMECBIO-Universidad de Guadalajara to rejuvenate a failed sawmill project that was initially run in the early 1970s. This is the only Ejido in the Reserve with a timber operation where trees can be harvested for commercial purposes. Ejido members of El Terrero do so on small clear cuts (<5 ha) mostly in *Quercus* forest located in the buffer zone (Jardel Pelaez et al., 1995a; Olvera Vargas & Figueroa-Rangel, 1999). In addition, the potential for eco-tourism is also being explored. Another

Ejido, Toxin, also located in Cerro Grande is in the process of developing an interpretative centre and low-impact camping facilities for tourists who want to learn about the rich diversity of the region. It is important to mention that nearly 35% of the total land of Cerro Grande falls within the core zone (mostly Toxin's Ejido ownership) whilst the remaining 65% is in the buffer zone.

2.2.3 Pleistocene vegetation history and origin of the flora

The present-day plant floristic composition in Manantlan includes three main elements; Holarctic, Neotropical and Endemic. The oak forests in particular contain a mixture of these three elements with relatively similar proportions of Neotropical and Holarctic and fewer endemic species (Rzedowskii, 1991). Holarctic plants increase from south to north and from low to high altitudes, whilst Neotropical ones do the opposite, and Endemic plants become more common with increasing aridity (Rzedowski, 1978). Oak forests in Mexico represent relicts from past eras when the climate was cooler than at present and this is mainly related to the advance of glaciers during the Pleistocene (Sarukhan, 1968).

Most of Mexico lies in the Neotropical realm with the majority of the flora coming from Central and South America (Raven & Axelrod, 1974); however, another line of reasoning suggests that the flora must have originated in Mexico migrating later to the south. Until quite recently it was believed that complex present-day vegetation in Mexico had originated during the Pleistocene (Deevey, 1949; Dressler, 1956) but there is now palynological evidence to support the idea that its foundation dates back to more ancient times, particularly the Tertiary (Steyermark, 1950; Braun, 1955; Martin & Harrell, 1957). Wend (1993) claimed that part of the Tropical element (*e.g. Clusia, Fuchsia, Hedyosmum* and *Oreopanax*) in the mountains of Mexico arrived in the Eocene from Eurasia, Africa via Eurasia and South America via Antillean routes during the spreading out of megathermal climates and during the Miocene and Pliocene from South America via the Panamanian land bridge.

A widely accepted explanation of the observed contemporary floristic patterns and their heterogeneous geographic locations is based on the idea that most forested areas transformed their ranges of distribution during the Pleistocene (Graham, 1999). A

number of hypotheses suggest that whilst the earth's tectonic plates were relatively stable and there were few significant large-scale geographical changes. Large parts of the earth experienced phases of wet (pluvial) and dry (interpluvial) climate cycles during the Pleistocene, in which massive sheets of ice scoured the earth alternating with warmer interglacial periods during which the ice retreated. Such glacial cycles had profound effects on most biotas causing large-scale modifications in their patterns of distribution and abundance (Cox & Moore, 2000). One of the most significant effects was to cause many species to shift, firstly from north south and then, to withdraw from the south to the north again. Subsequently, once the species reached new habitats, they developed adaptive mechanisms allowing them to colonise new and open environments following the cycle of glacial and interglacial periods (Gentry, 1982; Giesecke & Bennett, 2004; Kearney, 2006). In the montane tropics of Mexico climatic oscillations took the form of an altitudinal lowering and compression of vegetational zones due to the expansion of ice sheets. In contrast, in the lowland tropics, temperature oscillations associated with glacial advances were minimal but changes in precipitation were pronounced (Dressler, 1956; Perry et al., 2000). In the basin of Bogota, for instance, it has been estimated that oak forests occurred between 800 and 2200 m during glacial periods and between 1100 and 3300m during the interglacials; this altitudinal migration left patches of oak forest isolated at both low and high elevations (Hooghiemstra, 2006). For Mexico Lozano-Garcia & Ortega-Guerrero (1994) have reported an expansion of montane oak forests in Central Mexico associated with a humid Late Glacial.

When climatic fluctuations of the Pleistocene and physical barriers divided formerly continuous populations and confined them to more restricted geographic areas, this resulted in isolated patches of forest that were eventually reduced to small island-like regions called refugia. These so-called refugia would 'trap' species within geographically restricted zones until more favourable conditions allowed re-expansion their ranges in different directions and at different rates. Refugia in Mexico often showed high levels of species diversity and endemism and they were important sites for *in situ* speciation (Gentry, 1982). During the Pleistocene an epeirogenic elevation lifted the land from 3000 to 4000 feet in North Mexico providing a good refugium for retaining temperate elements and it provides the origin of high-altitude plants of today (Sharp, 1953).

Graham (1976) reported that temperate trees including genera such as *Abies, Acer, Carya, Cedrus, Cornus, Engeldhartia, Fagus, Fraxinus, Liquidambar, Liriodendron, Nyssa, Picea, Pinus, Platanus, Populus, Quercus, Tilia,* and *Ulmus* have been present since the Miocene in Chiapas and Veracruz. Throughout the Cretaceous and Early Tertiary some Holarctic elements (*Abies, Alnus, Cupressus, Pinus, Quercus* and *Crataegus*) had wider and more continuous distributions than at present; more recently during the Oligocene and Early Miocene climatic conditions were cooler and drier, which forced some temperate elements to migrate through pine and oak forest corridors. Such migrations were a consequence of colder climates in the south-eastern United States which forced elements from boreal coniferous forests to extend southwards (Gulf Coast) (Graham, 1999); the climatic cooling also caused constituents of the deciduous forest to be displaced further south in Mexico then, with the return of warmer conditions in the Holocene, remnants were trapped at mid-altitudes of the temperate zones of Mexico. With respect to the controversy over Pleistocene vs Tertiary origins of the Mexican flora, Rzedowski (1991) pointed out that the primary establishment of the Mexican flora was set in the Tertiary but the climatic fluctuations and physiographic changes that occurred in the Pleistocene contributed to the diversification that is seen today.

The global diversity of Quercus

Among trees, those in the genus *Quercus* L. FAGACEAE ("encino," "roble", "oak") have consistently been common constituents of the forests. After *Pinus,* oaks are one of the leading hardwood taxa with a large number of potential timber-producing species. All yield good-quality lumber for a number of purposes. Oaks are valued not only because of their durable and high quality timber used in furniture and wine barrel manufacturing, but also they are highly appreciated for their edible fruits, exceptional firewood quality, and they provide a great variety of habitats for wildlife. *Quercus* is one of the most important genera of angiosperms in America, Europe and Asia (Nixon, 2006). In America, *Quercus* species colonise large areas of land from southern Canada southwards to Colombia, with the greatest diversity in the Southern United States and the highlands of Mexico (Nixon, 1993a). In Europe, *Quercus* is found from the British Isles across continental Europe and the Mediterranean regions and extends to parts of northern Europe. In Asia it grows in the mountainous parts of southern Asia to

Kamchatka, Korea, Japan, and southwards to Southeast Asia and Malaysia (Jones, 1974; Nixon, 1993a). Based on existing treatments (*see for instance*: McVaugh, 1974; Rzedowski, 1978; Martínez, 1981) a reasonable estimate of oak species for the entire Western Hemisphere is about 200-225 species. By far the greatest concentration of *Quercus* species is in Mexico which has almost half of the world's oaks. Approximately 150 native oak species occur wholly or partially in the country (Nixon, 1993b). The wide ranges of physiographic and environmental heterogeneity along with the range of altitudinal variation are likely to be the major causes of such diversity. Oaks are distributed in Mexico along ridge tops, in high valleys, and on isolated peaks all over the country, except in the Yucatan peninsula. They are also found on a wide-range of biogeographic conditions and show a great variety of growth forms, ranging from a xerophytic habit in Chaparral vegetation, to quite big trees in Evergreen Cloud Forest (Rzedowski, 1978).

Quercus at the SMBR

Quercus is particularly abundant and highly diverse in the SMBR (González-Villarreal, 1986). *Quercus* species are common in almost all the vegetation types represented across the Reserve. Approximately, 31 species have been reported for the study area (Vázquez-García et al., 1995) which are differentiated into two major vegetation types: Dry oak forest (400-1500 m) characterised by trees reaching 5-15 m tall. The species in this group are mostly deciduous during the driest part of the year. Prominent species in this group are *Quercus castanea, Q. glaucensces, Q. magnoliifolia,* and *Q. rugosa.* Sub-deciduous oak forest (above 1500 m), is characterised by trees of up to 20-35 m tall that are deciduous for very short periods, but the different species do not lose their leaves at the same time. Amongst the main trees of this group are *Quercus candicans, Q. acutifolia*, and *Q. laurina* (Cuevas-Guzmán et al., 1997).

Quercus in the SMBR can be found in dense monospecific stands and also a number of the species frequently grow as isolated individuals intermingled with other broadleaved species particularly, in wet environments. However, most *Quercus* species typically co-occur in a variable mixture of species or small cohorts of single-tree species composition. But, species diversity, stand density and stem quality, greatly vary as a result of elevation, location and physiography within the Reserve (Olvera Vargas &

Figueroa-Rangel, 2000a). In favourable site conditions such as wet environments, on deep soils and gently slopping-terrain, middle to lower catenas and north-facing aspects (due to orographic-shade) some species (*e.g. Quercus xalapensis, Q. salicifolia, Q. laurina,* etc.) can reach more than 30 m tall and more than 1.30 cm in diameter at breast high (Olvera Vargas & Figueroa-Rangel, 1999). This is the case in certain localities within the Reserve such as Toxin, Los Mazos and Neverias. The oak species growing in these zones are typically represented by sub-deciduous oak forest of higher altitudes.

A number of studies carried out in the study area had suggested that even though some *Quercus* species might share key ecological and silvicultural characteristics such as their degree of shade tolerance, sprouting capability, fire resistance, low annual growth rates and timber characteristics (Jardel Pelaez et al., 1995b; Olvera Vargas & Figueroa-Rangel, 1998), most species differ in their habitat requirements (Figueroa-Rangel & Olvera Vargas, 2000a and b). Site and environmental conditions have important influences on key ecological processes. For example, Olvera Vargas et al. (1998) demonstrated that phenology, including seed production, varies between and within species. These processes are correlated to geographic location and to environmental surroundings where the different species grow.

It is assumed that the success of establishment after silvicultural cuttings depends on two key aspects: 1) an adequate seed supply which is mostly provided from mature trees whose average diameter is above 30-35 cm (Moreno Gómez et al., 1995) and 2) the vigour and quantity of coppice or root sprouts that grow after harvesting (Amador Ramírez, 1992) since depending on seed alone as means of re-establishing a new stand after harvesting is sometimes inadequate, especially with the species that do not produce seed regularly, as is the case of those *Quercus* species growing in the wettest habitats of Cerro Grande (*e.g. Q. laurina Q. scytophylla*) (Olvera Vargas et al., 1998). Species of dry habitats such as *Q. crassipes, Q. rugosa, Q. peduncularis* grow well in open environments and re-sprout well from both roots and cut stumps, they also produce little seed (Olvera Vargas & Figueroa-Rangel, 1998). Environmental factors such as precipitation and temperature largely determine species distributions and influence the establishment, growth and seed production in Manantlán (Muñoz Mendoza, 1992; Santiago Pérez, 1992).

2.2.4 The effect of disturbance processes on the vegetation of Manantlan

It is well known that natural- and/or human-induced forest disturbance regimes such as fires, flooding, grazing, logging and agricultural clearance have major impacts on determining the nature of ground vegetation (Oliver & Larson, 1996). Because of this, the role of disturbance regimes in maintaining species diversity is a central tenet of ecology (Frelich, 2002). And, since many early successional species are dependent on some sort of natural or anthropogenic disturbances, in recent years the maintenance of an appropriate level of perturbation has also become recognised as a general principle in conservation biology (Harrison et al., 2003). It has been shown (*e.g.* Rogers & Hartnett, 2001) that by disrupting the established plant canopy and altering resource availability (*i.e.* amount of light, moisture or soil nutrients) "regeneration niches" can be created which provide opportunities for less competitive species to become established and coexist in species-rich communities.

A considerable number of investigations have shown that present day vegetation is largely affected by a wide-array of both natural and human-induced disturbances which, in turn, are one of the main factors that trigger forest succession (Walker & del Moral, 2003). In the study area, forest communities experience continual floristic and structural change caused mainly by human-made disturbances. There are major disturbing factors that cause irreversible damage to the vegetation of the Sierra de Manantlan: 1) logging timber (Jardel Pelaez, 1991; Pineda-López & Sánchez-Velásquez, 1992; Pineda-López, 1998); 2) cattle grazing (Sánchez-Velásquez et al., 2002a) and 3) forest fires (Jardel Pelaez, 1991; Jardel Pelaez et al., 2003). The effect of these including their frequency, severity and size and the interactions amongst them on the local vegetation varies widely as the experience in the study area has shown.

The impact of logging

In the 1940s Mexico embarked on a period of rapid of industrialization which increased the need for timber, mainly for construction, electrification and industry. In these circumstances administrators saw unexploited forests as stores of raw material available for development of the economy (Raufflet, 2003). The Forest Law of 1940 brought back timber concessions, allowing tens of large contracts to extract logs (Brown &

Gurevitch, 2004). In the Sierra de Manantlan, including Cerro Grande, logging operations from both foreign and national lumber companies started early in the 1900s, a practice that was interrupted by the Mexican Revolution and by the Cristero War (1910–1925 and 1926-1929 respectively), starting up again in the 1940s. After 1940 it is estimated that almost 30 sawmills operated at different times around the Sierra, these activities ended in 1985 with the onset of the SMBR (Jardel Pelaez, 1996a). Empirical evidence suggests that valuable species were harvested from mountain mesophytic forest through selective cuttings. Most of the logging operations were conducted in pine forests through either clear cutting or selective cutting (except in Cerro Grande where logging was conducted to exploit oak).

For Cerro Grande in particular, written records derived from technical evaluations or forest management plans are largely unavailable so that it is difficult to establish past intensities of management and particularly which species were the most exploited. However, narrative evidence suggests that the study area was logged by at least two companies. According to Ayala Rodríguez (1988) and Jardel Pelaez (1996a), "The Colima Lumber" a US Company, exploited the Cerro Grande plateau almost entirely during the early 1900s. The harvested timber, was loaded into small trucks, taken to the Manzanillo port (ca 100 kilometres from the capital of the Colima state) and then shipped to the US. "Maderas de México" also heavily exploited the remaining forests between1946-1952, but mostly leading the cuttings over the pine stands.

In addition, according to local informants around the Ejidos of El Terrero and Toxin, the Colima Lumber had no target species for harvesting, particularly in the oak-dominated forest so that these areas were mostly exploited through high-intensity methods such as clear cutting. In addition, in the mountain mesophytic forest, a common practice was to harvest only the most valuable timber species including *Fraxinus uhdei, Tilia mexicana, Carpinus tropicalis*, and several species of *Quercus* such as *Q. candicans* (personal communication with several farmers in the study area). The effect of such practices on the structure and species composition, as previously indicated, was poorly documented. However, field observations suggest that both cutting methods, in combination with grazing, fire, agriculture and road construction into the forest had adverse impacts upon the dynamics and functioning of these ecosystems. According to local informants, one of the most obvious consequences,

which is reflected in the present day vegetation, was on the local species diversity, species abundance and in the expansion of forest cover extension, which was seriously reduced.

In addition, the pattern observed today in the stands where clear cutting was carried out suggests that one of the main causes of forest degradation was because the cut areas were not fenced to protect them from cattle grazing or agriculture. Reestablishment of trees has consequently been very slow and erratic. There are a number of sites across Cerro Grande in which little or no regeneration has occurred since clearcuts were created more than 35 earlier. The most likely cause of these patterns is overgrazing, forest fires and repeated agricultural cultivations. Such circumstances have lead to the replacement of existing vegetation by secondary vegetation of grasses and shrubs or developed into a highly fragmented forest made up of ecologically complex stands in terms of structure and species composition, including stands of variable diameter frequency distributions.

With regard to the effect of selective logging applied in other parts of the Reserve Pineda-López & Sánchez-Velásquez (1992), via stand history reconstructions and stand structure chronosequence analyses (Pineda-López, 1998) in pine-oak dominated stands showed that selective logging may also have rather erratic effects on the overall dynamics of this vegetation type. The authors observed that soon after the completion of a selective logging operation in a pine-oak dominated stand there are often satisfactory pulses of *Pinus* and *Quercus* seedling recruitment. However, their effectiveness is variable and depends upon the intensity of the felling and the physical and biological environments in which the selective logging was carried out.

Even when this type of harvesting appears to favour prompt and rapid pine and oak establishment, the number of individuals recruited of both species may not be sufficient for a full recovery. The authors claim that one of the main silvicultural effects of selective loggings is a gradual decline in the abundance of pines accompanied by gradual increase in oaks, and a decline in the average diameters of the trees and in volume increment of the stand. One of the main reasons for this, apart of the intensity of cutting and the size of the openings, appears to be the time intervals between successive

cuttings were too short to allow the stands to recover their original diameter distributions and maturity conditions.

It has also been observed (Jardel Pelaez, 1985; Snook & Negreros, 1987) elsewhere in Mexico that selective logging, when applied exclusively on pines to pine-oak dominated forest (as in the study area), severely modifies the relative dominance of pines and oaks. Low-intensity selective logging encourages successional processes of replacement of pines by oaks, whilst high-intensity logging (e.g. clear cuttings) has the reverse effect. Snook & Negreros, (1987), for example found that after a low-intensity selective cutting of pines in pine-oak forests; pine regeneration is inadequate to provide for the replacement of the harvested trees. Selective cutting encourages the successional replacement of pines by oaks. Jardel Pelaez (1985) claimed that the effect of low-intensity selective logging in pine-oak forests in the Sierra de Juárez Oaxaca follows a similar pattern. Jardel Pelaez (1985) shows that after selective cutting in pine-oak forest, there a relative increase in the proportion of oaks which modified the structure and yield of the harvested area. Negreros & Snook (1984) found that natural forest pines occupied 54% of the basal area as compared to the 39% for oaks. In stands that were clear-cut (areas that were opened to establish power lines or in former agricultural fields) pine regeneration represented 87% of the total basal area and oaks represented 13%, suggesting that selective logging encourages the replacement of intolerant species (pines) by tolerant ones (oaks).

The impact of grazing

Uncontrolled grazing, mostly by cattle, horses, pigs and some goats has, for years been one of the most disturbing factors that first modified and eventually eliminated a number of forest communities in the study area. This comes from both personal observations and several empirical studies. For example, in 1988 within the Manantlan-Las Joyas core zone, a fence was erected to enclose 1,350 ha in which a Scientific Station was established. This fence has protected the area from hunting, gathering of non-woody forest products, logging and especially from grazing by domestic animals including the total exclusion of domestic cattle. Visual cross-fence comparisons suggest that grazing is one of the most detrimental factors to ecological processes including natural regeneration.

In Cerro Grande, although a substantial number of families has domestic animals (mostly cows and pigs), cattle raising is not seen as an economic activity of any importance. There is no formal strategy for managing domestic animals in the area (Olvera Vargas et al., 2000). Except for the core zone, the most common practice is to let the animals forage freely over the ejido's land the whole year with no plan to rotate the animals from place to place (Jardel Pelaez & Cruz Sandoval, 2000). The only attention given to them is to provide a minimum supply of water during the dry season as there is no standing water in the study area. The radius of the area used by cattle has not been estimated. However, personal observations and communication with several "Ejidatarios" (Olvera Vargas et al., 2000) indicates that most animals, mainly cows, move several km into the forest to feed, browsing on almost anything they pass. Climatic seasonality alters the temporal and spatial availability of sources of forage. In the wet season the animals tend to be selective about what they consume, mostly browsing grasses and fresh leaves. In the dry season the availability of food greatly diminishes and cattle become more generalist. The situation becomes critical when herds of pigs or goats, mostly foraging near human settlements, consume young seedlings and almost the entire seed-crop already on the forest floor. This has a profound effect on the natural dynamics of the forest. The most obvious evidence of damage, apart of soil erosion, is that natural regeneration is practically eliminated either by consuming seeds or eating young seedlings. There is evidence (*personal observations*) that cows and pigs are selective about the food they consume if they have the choice. For example, *Ternstroemia lineata* and *Prunus serotina* are species which seem not to be eaten if there is a choice other species (*e.g.* young seedlings of *Quercus*). It is common to see areas where severe grazing has taken place yet there are regenerating individuals of *T. lineata* and *P. serotina*, but not of *Quercus*. This will have a substantial effect on species diversity, abundance and the future structure of the stands. It is not known why cattle and pigs prefer to eat seedlings of *Quercus*.

Several studies undertaken in the study area aiming to assess the effect of grazing on different vegetation types across the Sierra support the observations made in Cerro Grande. In particular, Hernández-Vargas et al. (2000) carried out an evaluation of the impact of grazing on the local vegetation through the installation of permanent sample plots on three different vegetation types in fenced and unfenced sites. They found contrasting patterns of regeneration (mainly abundance) and species composition in

fenced and unfenced areas. The authors state that several species practically disappear from the unfenced areas; they also discovered that a number of species were not eaten by cattle. This resulted in major differences in the number of individuals established as well as in the species diversity between the two areas. The authors concluded that cattle grazing significantly affected successional processes.

Other studies (Sánchez-Velásquez et al., 2002b; Carranza-Montaño et al., 2003) have recognised other effects of grazing across the Sierra de Manantlan: soil compaction, erosion, differential selection of preferred forage species, elimination of rare or preferred species, and increases in the dissemination of seeds the species that are eaten most to open areas or habitats in the forest interior and sites disturbed by cattle. In addition, according to local informants, the abundance and the geographic distribution of a number of valuable timber species such as *Tilia mexicana, Magnolia illtisiana,* and *Fraxinus uhdei* have been reduced dramatically due to the combined effect of illegal logging (mimicking selective cuttings) and intensive cattle grazing. This may have impacted significantly upon the regeneration processes of these species as the results of research described in this thesis suggests (*see* Chapter 4).

The impact of fire

Frequent forest fires are one of the most important ecological components in the dynamics of the vegetation of the study area. Fires can cause irreversible damage to the vegetation, mainly to regeneration. Research on fire history reconstruction for Manantlán suggests that forest fires occur at mean intervals of between 5 and 14 years. A similar time interval has been estimated for other forested regions in Mexico (Jardel Pelaez et al., 2003). The study forests are considered to have a long-history of intensive human-disturbance. Over the past 4000 years, forest fires have shaped the structure and functioning of the vegetation of the Sierra de Manantlan (Figueroa-Rangel, in preparation). Present-day small-scale fires occur almost every year, most of them start as a result of uncontrolled burning from agricultural systems, to promote the establishment of pasture for cattle or even intentionally as a pretext to claim for a change in land use from forestry (*personal observations*).

A revision of ecological research concerning the effects of frequent fires on the flora, but mainly focusing on pine-oak dominated forests, has been made by Jardel Pelaez et al. (2003). Generally, in fire-derived gaps abundant pine seedlings of species such as *Pinus pseudostrobus, P. douglasiana, P. oocarpa, P. devoniana* and some *Quercus* (e.g. *Q. scytophylla, Q. castanea*) and other broadleaved species such as *Arbutus xalapensis,* are readily established and successfully regenerated. Low-intensity fires also promote pine dominance over both shade-tolerant and fire-sensitive species such as *Abies religiosa, Carpinus tropicalis, Cornus disciflora, Fraxinus uhdei, Magnolia iltisiana, Persea hintonii* and *Zinowiewia concinna.* Species tolerant to shade tend to increase in dominance on sites where fire has been excluded for several years (Jardel Pelaez et al., 2003). If constant low-intensity fires occur, these species would be replaced by pines, and such fires consequently have a major impact on succession (Anaya Corona, 1989; Sánchez-Velásquez & García-Moya, 1994).

Observations carried out in permanent sample plots suggest that low-intensity fires can accelerate self-thinning in over-crowded pine stands by eliminating suppressed individuals (Jardel Pelaez et al., 2003).

However, fire is also an essential ecological factor that constitutes an important part in the dynamics of several forest ecosystems. Periodic fires are a central component in the evolution and maintenance of many plant species, especially in fire-prone grasslands. For example, Sánchez-Velásquez et al. (2002a) found that if populations of *Zea diplopernnis*, a wild relative of maize that is endemic to the Sierra de Manantlan, are not disturbed by fires at least once every five years the species becomes locally extinct.

A number of oak species appear to be favoured by periodic, medium intensity fires. After harvesting, coppice growth of species such as *Quercus crassipes, Q. rugosa,* and *Q. castanea* is stimulated by fire though for species such as *Q. laurina, Q. candicans,* and *Q, scytophylla* fires of any intensity represent a serious disturbing factor (*personal observations*).

2.3 Research methods

2.3.1 Sampling design, Site selection and plot establishment

Sampling design

The database used in this research is derived from a system of 105 permanent sample plots (0.05-ha) established in stands classified as representative of one of the several oak (*Quercus*) forest types found in Cerro Grande. High floristic heterogeneity and physiographic irregularity limited the application of a traditional forest inventory (*e.g.* systematic sampling). Therefore, a major challenge was to design a reliable and versatile sampling strategy that would capture the complete range of floristic and environmental variation and, at the same time, allow efficient long-term monitoring. To accomplish this, preliminary ground-truthing reconnaissance was undertaken across the study area. The main aim was to locate oak areas that showed floristic and environmental characteristics of interest. After subjectively locating areas dominated by oak, a calibration inventory was carried out in 1989 by means of temporary sample plots using an angle-count sampling approach (Bitterlich, 1984). An oak dominated area, for the purpose of this research, was defined as a portion of the forest dominated by at least one *Quercus* species either in terms of density (more oak individuals than any other species), in the canopy (dominant or codominat canopy trees), or in basal area (in some stands one or a few big trees contributed the largest proportion of basal area, but another species was dominant in number of trees). This preliminary survey was undertaken with the aim of restricting a further forest inventory to specific oak areas based on the criteria of:

i. Relatively homogeneous species composition but in which *Quercus* species were always the dominant genus;

ii. A relatively homogeneous range of stand structural variability, both horizontal and vertical;

iii. All possible physiographical environments with *Quercus* species;

iv. Areas large enough to allow the establishment of at least two to three clusters of nested (explained below) sampling units of 500 m^2 each within a similar oak area.

v. No evidence of current major anthropogenic disturbance such as charcoal production, harvesting, forest fires or domestic animal grazing.

During the preliminary survey, 70 temporary sample plots were set up (using a 2.2 m^2 factor angle gauge). This yielded a provisional forest classification based on subjective observations of the interactions of micro-relief and the existing vegetation. The results and main findings are reported elsewhere (Olvera Vargas & Moreno Gómez, 1992), but broadly this work showed that:

i. The spatial distribution of the vegetation seemed to be organised along complex environmental gradients. Some species, for instance, *Zinowewia coccinea, Fraxinus uhdei,* and *Ostrya virginiana*, were observed growing just in specific localities.

ii. A wide range of compositional and structural variability was evident and it was found that such variation might occur over short distances.

iii. There was a lack of seedling regeneration in some localities, mainly in spots nearest to human settlements or areas subject to grazing by domestic animals.

Site selection and psps establishment

In 1991 a forest inventory was initiated based on clusters of three circular permanent sample plots (psps) of 500 m^2 each (0.05-ha; 12.6 m radius). Sampling clusters provide an opportunity to spread out a small sample more than would be the case for a single plot of the same total size, thus reducing between sample variance (Ghosh & Innes, 1996). The circular permanent sample plot was adopted because they are laid out more easily and quickly than rectangular or square ones. In addition, circular plots have fewer edge effects and potentially fewer 'doubtful trees' on the plot perimeter. This sample size best suited the vegetation structure of CG, even in areas of mesophytic vegetation in which most of the trees tend to be of bigger dbh than in non-mesophytic vegetation, to sufficiently accommodate the local floristic variability. All the clusters of psps were

laid out from random starting points within homogenous oak areas, and located on the ground by walking along a fixed compass bearing. Based on the preliminary survey it was established that the vegetation could be stratified into at least three-oak floristic zones. Thus, such stratification was carried out at two levels: one based on relatively temporary biotic stand characteristics such as species composition (presence of oak species), stand density and developmental stage, and another based on permanent abiotic landscape components such as landform, aspect, catena, topography, etc. Within each stratified oak area, the distance between each cluster of three plots was at least 500 m but not further than 1000 metres (Figure 2.2). Based on preliminary observations on the general floristic conditions of the vegetation of CG, it was thought that longer separation between plots would prevent to establish cluster repetitions within each different vegetation type due to the high forest fragmentation in the study area.

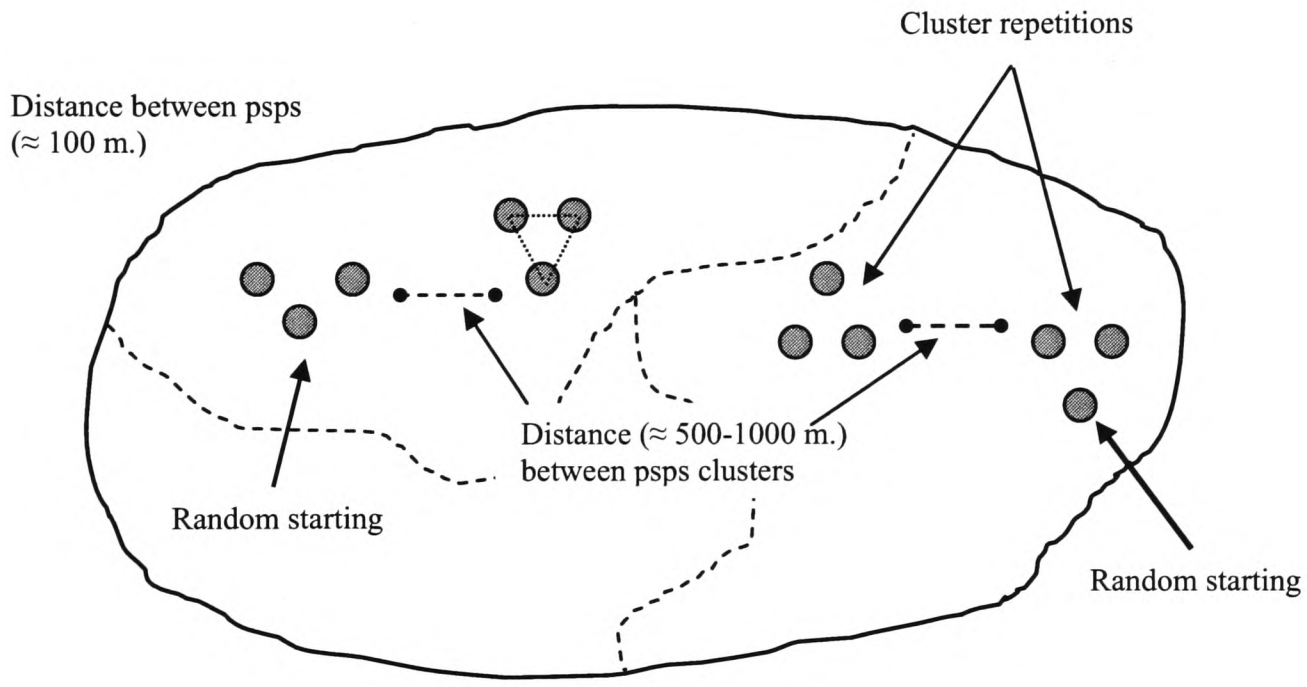


Figure 2.2 Hypothetical stratified sampling areas delimited by different vegetation type or by changes in physiography. Circles represent permanent sample plots distributional arrangement. Dashed lines represent two supposed adjacent but different oak-dominated zones base on differences in vegetation, physiography or both.

In the event that the selected spot fell in a forest gap, on an abandoned track, close to a forest edge or to any other undesirable situation (*e.g.* the presence of a fence or a road), the point was moved 50 metres from the original point along the initial compass direction. Psps belonging to the same nested group were set 100 to 150 m apart from each other, in a triangular arrangement (Figure 2.3).

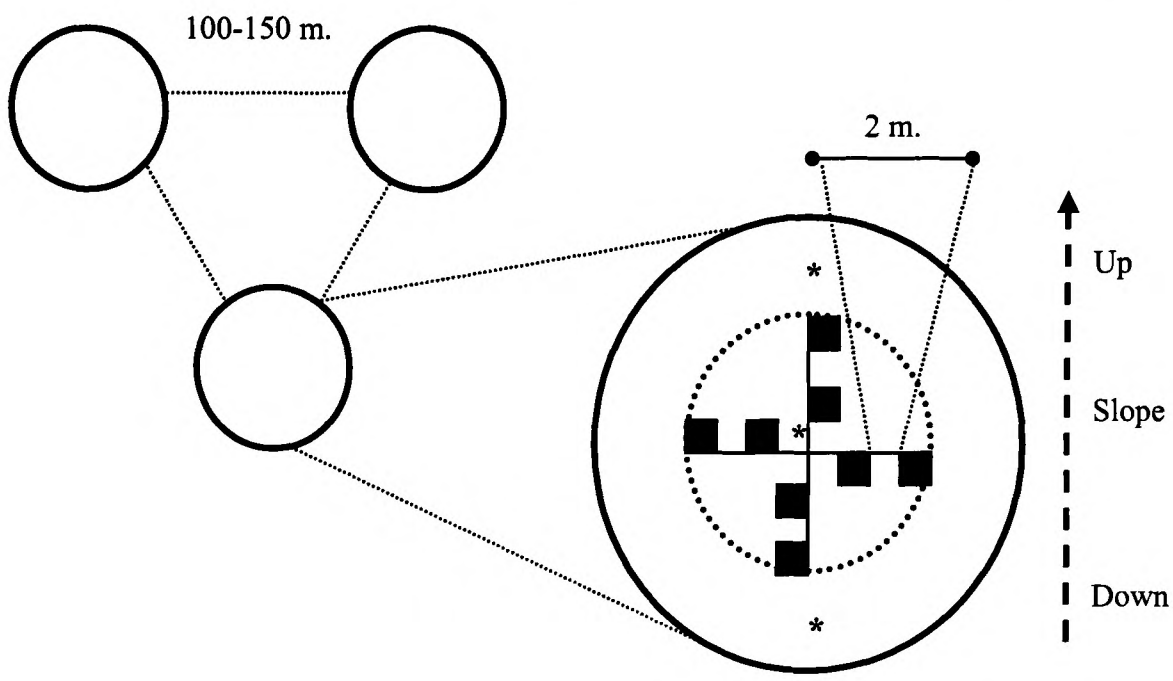


Figure 2.3 Schematic representation showing the triangular survey nested-plots along with sub-sampling units for saplings and seedlings. ___ Plot for the recording of adult trees (500 m^2; radius 12.6 m). .... Subplot for the recording of saplings (50 m^2; radius 4 m). ■ Subplot for the recording of seedlings (1 x 1 m^2). * Points of soil sample collection.

The overall forest inventory was carried out using a modification of the Successive Sampling with Partial Replacement (SPR) methodology. SPR initially was introduced by Ware & Cunia (1962) based on work pioneered by Patterson (1950). In implementing a SPR, a conventional forest inventory is carried out during the primary stage of sampling. Then, in a second phase of the forest inventory a percentage of the initially established psps are re-measured, but a set of new plots is added to the psps network. The re-measured plots can eventually be used to develop regression relationships to update estimators of importance for those un-measured plots. According to Köhl et al. (1993) a significant attribute of the SPR approach is that the forest stands are sampled on more than two occasions. This reduces the risk of obtaining a poorly distributed sample. Moreover, the sample size is periodically increased leading to a better representation of the population. Thus, periodic surveys permit precise estimates of the components of forest dynamics, besides the statistical advantages of independence of samples (but *see* Legendre & Fortin, 1989); it also offers the advantage of collecting information about the dynamics of the stand including diameter growth, survival, mortality and ingrowth (Cunia & Chevrou, 1969; Van Deusen, 1989; Scott & Köhl, 1994; Johnson et al., 2003).

Study plots and measurements

History of the Permanent Plot Network in Cerro Grande

All data used in this thesis was produced as part of a project 'Silviculture of oaks in the Sierra de Manantlán', initially financed by the University of Guadalajara, Mexico and subsequently by the Comisión Nacional para Uso y Conocimiento de la Biodiversidad (CONABIO). This is a long-term research project that emerged from the need to produce baseline ecological and silvicultural information on species-rich oak-dominated forest ecosystems. This included forest stand dynamics, the assessment of species tree growth, phenological patterns as well as tracking potential fluctuations in regeneration over time. So far, a total of 105 psps have been established: 32 in 1991; 28 1994 and 45 in 1998. In 2002, 86 of the 105 psps were re-measured (Figure 2.4).

The Sampling layout corresponds to three main floristic areas observed across the study area. Thus, the plot grouping represents three relatively different floristic, ecological and environmental spots observed to occur in Cerro Grade. In floristic and ecological terms, the three groups of plots differentiate from each other as follows:

i. One group of plots was established across a relatively species-poor and xeric zone of the study area. Stands in this group are represented by three or four different species at most, but generally most of them are canopy-dominated by *Quercus crassipes*. This group was called as such (*Quercus crassipes* (**Qc**)). Commonly, the species contained by this group of plots are of inferior stature and smaller diameter sizes than the ones growing in the wet zone. In general terms, it has more gently physiography, shallower soils and considerable less environmental humidity.

ii. The second group was established across the most species-rich spots of the study area. Such spots correspond essentially to mountain mesophytic (**Mm**) vegetation, floristically representing the most heterogeneous stands containing the biggest proportion of tolerant to shade species. These are stands of irregular diameter structures with the biggest mean diameters and the tallest trees. Environmentally, this is the wettest zone across Cerro Grande with the more

complex physiography that includes deepest organic soils. Most of the plots in this group were established within one of the core zones of the SMBR.

iii. The third group was established across a zone that visibly showed intermediate floristic and environmental characteristics between the two previously described areas therefore was intuitively considered to be a intermediary floristic zone (**It**) between the two major vegetational zones. It is important to stress that the idea of establishing the psps across environmentally distinct vegetational zones was aiming at capture the complete range of floristic and environmental variation of the study area.

The, length of monitoring differences between plots ranged from 4 years for the most recently established plots to 11 years for those established at the start of the study. The difference in the starting times was a result of the availability of funds to develop the project, and also for producing baseline information for the areas where forestry practices have been carried out.

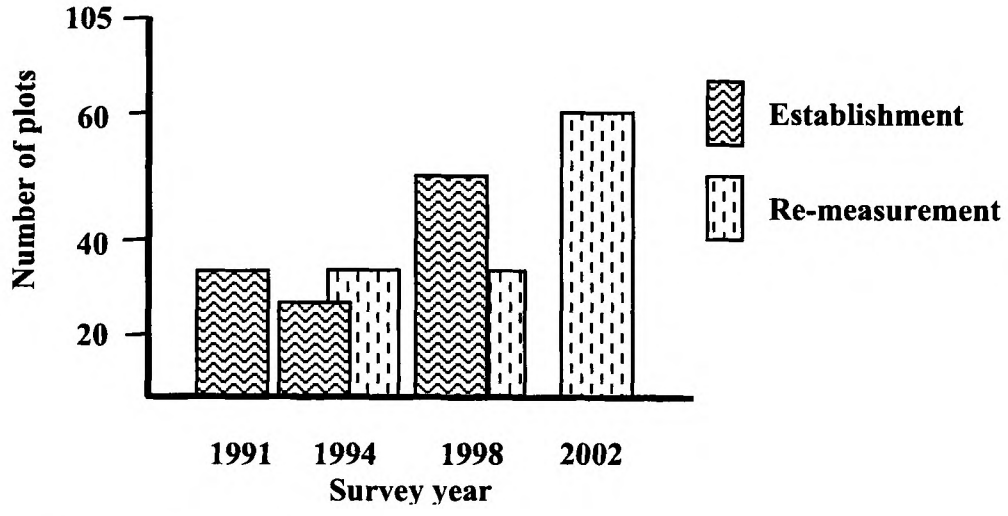


Figure 2.4 Sampling effort representing the number of permanent plots (n=105) and period of establishment and re-measurement.

2.3.2 Plot Monumentation and Maintenance

All the psps were established and made permanent by numbering and tagging all live trees found in a radius of approximately 12.62 m. The radius varied slightly among the psps according to the slope factor correction used. Slope was corrected only if the inclination of the terrain within a plot was more than 30%. Ignoring the correction for

sloping terrain leads to a biased estimate of forest parameters (Beers, 1969). A durable colour-painted post was placed in the centre of each psp to help in delimiting the psps' boundary as well as to aid in the location of the plot during subsequent visits. To ensure an accurate position of the psps' centre, in case the central post was lost, the distance and the azimuth of at least three "reference trees" near to the plot's centre were recorded. A numbered aluminium tag was nailed (15-20 cm above ground level) to each tree to identify and locate the trees in psps. In addition, all trees were labelled with white water-proof silicon paint at least 10 cm above the dbh measurement (Photo 2.1). All psps were geo-referenced to Universal Transverse Mercator (UTM) from geographical coordinates taken with a hand-held Global Positioning System receiver (GPS 12XL, Garmin International, Inc., Olathe, Kansas, USA). Supplementary notes on each psp consisted of a description of the physical surroundings, the local name of the forest spot, along with a brief description about the route followed to reach the spot, including the travel time from a known spot. This information enabled the plots to be relocated relatively easily in subsequent visits.

Photo 2.1 Tree indelibly labelled with white water proof silicon paint (green arrow) marked at least 10 cm above the point of dbh measurement.

2.3.3 Vegetation categorisation

All woody tree species encountered in the sample area were classified into three size categories:

a) *Adult trees* (individuals ≥ 5 cm dbh and ≥ 1.30 m height) were recorded in a plot of 500 m^2 (≈12.62 m radius).

b) *Saplings* (individuals > 1.30 m height and < 5 cm dbh) in a plot of 50 m^2 (4 m radius) in the centre of the 500 m^2 plot.

c) *Seedlings* (individuals < 1.30 m height) were sampled in eight plots of 1 x 1 m^2 each; four were situated across the slope and four perpendicular to the slope (*see* Figure 2.3).

Notes on the presence and percentage of shrubs and herb abundance within each 500 m^2 plot were also made, as described later is this section.

Adult trees

Information collected for each individual adult tree is shown in Table 2.1. In additi silvicultural characteristic such as merchantable stem height, the presence and posit of forks was also recorded even though this information is not shown in Table 2.1.

Most tree dbhs were measured at 1.3 m above ground level, except when a tree l buttresses, deformations or any physical damage at this level. In such cases, dbh v usually measured 30 cm above breast height. If so this was recorded in the datashee order to ensure that the measurement was made in the same position in furt inventories. A permanent breast height mark was made with white water-proof sili paint on each tree (Photo 2.2) in order to make sure that measurements were made at same point. All repeated inventories were undertaken between January and June. T facilitated the estimation of components of forest dynamics on an annual basis.

Table 2.1 Descriptive qualitative and quantitative variables recorded on adult trees within the 500-m^2 permanent sample plot. Numbers between brackets represent classes.

Code	Variable name	Measured Units	Variable type	Observations
SP	Species			Commonly identified in field, otherwise samples were collected and later identified
DN	Diameter	Centimetres	Interval	For trees with multiple stems coming from a single root-collar, each stem was counted as a separate individual tree.
HT	Height	Metres	Interval	Height of the top of live crown measured to the nearest 10 cm, with a clinometer.
BTHI	Bark thickness	Centimetres	Interval	Two records were taken from each tree, one facing up slope the other down slope.
CRCL	Crown social class position [4]	1. Dominant 2. Codominat 3. Intermediate 4. Overtopped	Nominal	Following Kraft classification (Smith, 1986); it was an evaluation of the tree's position relative to its neighbouring trees.
CRCP	Crown competition	Percentage	Ratio	Percentage of crown overlapping neighbouring trees, visually estimated.
CRLH	Crown length	Percentage	Ratio	Crown length was estimated as the percentage of the difference between the total tree height and the height of the lowest living branch.
BICO	Biological condition [3]	1. Alive 2. Dead 3. Harvested	Nominal	Dead trees observed during the initial psps establishment were not taken into account
DAME	Visible damage [13]		Nominal	Following the criteria given in Olvera Vargas et al. (1996).

Photo 2.2 Permanent breast height mark (commonly at 1.3 m.) marked with white water proof silicon paint (green arrow).

Saplings

Saplings (individuals > 1.30 m height and < 5 cm dbh) were individually identified and counted by species, stem-diameter, total height, vitality and their position in relation to canopy stratum. For saplings the same measures as for the adult category were taken. Stem-diameter was recorded to the nearest millimetre using a high-precision industrial calliper. Two diameter records were taken if the height of the sapling was less than 10 cm above the minimum height limit (1.30 m), one at 1.30 m and other approximately 10 cm above the ground, otherwise only the second diameter was recorded. Total sapling height was taken to the topmost live part and measured to the nearest centimetre. Sapling canopy position was evaluated in the 40 m^2 subplot, considering their position in relation to the crown canopy based on vertical upwards sighting. Categories used were: a) beneath the canopy, b) canopy edge and, c) canopy gap (Figure 2.5).

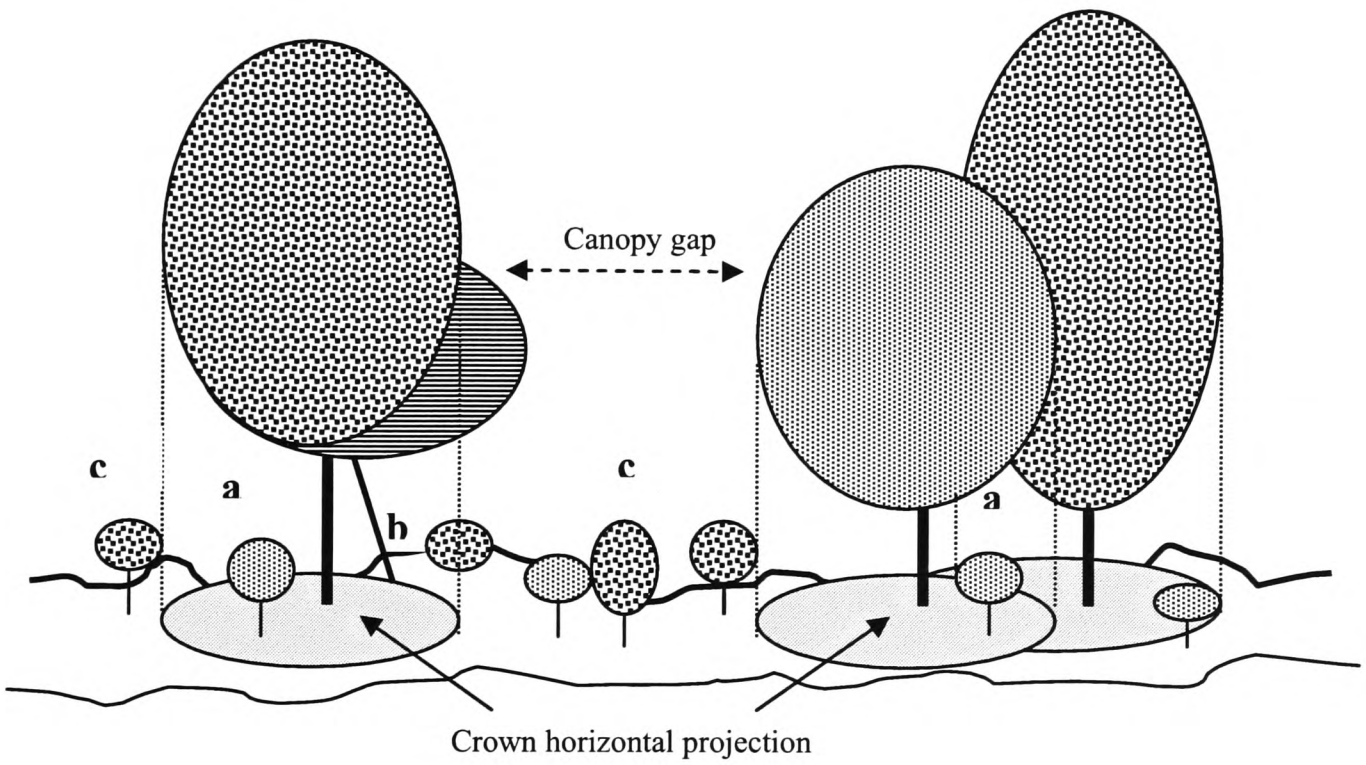


Figure 2.5 Seedling and sapling positions in relation to the overhead canopy. Estimates were based on vertical sighting. For saplings, each plant was individually evaluated, for seedlings using the 1 m^2 sub-sampling plot centre. **a** -beneath the canopy, **b** -at the canopy edge and **c** -canopy gap.

methodologies exist for transforming sun-aspect into categorical units. For example, Zerihun et al. (1989) used a different approach to convert aspect into scalar units, which represent a scale of total solar energy given by N=0, E=2, S=4, W=2.5. Judging by the higher weighting given to southern and western aspects, Zerihun's methodology seems that it was developed for its application mostly in the Southern Hemisphere. However, it is a rather ambiguous technique and the authors do not provide any further explanation for the coding they use.

CHAPTER 3 - Floristic patterns and species coexistence

3.1 Introduction

One of the most fundamental present-day enquires in vegetation ecology is establishing what mechanisms shape patterns of floristic distribution and coexistence in species-rich ecosystems. A traditional view maintains that species distribution is due to, and species coexistence is possible because of, the existence of heterogeneous environments. A recent theory suggests that a neutral landscape model, wherein species distribution is determined by species drift across the landscape, may explain patterns of floristic distribution and coexistence. In this neutral model, habitat partitioning does not determine the structure of species–rich forest communities. In this chapter it is examined whether evidence of discrete communities exists, by looking at the spatial distribution of 9 sympatric *Quercus* species growing mixed with 29 allied timber species, and the corresponding site environmental factors, in a high altitude mountain forest in western Mexico.

3.1.1 Background

In plant ecology, a major query has been whether tree species are sorted into discrete communities as opposed to being accidental collections of individuals across the landscape, resembling a compositional drift. It has also been of great interest to discover whether general assembly rules determine the structure of natural communities (Gotelli & McCabe, 2002). A community is said to have structure or a defined pattern if the species it contains are a non-random subset of the local pool of species (Law & Morton, 1996). Thus, community assemblage provides a conceptual foundation for understanding the processes that determine which species live in a particular locality. However, the patterns of community assemblage have traditionally been a controversial issue. There has been an ongoing debate about whether the species in species-rich forest ecosystems can be assigned to floristic groups, each with specific characteristics, such it can be differentiated from another group. In this context, the discrete-community concept in ecology sees plant 'communities' as distinct entities: sizable areas of relatively uniform vegetation, with rapid transitions between them. The alternative self-

similarity view maintains that discrete communities do not exist – floristic variation occurs equally on all scales (Bastow & Alessandro, 2000). There is a range of ideas about the main causes for the distribution of plant species and the kinds of temporal and spatial patterns they follow over time (Tuomisto et al., 2003a). For example, Hou et al. (2004) sustain that floristic patterns can arise because of a combination of factors ranging from environmental heterogeneity to natural and human disturbances, intra- and inter-specific competition, and life history strategies so that different processes can induce specific spatial patterns. One view proposes that there is a one-to-one match between the environment and the species in forest communities. In this case, species composition should converge towards a similar floristic structure in two comparable environmental locations. A contrary belief maintains that species differ in environmental requirements so that they have divergent community structures (Chase, 2003). These notions have been the subject of intense dispute since early in the 20th century *e.g.* Tansley (1904); Clements (1916) and Grinnell (1917a); among others.

Recent empirical and theoretical investigations, mostly carried out in lowland tropical forests, have suggested that niche differentiation, one of the most influential ecological views addressing mechanisms of species richness and coexistence, is unimportant in structuring forest ecosystems at local scales. Instead the dispersal limitation view has been variously tested to explain a lack of discreteness over a wide-range of vegetation types, including Mediterranean vegetation, as in the investigations carried out by Auerbach & Shmida (1993), in northeastern Israel; as well as non-vegetational studies such as those described by McAbendroth et al. (2005) in macroinvertebrates. One of the major arguments given to reject the need for niches as a mechanism promoting species diversity and coexistence, mainly in plants, derives from the fact that it has been repeatedly stated that environmental heterogeneity has a weak or no effect at all on patterns of floristic distribution. This has led some researchers to propose that neutral processes (*op. cit.*) play a major role in determining floristic composition.

The objectives in this chapter were threefold: (**1**) to establish whether *Quercus* and allied timber species constitute discrete communities or are better represented by a compositional drift; (**2**) to elucidate whether patterns of species variation correlate to specific environmental heterogeneity; (**3**) to discuss the ecological paradigm that best explains their coexistence.

3.1.2 Hypotheses to be tested

In this chapter the following hypotheses are tested:

Ho_1. *Quercus* and allied timber species do not constitute a compositional drift; instead the tree species richness in this forest ecosystem is assorted into discrete communities across the study area.
Ho_2. Environmental heterogeneity does explain community differentiation in *Quercus* dominated forests.
Ho_3. The niche paradigm rather than the neutral paradigm (or compositional drift) explains species coexistence.

3.2 Research methods

3.2.1 Data description and processing

In this chapter the main goal is to reveal whether patterns of floristic variation in adult tree communities exist and to discover the extent to which the prevailing environmental heterogeneity explains such patterns of floristic variation. Only data for the adult trees (trees $\geq$ 5 cm dbh and $\geq$ 1.3 m tall) along with the environmental information collected for the last 86 inventoried permanent sample plots (psps) in 2002 was used.

3.3 Data analyses

3.3.1 Floristic patterns of variation

Ordination methods in community ecology

Ordination in community ecology is a collective term given to a group of multivariate techniques that endeavour to represent sample-species relationships in a low-dimensional space (Orlóci, 1975; Greig-Smith, 1983; ter Braak, 1995). The fundamental aim of ordination techniques is to summarise numerical patterns while retaining as much information as possible from the original data. The end product of the ordination

methods is a graph on which similar samples are plotted near each other, and dissimilar ones are positioned far apart, representing the position of *n* species on *m* environmental gradients represented by axes (Gauch, 1982). Potentially, there may be as many axes as there are explanatory variables in the data set. However, since this may complicate interpretation it is not practical to draw an ordination diagram with more than two or three axes (Palmer, 1993), even though it is a valid mathematical construction (Legendre & Legendre, 1998).

There are two main groups of ordination methods: (*i*) Direct ordination methods that make use of floristic and environmental data in a single, integrated analysis. Their main aim is to display vegetational trends in relation to environmental gradients and; (*ii*) indirect ordination, which typically describes patterns of floristic variation based on features derived from the vegetation itself. Generally, indirect ordination diagrams do not represent environmental gradients. However, once major sources of vegetation variation have been revealed, it is possible to relate them to environmental information (Kent & Coker, 1998) in order to explain the underlying causes of patterns in species composition.

Ordination-based ecological research has led to a dilemma of choice among the most commonly used techniques. It is beyond the scope of this thesis to describe in detail each of the methods listed in the scientific literature, but the methods that will be applied in this chapter are described.

Non-metric Multidimensional Scaling

Multidimensional Scaling (MDS) describes a family of multivariate methods for the analysis of proximity information. This technique was developed by Kruskal (1964) for applications in psychology and sociological science research. Recently, due to its robustness, MDS has been applied to span a wide-range of scientific disciplines, particularly in vegetation science. In this chapter, because of the relative novelty of its use in community ecology, a brief description follows:

MDS is an indirect, non-linear, heuristic, multivariate ordination method that seeks to arrange samples (in the case of this investigation, permanent sample plots based on their

species composition), so that each pair of samples is in a rank-order according to their dissimilarity. Mathematically, MDS embeds points in Euclidean space in such a way that the distances between points preserve a rank-order between those points (Prentice, 1977; Clarke, 1993). MDS constructs a 'map' (graph) by interpreting the dissimilarity (*e.g.* differences in species composition, although it can be any other vegetational attribute) as distance points between observations (permanent sample plots in the case of this thesis). The graphical display provided by MDS enables the data analyst to literally "look" at the data and to explore and interpret their structure visually. On such a map MDS produces a set of vectors in a *p*-dimensional space in which the Euclidean distances among points corresponds as closely as possible to a function of the input matrix according to a criterion called *STRESS* (*S*tandardised *R*esidual *S*um *of S*quares of the observations) (Mead, 1992). Technically, *STRESS* can be interpreted as an inverse measure of fit between distances in ordination space and differences in species composition.

The range of *STRESS* lies between 0 and 1, the closer a value comes to 0 the better the configuration is, indicating a good fit. A rule of thumb for *STRESS* interpretation is: <0.05 is excellent, <0.1 is good, <0.2 is potentially useful, >0.2 is possibly a random placement of points and is likely to yield plots that could be dangerous to interpret (Clarke, 1993). Depending on the software utilised, *STRESS* is expressed on a scale from 0-1, but PC-ORD v.4 (the one used in this thesis) uses a scale of 0-100 (McCune & Mefford, 1999).

Despite the fact that NMDS has been criticised because it is judged to be computationally demanding and apparently lacking in stability (Clarke, 1993), in general terms, MDS is a robust methodology that affords effective solutions when analysing large and complex ecological databases. Some commonly cited attributes of MDS are:

1. It is flexible because it is not limited to Euclidean distance, an attribute that allows MDS to produce ordinations from almost any metric distance matrix (Kenkel & Orlóci, 1986); for example PC-ORD v.4 handles at least eight distance metrics.

2. It is independent of parametric assumptions; therefore MDS succeeds well with data that is not normally distributed or in discontinuous scales (McCune et al., 1997a).
3. MDS is not derived from a model of species responses to gradients such as CCA (Palmer, 1993), therefore MDS axes are not necessarily interpreted as environmental gradients.
4. MDS can perform reliable ordinations with missing pair-wise information (Legendre & Legendre, 1998) or when the data is lacking replication such as plot-to-plot or year-to-year observations.
5. In NMDS the 'arch effect' rarely occurs. This is a mathematical artefact corresponding to an unreal structure in the data in which the second axis is an arched function of the first axis (Palmer, 2000).

Canonical Correspondence Analysis

Canonical Correspondence Analysis (CCA) is one of the most accepted gradient analyses in ecology (Palmer, 1993). It is well documented in a wide-range of overviews, but the mathematical details and its methodological foundation along with general applications are described in depth by ter Braak (1994); Kent & Coker (1998) and Guisan et al. (1999). CCA is a direct ordination method in which gradients of community composition are directly related to underlying variations in a set of 'external' variables. CCA represents a special case of multivariate regression with site scores as the dependent variable, and the environmental variables as the independent variables (Palmer, 1993). CCA provides a measure in eigenvalues that are used to estimate a gradient's length, a feature not performed by NMDS. Eigenvalues are unitless numbers that may be positive or negative. Large positive numbers indicate sample points with strong positive relationships to the CCA axis, while large negative numbers indicate strong negative relationships. One of the most acknowledged attributes of CCA is its rapid computation (relative to NMDS); CCA also excels in ordinating vegetational and environmental data almost without bias. Furthermore, it is one of the best techniques to apply where species response to environmental gradients is unimodal and when a wide range of environmental variables have been measured (McCune, 1997).

NMDS versus CCA

From the above review it seems that indirect and direct ordination may appear rather analogous multivariate methods as both generate similar ordination diagrams. Indeed, they are both quite frequently used to portray vegetation patterns as well as to elucidate the environmental variables underlying these patterns. However, NMDS and CCA are fundamentally different gradient analyses serving two distinct purposes in ecological research (Økland, 1996). Their joint use may depend on the objectives of the study, yet it is startling that on very few occasions have these two methodologies been used as complementary analytical tools (but *see* Rettie et al., 1997; De' Ath, 1999 and; Small & McCarthy, 2002). Økland (1996) points out that many ecologists use either NMDS or CCA as if they are similar techniques, while in fact they have quite different applicability. According to McCune (1997) performing ordinations on only the community data (indirect ordination) and subsequently relating the ordination to the environmental variables (direct ordination), allows an expression of pure community gradients, followed by an independent assessment of the importance of the environmental variables.

3.3.2 Ordination of the Permanent Sample Plots

Statistical treatment

Floristic-derived data sets are commonly acknowledged to be complex. Random variation and unknown structure are typical sources of noise in this type of information (Oksanen, 1983; Vanclay, 1991). Because of this, inconsistent and unpredictable outcomes to their analysis are a common problem. For example, Strayer (1999) found that presence-absence data generally have low power to perceive population declines and that detection is dependent upon the spatial pattern of the population under study. (Manel et al., 2001) compared the efficiency of abundance and presence-absence data to predict species distribution and the authors discovered that the predictive accuracy is affected by the frequency of occurrence of the target organism in the database arguing that many evaluations of presence-absence data models are misleading (*cf.* Cushman & McGarigal, 2004). In order to examine the implications of using distinct ecological

parameters in discovering vegetational patterns, the data set was explored using three distinct plot-level indices, two of them commonly used in community ecology:

- Presence-absence (P/A) as a measure of species frequency.
- Basal Area (BA = $\sum di^2$*0.7854) as a measure of species abundance.

and an importance index called Index of Performance (I^P) that was derived in this thesis as:

- Relative Volume + Relative Density (*Rel.Vol.* + *Rel.Den.*) as a measure of species dominance.

The I^P was extracted as:

$$I^P = (\mathrm{Re}\,lativeDensity) + (\mathrm{Re}\,lativeVolume) \qquad 3.1$$

Thus:

$$\mathrm{Re}l.Den. = \left(\frac{DSp_i}{\sum DSp_i}\right) * 100 \qquad 3.2$$

$$\mathrm{Re}l.Vol. = \left(\frac{VolSp_i}{\sum VolSp_i}\right) * 100 \qquad 3.3$$

***Where*:** DSp_i is the number of individuals of species *i* in plot *j*; VolSp*i* is the volume of species *i* in the plot *j*. Hence, Vol. was calculated according to Husch et al. (1982) as follows:

$$Vol = (\bar{h})(G)(f) \qquad 3.4$$

Where:

$$\bar{h} = \frac{n_1 g_1 h_1 + n_2 g_2 h_2 + ...n_Z g_Z h_Z}{G} = \frac{\sum_{i=1}^{z} n_i g_i h_i}{\sum_{i=1}^{z} n_i g_i} \qquad 3.5$$

Where: n_i is the number of trees per species per diameter class, g_i is the average basal area per species per diameter class, and h_i is the average height per species per diameter class; G is the total basal area per plot; *f* is the form factor which was set as 0.5 for all species. Diameter class limits were 5 cm.

The last relationship was defined as an *Index of Performance* (I^P) using the reasoning that combining density and volume parameters would provide a more objective indicator of species' ability to colonise and to become established (number of individuals established = density) and to grow (volume) over the prevailing range of environmental conditions. According to Daehler (2003) the most common measure of plant performance is growth because it involves both radial increment and vertical dominance (height). Since I^P is comprised of tree features that are affected by site conditions (*e.g.* soil fertility, humidity) it is assumed to represent an objective measure for species differentiation, even when growing under similar conditions. Whilst P/A and BA may also offer an objective measure of species' representativeness and dominance and, indeed in spite of the above cited, both parameters are well accepted as reliable metric indices; in this thesis they were assumed to be poorer ecological indicators (or measures) than I^P. BA has been shown to be relatively insensitive to subtle changes in diameter increment; this has been particularly demonstrated for small dbh classes (Harcombe et al., 2002). P/A is insensitive to the extent to which trees within the stand are using the space available to them, as well as in the quantity of each species is present.

Each of the above plot-level indices (P/A, BA and I^P) was explored via three variants:

i. Using all plots and species (86 psps and 38 species);

ii. Excluding infrequent species (species that occurred only in one plot or species with fewer than five individuals in all the plots) and;

iii. Excluding common and rare species. These were species with more than 2 standard deviations from the general mean (either in BA or I^P) (*summary* command PC-ORD v.4).

3.3.3 NMDS ordinations

Prior to performing indirect ordinations, to comply with the analysis assumptions, all of the matrices described above along with their respective variants (*i, ii* and *iii*) were tested for normality using the *Summary* command for descriptive statistics provided in the PC-ORD v.4 package. When necessary, if normality assumptions were violated, the abundance and dominance data matrices were transformed by *Binary Relativization with respect to the Mean* (PC-ORD V.4; McCune & Mefford, (1999)) and checked again for normality.

Dimensionality in relation to the data set

NMDS is a straightforward ordination technique in which, to determine a reliable dimensionality (number of axes to be used during the analysis), to test its statistical significance and to avoid local minima, requires an interactive approach that has to be performed several times. There is no standard procedure to accomplish this, but general guidance is given in McCune & Mefford (1999). Local minima refer to situations in which no 'small' change in the configuration will improve the fit between ordination distances and dissimilarities even though other configurations do exist for which *STRESS* is lower (Bowman & Minchin, 1987). The one applied in this thesis follows and the operational framework is given in appendix 3.1:

- *Step one* **A calibration starting process**

This is an initial phase that aims at determining the best dimensionality with the greatest possible *STRESS* reduction. To undertake this, the slow and thorough autopilot mode of NMDS was carried out. This procedure performs 40 runs with real data and 50 runs with randomised data while automatically stepping down from 6 to 1 dimension. Then, the same procedure was manually repeated stepping down from 6 to 1 dimension. Both the autopilot and the manual

methods were carried out at least five times to avoid this interactive procedure becoming trapped in local minima. All the *STRESS* graphs produced during this phase were compared with each other so that when a number of graphs showed similar patterns in which the *STRESS* line had flattened out, then it was assumed that NMDS had stabilised.

- *Step two* **Application phase**

Once the dimensionality was determined, NMDS was newly achieved; setting the number of axes that gave the lowest *STRESS* reduction; first using random starting coordinates and then specifying the configuration with the lowest *STRESS* reduction. This operation was also carried out at least five times to ensure the final solution was stable and represented the best possible *STRESS* reduction.

- *Step three* **Testing phase**

  Finally, a verification of the spatial configuration was carried out by repeating step two for successive interactions until a number of graphs showed similar patterns of psps and species positions on the ordination space so that it was assumed that the NMDS ordinations had stabilised.

In each run, five hundred interactions were used to evaluate instability. Multiple interactions are performed seeking to minimise *STRESS* between ordination distances (Bowman & Minchin, 1987). Monte Carlo permutation tests were also carried out on each NMDS run to determine whether reductions in *STRESS* were greater than those expected from random shuffling of the data. Sørensen (Bray-Curtis) index of similarity was used as a measure of dissimilarity between all pairs of psps. The Sørensen's index was used because it has been reported (Faith et al., 1987) that it gives less weight to extreme observations and it has been shown (Kenkel & Orlóci, 1986; De' Ath, 1999) to be stronger than other distance dissimilarity measures in NMDS. The percentage of variation in the original data that was explained by the ordination was estimated through Pearson's r^2, correlating the distance between the plot scores in the ordination space and the distance in the original matrix.

The three-dimensional (axes) solution for I^P data and the two-dimensional solutions for P/A and BA respectively, were observed to be more parsimonious in explaining the variability of the data so that the distance between psps in the ordination space congruently represented the dissimilarity in species composition among psps. It was observed that additional dimensions provided only slight improvements in *STRESS* reduction indicating that the first axes captured the majority of information.

3.3.4 CCA ordinations

Canonical Correspondence Analysis (CCA) (CANOCO v.4 (ter Braak & Smilauer, 1998)) was achieved next, with the aim of investigating the relative importance of the measured environmental variables on spatial patterns of species composition. Ecological investigations often differ in the ratio of the number of observations relative to the variables involved in the analysis. A number of investigations recognise the importance of having a ratio of 3:1 (King & Jackson, 1999) or greater to provide a stable solution when correlating the environmental variation to the floristic information. However, within data sets there may be groups of variables that are highly correlated with one another, but uncorrelated with other groups (Jackson, 1993). In this thesis, a total of 26 explanatory variables separated into three subsets denoted as: 1) physiographic, 2) biological and 3) edaphic (including soil chemical properties) were explored. Each subset incorporated interval and nominal variables (Table 3.1). In CCA, as in many areas of numerical ecology, when a relatively large number of explanatory variables are involved a generalised concern is that there is an increased likelihood of finding one or more significant correlations due to chance alone (Type-error I) as the number of variables increase (Rice, 1989). Hence, in an attempt to avoid multicolinearity and produce the most parsimonious CCA ordinations, Kendall's correlation coefficient (due to non-linear relationship of some bivariate association) was estimated. Kendall's correlation coefficient is a nonparametric measure of association for nominal or ranked variables that takes ties into account. The sign of the coefficient indicates the direction of the relationship, and its absolute value indicates the strength, with larger absolute values indicating stronger relationships. Possible values range from -1 to 1.

This approach yielded a correlation coefficient matrix that served as a preliminary delimitation of highly and weakly correlated variables. The sequential Bonferroni-adjusted probabilities test were then performed (p = 0.05) on the resulting correlation matrix (Table 3.2) The Bonferroni-adjustment is an efficient procedure for removing highly correlated explanatory variables, minimising the likelihood of finding significant correlations due to chance. Thus, for the Bonferroni-adjustment the (Legendre & Legendre, 1998) method was used as:

$$p' = (k - i + 1)p \qquad 3.6$$

Where: p' is the adjusted p value, k is the number of p values and i is the rank of a p value.

Table 3.1 Codes and definitions of explanatory variables used in CCA ordinations presented by subset. For nominal variables (N) the numbers of categories in which the

Code	Variable	Type	Measured unit	Observations
SUBSET PHYSIOGRAPHICAL				
ELEV	**Elevation**	I	Metres	Range sampled 2020-2350 m
SLOP	**Slope terrain**	I	Percentage	
ASPE	**Sub-aspect**	I	Degrees	Log-transformed (Beers, 1969)] into a continuous variable
TOP[2]	**Topography**	N		A measure of the terrain evenness
	Top1			Even terrain
	Top2			Uneven terrain
CAT[7]	**Catena**	N		
	Cat0			Flat terrain
	Cat1			Ridge slope
	Cat2			Upper slope
	Cat3			Middle slope
	Cat4			Lower slope
	Cat5			Base slope
	Cat6			Gully/dicth
SUBSET BIOLOGICAL				
MAT[4]	**Canopy maturity**	N		
	Mat1		Immature	
	Mat2		Young reproductive	
	Mat3		Mature	
	Mat4		Old-growth	
CALA[3]	**Canopy layers**			(*cf.* Smith, 1986)
	CaLa1		One horizontal layer	
	CaLa2		Two horizontal layer	
	Cala3		No obvious layer	
SUBSET EDAPHIC				
OMC	**Organic matter content**	I	Percentage	Determined in laboratory as % loss on ignition.
CEC	**Cation- Exchangeable Capacity**	I		
P	**Phosphorous**	I		mg/100g dry weight
Texture[3]		N		Determined in the field
	Tex1			% of Sand particles
	Tex2			% of clay particles
	Tex3			% of silt particles

variable was partitioned are given in square brackets after the code name. For interval (I) variables the units of measurement are provided.

Table 3.2. Kendall's (*tau*_b) rank correlation coefficients between all pairs of environmental variables (n=26). *tau* is given with two levels of probability. * = 0.05; ** = 0.01. Numbers in bold indicate significant values (p<0.0001) after the Bonferroni-sequential correction. OMC = organic matter content; CEC = cation exchange capacity; CALA = canopy layers; CRCP = crown competition.

	Elevation	**Slope**	**Aspect**	**Humus**	**Litter**	**OMC**	**pH**	**CEC**	**Sand**	**Clay**	**Silt**	**Texture**	**Nitrogen**	**Phosphorous**	**Potassium**	**Catena**	**Topography**	**Rocks**	**Stones**	**Twigs**	**Branches**	**Erosion**	**Grazing**	**CALA**	**CRCP**	**Maturity**
Elevation	1.00																									
Slope	-0.11	1.00																								
Aspect	0.17*	-0.16*	1.00																							
Humus	-0.04	0.03	0.05	1.00																						
Litter	-0.01	0.06	-0.03	0.33**	1.00																					
OMC	0.02	-0.06	0.01	-0.11	-0.03	1.00																				
pH	-0.02	-0.13	-0.03	0.11	0.16*	-0.01	1.00																			
CEC	-0.19**	0.03	0.03	-0.11	-0.22**	-0.17*	-0.02	1.00																		
Sand	-0.23**	-0.02	-0.04	-0.07	-0.16*	-0.21**	0.02	0.43**	1.00																	
Clay	-0.04	0.08	0.07	-0.05	-0.16*	0.13	-0.02	0.17*	0.10	1.00																
Silt	0.22**	-0.01	0.01	0.07	0.19**	0.14*	-0.01	-0.44**	-0.84**	-0.27**	1.00															
Texture	-0.22**	0.05	0.02	0.03	-0.05	-0.06	-0.06	0.21**	0.23**	0.06	-0.20*	1.00														
Nitrogen (N)	0.13	-0.06	0.04	-0.02	0.09	0.16	-0.10	-0.29**	-0.37**	-0.17*	0.37**	-0.16*	1.00													
Phosphorous (P)	0.07	-0.18**	0.04	0.01	-0.05	0.10	0.09	-0.14*	-0.16*	-0.07	0.16*	-0.03	0.34**	1.00												
Potassium (K)	-0.14*	0.10	-0.06	0.02	-0.17*	-0.17*	-0.09	0.44**	0.28**	0.13	-0.28**	0.15	-0.19**	0.00	1.00											
Catena	-0.07	-0.06	-0.16*	-0.05	0.04	-0.06	0.03	-0.01	0.11	-0.02	-0.06	-0.06	-0.16*	-0.08	-0.02	1.00										
Topography	-0.01	0.14	-0.03	-0.08	-0.08	0.11	0.00	-0.04	-0.03	0.19*	-0.02	0.19	0.06	0.18	0.07	-0.13	1.00									
Rocks	-0.09	0.15	0.03	-0.05	0.17*	0.03	-0.02	-0.13	-0.05	0.02	0.04	-0.13	0.11	0.02*	-0.13	0.11	0.17	1.00								
Stones	-0.20**	0.21**	0.00	-0.10	-0.02	-0.05	0.06	-0.21	0.11	0.10	-0.11	0.05	0.03	0.01	0.09	0.02	0.33**	0.40**	1.00							
Twigs	0.22**	-0.08	0.17*	-0.13	-0.20**	0.11	0.01	0.07	-0.08	-0.09	0.09	-0.06	0.18*	0.18*	0.00	0.02	-0.07	-0.11	-0.10	1.00						
Branches	0.27**	-0.10	0.12	0.05	-0.12	0.00	0.01	-0.02	-0.15	-0.05	0.15*	-0.08	0.08	0.16*	0.01	0.08	-0.03	-0.14	-0.11	0.47**	1.00					
Erosion	-0.34**	0.18*	-0.03	-0.02	-0.36**	-0.05	-0.09	0.45**	0.27**	0.27**	-0.31**	0.38**	-0.27**	-0.04	0.37**	-0.10	0.18	-0.11	0.12	0.03	0.03	1.00				
Grazing	-0.20**	-0.01	0.11	-0.06	-0.40**	-0.02	-0.19*	0.45**	0.23**	0.31**	-0.27**	0.26**	-0.14	-0.01	0.32**	-0.11	0.14	-0.17	0.02	0.17*	0.10	0.71**	1.00			
CALA	-0.14	0.03	0.07	0.08	-0.14	-0.07	-0.17*	0.27**	0.12	0.09	-0.13	0.22*	-0.05	0.05	0.12	-0.08	0.11	-0.12	-0.06	0.17	0.27**	0.43**	0.45**	1.00		
CRCP	0.24**	-0.19*	0.11	0.13	0.07	-0.14	0.00	-0.20**	-0.17**	-0.10	0.17*	-0.22*	0.15	0.14	-0.22**	0.06	-0.05	-0.18	-0.25**	0.09	0.18*	-0.26**	-0.17	0.04	1.00	
Maturity	-0.21**	0.07	-0.11	0.12	0.04	0.02	0.12	0.09	0.18*	0.01	-0.16*	0.04	-0.01	-0.04	0.02	0.01	-0.05	0.01	0.16	-0.10	-0.09	0.11	0.04	0.16	0.06	1.00

Following the Bonferroni-adjustment first, unconstrained ordination with the forward selection of independent variables and unrestricted Monte Carlo Permutation test was run on the data set listed on Table 3.2. Unconstrained ordination aims fundamentally to identify 'any' variable contained in the data set that explains best the species composition (Lepš & Šmilauer, 2003). Subsequently, a number of constrained ordinations were carried out restricting in each case, the strongest variable in explaining species composition. This approach (also known as variation partitioning) is recommended by Borcard et al. (1992) with the aim of achieving more reliable ordinations. It endeavours essentially to quantify the relative importance of a set of environmental variables in explaining, in the case of this thesis, patterns in species composition. This is a good approach for determining which is the real contribution of each individual variable involved in the analysis to the total explained variance.

Unlike NMDS, the effect of outliers and rare species was assessed by the downweighting procedure available in CANOCO with the aim of reducing the weight of dominant species. The species relative dominance values per plot (I^P) were log-transformed. CCA runs were tested with the Monte Carlo Permutation test following a stepwise forward selection for all the variables involved and using 499 permutations. The reason for using this number is that the power of the test to detect deviations from the null hypothesis increases with the number of permutations undertaken. ter Braak & Smilauer (1998) suggest carrying out at least 199 for a 5% significance level; however, a larger number of permutations are preferable, only being constrained by the availability of computing power. All other default options offered in CCA (CANOCO v.4) such as: *Focus scaling on*: inter-sample distances; *scaling type*: biplot-scaling; *transformation of the species data*; Log-transformation –Y'=log A*Y+B-; *automatic selection*: for the Monte Carlo Permutation test (in unconstrained ordinations) were used during the analyses (*see* ter Braak & Smilauer (1998) for a more throughout explanation).

3.4 Results

3.4.1 The floristic variation of the adult community

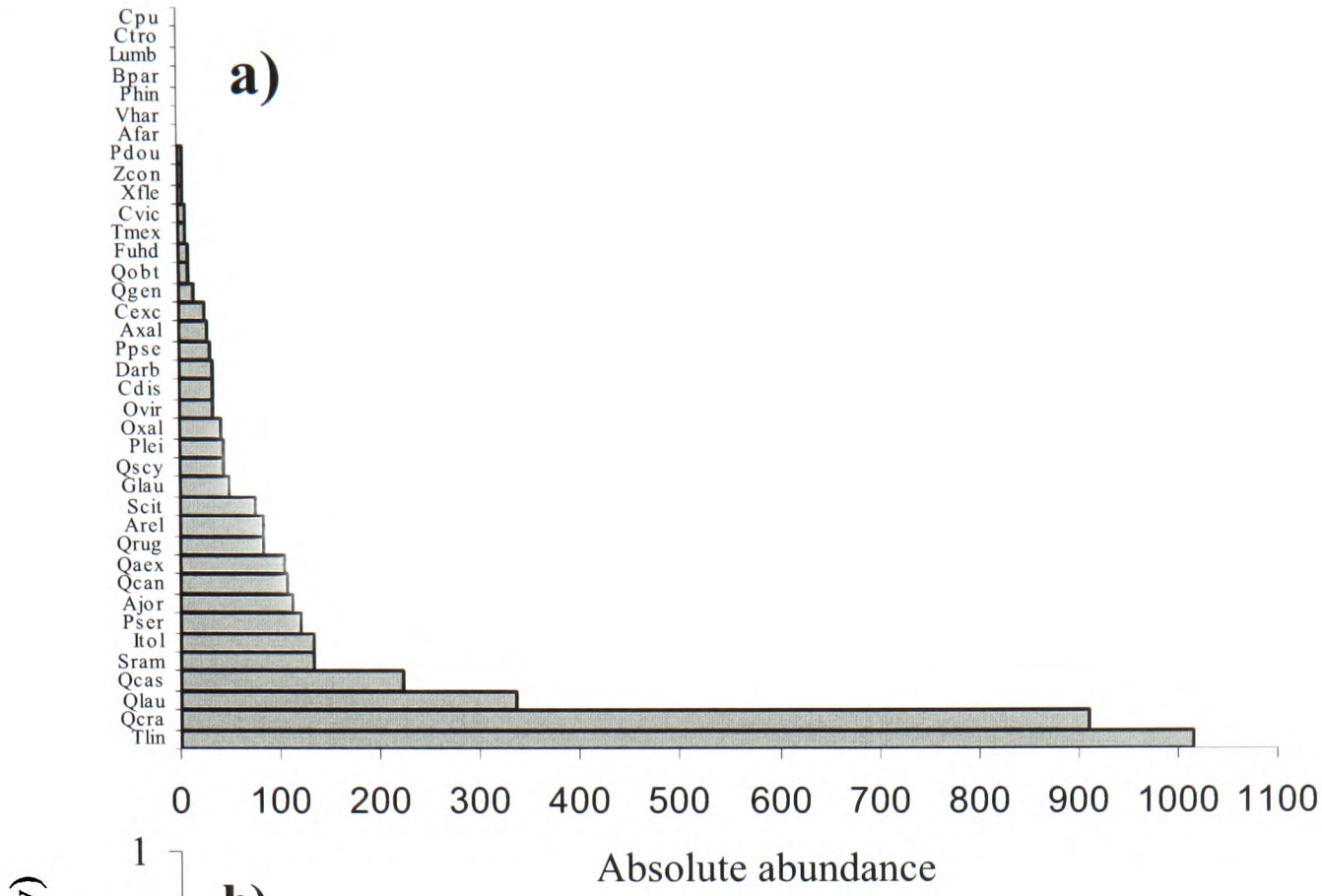
In 2002, a total of 38 adult tree species (≥ 5 cm dbh and ≥ 1.30 tall), including 9 species of *Quercus*, from 28 genera and 22 families were recorded whilst re-inventorying 86 of the 105 psps (Table 3.3). Two species, *Ternstroemia lineata* and *Quercus crassipes*, were widespread and outstanding in the data, accounting for 26.0% and 23.3%, respectively of the total number of individuals. These two species had individuals in 48 and 40 of the last 86 re-inventoried plots, respectively. There was a high heterogeneity in species frequency, so that the third most prominent species was *Quercus laurina* with 8.6% of the total number of individuals and recording in 28 plots. Several other taxa were counted occasionally in the psps, for instance, *Carpinus tropicalis, Crataegus pubescens* and *Lippia umbellata* were inventoried only once each in all the psps. Evidently, the most common genus in terms of number of species and dominance was *Quercus*; its relative frequency ranged from less than 1 % to 100%. Histograms of species relative abundances, both absolute and rank-abundance (Magurran, 2004) are shown in Figure 3.1a and b.

Ternstroemia lineata was the unique species recognised as an extreme observation in the adult community, with an average distance of -2.104 standard deviations (Sørensen distance measure) higher than the average distances of the rest of the species, however this arises only in the I^P data. Though most species had dominant individuals in the upper canopy, *Ternstroemia lineata, Prunus serotina, Styrax argenteus* and *Cornus excelsa* are commonly elements of smaller stature only represented in the sub-canopy, while *Buddleia parviflora, Xilosma flexuosum* and *Acacia farnesiana* seldom reach the sub-canopy stratum, behaving as understory trees.

Table 3.3 List of species (n=38), along with three-letter code, present in oak and mixed-oak forest in Cerro Grande Sierra de Manantlán, Western México. (Altitudinal range 2020-2235 m a.s.l.). **ld** = light demanding; **t** = shade tolerant; **i** = intermediate; **pa** = phytogeographical affinity; **ds** = seed dispersal syndrome; **Resprout** = ability of resprouting after harvesting. **r** = resprouts; **nr** = does not resprout. Species authorities for are shown in bold to the right of the species.

Species*	Code	Family	pa[+]	Habitat type	ds**	st[ℓ]	Resprout***
Abies religiosa **(H.B.K.) Schlecht. & Cham** *var.* religiosa **Loock et Martínez ex Martínez**	*Arel*	Pinaceae	Holarctic	Mesic	Anemochory-w	t	nr
Acacia farnesiana **(L.) Willd**	Afar	Fabaceae	Neotropical	Transition	Barochory	ld	r
Alnus jorullensis subsp. *Lutea* **Furlow**	Ajor	Betulaceae	Holarctic	Xeric	Barochory	ld	r
Arbutus xalapensis **H. B. K.**	Axal	Ericaceae	Holarctic	Mesic	Endozoochory	t	r
Buddleja parviflora **H. B. K.**	*Bpar*	Buddlejaceae	Neotropical	Mesic	Barochory	t	nr
Carpinus tropicalis **(Donn. Sm.) Lundell**	*Ctro*	Betulaceae	Holarctic	Mesic	Barochory	t	nr
Clethra vicentina **Standl.**	Cvic	Clethraceae	Malayo-American	Mesic	Anemochory-s	ld-i	nr
Comarostaphylis discolor **(Hook.)** subsp. *Discolor* **Diggs**	Cdis	Ericaceae	Neotropical	Mesic	Endozoochory	t	r
Cornus excelsa **H. B. K.**	Cexc	Cornaceae	Holarctic	Mesic	Endozoochory	t	r
Crataegus pubescens **(H.B.K.) Steud.**	Cpub	Rosaceae	Holarctic	Transition	Endozoochory	ld	r
Dendropanax arboreus **(L.) Decne. & Planch.**	Darb	Araliaceae	Pantropical	Mesic	Endozoochory	ld	nr
Fraxinus uhdei **(Wenzig) Lingelsh.**	Fuhd	Oleaceae	Holarctic	Mesic	Anemochory-w	t	r
Garrya laurifolia **Hartweg ex Benth.**	Glau	Garryaceae	Holarctic	Mesic	Anemochory-s	t	nr
Ilex tolucana **Hemsl.**	Itol	Aquifoliaceae	Cosmopolitan	Mesic	Endozoochory	t	r
Lippia umbellata **Cav.**	Lumb	Verbenaceae	Afro-American	Mesic	Endozoochory	t	r
Oreopanax xalapensis **(H. B. K.) Decne. & Planch.**	Oxal	Araliaceae	Neotropical	Mesic	Endozoochory	t	nr
Ostrya virginiana **(Mill.) K. Koch**	Ovir	Betulaceae	Holartic	Mesic	Barochory	t	nr
Persea hintonii **Allen**	Phin	Lauraceae	Malayo-American	Mesic	Endozoochory	t	nr
Pinus douglasiana **Martínez**	Pdou	Pinaceae	Holarctic	Xeric	Anemochory-w	ld	nr
Pinus leiophylla **Schlecht. & Cham.**	Plei	Pinaceae	Holarctic	Xeric	Anemochory-w	ld	nr
Pinus pseudostrobus **Lindl.**	Ppse	Pinaceae	Holarctic	Xeric	Anemochory-w	ld	nr
Prunus serotina **Ehrh.** subsp. *capuli* **(Cav.) McVaugh**	Pser	Rosaceae	Holarctic	Xeric	Endozoochory	ld	r
Quercus aff. *excelsa* **Liebm.**	Qaex	Fagaceae	Holarctic	Mesic	Barochory-Endozoochory	t	nr
Quercus candicans **Née**	Qcan	Fagaceae	Holarctic	Mesic	Barochory-Endozoochory	t	nr
Quercus castanea **Née**	Qcas	Fagaceae	Holarctic	Mesic-Transition	Barochory-Endozoochory	i	r
Quercus crassipes **Humb. & Bonpl.**	Qcra	Fagaceae	Holarctic	Xeric	Barochory-Endozoochory	i	r
Quercus gentryi **C. H. Muller**	Qgen	Fagaceae	Holarctic	Mesic	Barochory-Endozoochory	t	nr
Quercus laurina **Humb. & Bonpl.**	Qlau	Fagaceae	Holarctic	Mesic	Barochory-Endozoochory	t	nr
Quercus obtusata **Humb. & Bonpl.**	Qobt	Fagaceae	Holarctic	Mesic-Transition	Barochory-Endozoochory	t	nr
Quercus rugosa **Née**	Qrug	Fagaceae	Holarctic	Mesic-Transition	Barochory-Endozoochory	t	r
Quercus scytophylla **Liebm.**	Qscy	Fagaceae	Holarctic	Mesic	Barochory-Endozoochory	t	nr
Styrax ramirezii **Greenm.**	Sram	Styraceae	Malayo-American	Mesic	Endozoochory	t	r
Symplocos citrea **Lex.**	Scit	Symplocaceae	Malayo-American	Mesic	Endozoochory	t	nr
Ternstroemia lineata **DC.** subsp. *lineata*	Tlin	Theaceae	Pantropical	Mesic-Transition	Barochory	i	r
Tilia mexicana **Schlecht.**	Tmex	Tiliaceae	Neotropical	Mesic	Barochory	t	r
Viburnum hartwegii **Benth.**	Vhar	Caprifoliaceae	Holarctic	Xeric-Transition	Endozoochory	t	r
Xilosma flexuosum **(H. B. K.) Hemsl.**	Xfle	Flacourtiaceae	Pantropical	Xeric	Endozoochory	ld	r
Zinowewia concinna **Lundell.**	Zcon	Celastraceae	Neotropical	Mesic	Anemochory-w	t	nr

*Vázquez-García et al. (1995); **Vázquez-García & Givnish, (1998); [+]Rzedowski, (1978); [ℓ] *** personal observations.



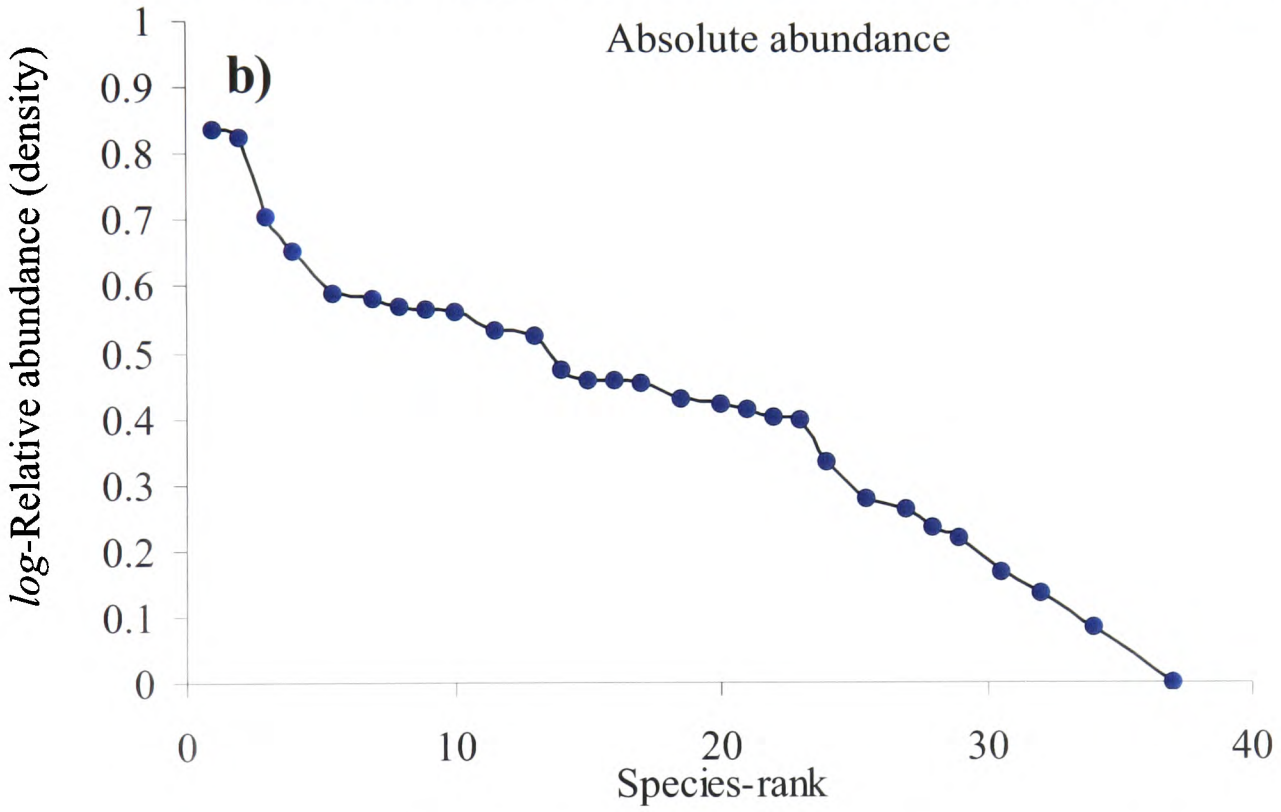


Figure 3.1 Variation in absolute abundance (a) and species *log* rank abundance (b) for adult trees (individuals ≥ 5 cm dbh and ≥ 1.30 tall) in the 86 psps. Species name are abbreviated as follows: **Arem** = *Abies religiosa var. emarginata;* **Arel** = *Abies religiosa var. religiosa;* **Afar** = *Acacia farnesiana;* **Ajor** = *Alnus jorullensis subsp. lutea;* **Axal** = *Arbutus xalapensis;* **Bpar** = *Buddleja parviflora;* **Ctro** = *Carpinus tropicalis;* **Cvic** = *Clethra vicentina;* **Cdis** = *Comarostaphylis discolor subsp. discolor;* **Cexc** = *Cornus excelsa;* **Cpup** = *Crataegus pubescens;* **Darb** = *Dendropanax arboreus;* **Eama** = *Eupatorium aff. mairetianum;* **Fuhd** = *Fraxinus uhdei;* **Glau** = *Garrya laurifolia;* **Itol** = *Ilex tolucana;* **Lumb** = *Lippia umbellata;* **Mcil** = *Monnina ciliolate;* **Oxal** = *Oreopanax xalapensis;* **Ovir** = *Ostrya virginiana;* **Plot** = *Perrottetia longistylis;* **Phin** = *Persea hintonii;* **Pgue** = *Picramnia guerrerrensis;* **Pdou** = *Pinus douglasiana;* **Plei** = *Pinus leiophylla;* **Ppse** = *Pinus pseudostrobu;* **Pser** = *Prunus serotina;* **Qaex** = *Quercus aff. excelsa;* **Qcan** = *Quercus candicans;* **Qcas** = *Quercus castanea;* **Qcra** = *Quercus crassipes;* **Qgen** = *Quercus gentryi;* **Qlau** = *Quercus laurina;* **Qobt** =*Quercus obtusata;* **Qrug** = *Quercus rugosa;* **Qscy** = *Quercus scytophylla;* **Sram** = *Styrax ramirezii;* **Scit** = *Symplocos citrea;* **Tlin** = *Ternstroemia lineata subsp. lineata;* **Tmex** = *Tilia mexicana;* **Vhar** = *Viburnum hartwegii;* **Xfle** = *Xilosma flexuosum;* **Zcon** = *Zinowewia concinna.*

3.4.2 Species assembly: discrete communities or a compositional drift?

The three metric indices used (P/A; BA and I^P) yielded relatively similar results however, floristic patterns of distribution will be described based on I^P results. The main motivation of considering I^P rather than P/A of BA is that the former provided more clear-cut graphic separation in the NMDS ordination diagrams between the main floristic zones.

Strictly based on pair-wise shared species composition, NMDS separated the 86 psps and 38 species into at least two main vegetational discontinuities, and a third group of psps that could be classified as a transitional 'contact' zone located between the two major floristic zones (Figures 3.2 and 3.3). A topographic map showing the overall vegetation of the study area, along with the GPS derived psps' position and their respective Shannon's diversity index (different colours) is presented in Figure 3.4. The first three NMDS axes explained 77.7% of the variability in the data (p>0.005; *STRESS* 14.5). As is evident in the NMDS ordination diagrams and in the map, it can be strongly argued that although there is no a sharp division between the two main vegetation zones, there are evidences of floristic patterns across the study area. Therefore, taking into consideration the species' ecological traits presented in Table 3.3, along with their phytogeographical affinities, the results can intuitively be interpreted as the existence of at least two main vegetational gradients extracted by NMDS, joined by a contact floristic zone containing elements from the two main floristic gradients. Considering the two biggest vegetational zones the results suggested that one floristic gradient which is species-poor, runs along the most xeric zones of Cerro Grande; while a second gradient, which is larger and richer in species runs along the most mesic zones of Cerro Grande. The putative xeric group, hereafter labelled as such, was tightly clustered and positioned at the upper right end of axis one (Figure 3.2) explaining 36.7 % of the variation in species composition. While the second main group (which was labelled as the mesophytic group), although if compared with the previous group was rather loose as seen by the scattered distribution of the plots and species over the ordination diagram included most of the remaining species. *Q. candicans, Q. laurina, Q. gentry* and *Q. scytophylla, Persea hintonii, Ilex tolucana* and *Styrax ramirezii* were the most common species in this group, and were evenly distributed in the middle lower part of axis one (Figure 3.2) which in turn explained 16.7% of the variation in species composition.

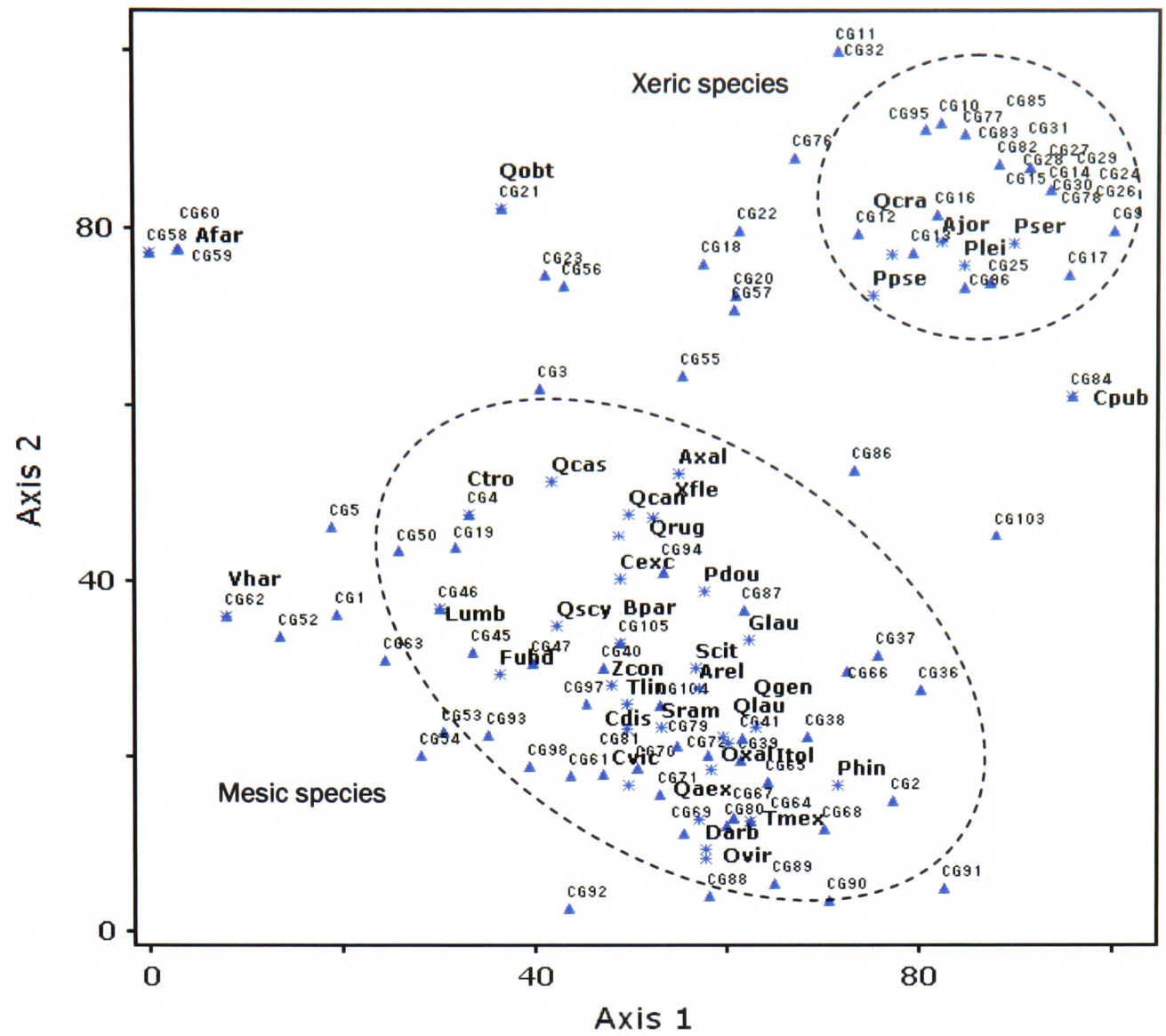


Figure 3.2. First two axes of non-metric multidimensional scaling for the complete data set (86 psps x 38 species) (*STRESS* 14.5; $p = 0.019$) showing groups of plots that share similarities (Sørensen index). Asterisks indicate relative position of species on the axes. Solid triangles represent the relative position of the psps on the same axes according to their relative species dominance (I^P). Lines surrounding groups of plots and species are approximate boundaries between zones. Geographic range distance between psps 0.0010-10.5 km. **Arem** = *Abies religiosa var. emarginata;* **Arel** = *Abies religiosa var. religiosa;* **Afar** = *Acacia farnesiana;* **Ajor** = *Alnus jorullensis subsp. lutea;* **Axal** = *Arbutus xalapensis;* **Bpar** = *Buddleja parviflora;* **Ctro** = *Carpinus tropicalis;* **Cvic** = *Clethra vicentina;* **Cdis** = *Comarostaphylis discolor subsp. discolor;* **Cexc** = *Cornus excelsa;* **Cpup** = *Crataegus pubescens;* **Darb** = *Dendropanax arboreus;* **Eama** = *Eupatorium aff. mairetianum;* **Fuhd** = *Fraxinus uhdei;* **Glau** = *Garrya laurifolia;* **Itol** = *Ilex tolucana;* **Lumb** = *Lippia umbellata;* **Mcil** = *Monnina ciliolate;* **Oxal** = *Oreopanax xalapensis;* **Ovir** = *Ostrya virginiana;* **Plot** = *Perrottetia longistylis;* **Phin** = *Persea hintonii;* **Pgue** = *Picramnia guerrerrensis;* **Pdou** = *Pinus douglasiana;* **Plei** = *Pinus leiophylla;* **Ppse** = *Pinus pseudostrobus;* **Pser** = *Prunus serotina;* **Qaex** = *Quercus aff. excelsa;* **Qcan** = *Quercus candicans;* **Qcas** = *Quercus castanea;* **Qcra** = *Quercus crassipes;* **Qgen** = *Quercus gentryi;* **Qlau** = *Quercus laurina;* **Qobt** =*Quercus obtusata;* **Qrug** = *Quercus rugosa;* **Qscy** = *Quercus scytophylla;* **Sram** = *Styrax ramirezii;* **Scit** = *Symplocos citrea;* **Tlin** = *Ternstroemia lineata subsp. lineata;* **Tmex** = *Tilia mexicana;* **Vhar** = *Viburnum hartwegii;* **Xfle** = *Xilosma flexuosum;* **Zcon** = *Zinowewia concinna.*

Figure 3.2 also shows, at the upper left side of the ordination diagram on axis 2, a small group of plots (CG58-CG60) represented by *Acacia farnesiana* which were separated from the two main dominant vegetational trends. This last group of plots exhibited the lowest species abundance and diversity and, at the same time this groups was geographically situated at the lowest (≈2020-2040 m a.s.l) altitudes of the range sampled. These psps are the most exposed to solar radiation, have shallow soils and represent the most xeric *Quercus* zones in the study area. The above-described vegetational patterns also arose when both common and uncommon species were excluded (Figure 3.3) and, even when distinct types of data matrices (*e.g.* P/A or BA; *see* Appendix 3.2) were examined. Indirect ordinations were achieved just on the vegetation data, independently of the measured environmental variables. Thus, the vegetational patterns identified fairly represented the underlying patterns in species composition.

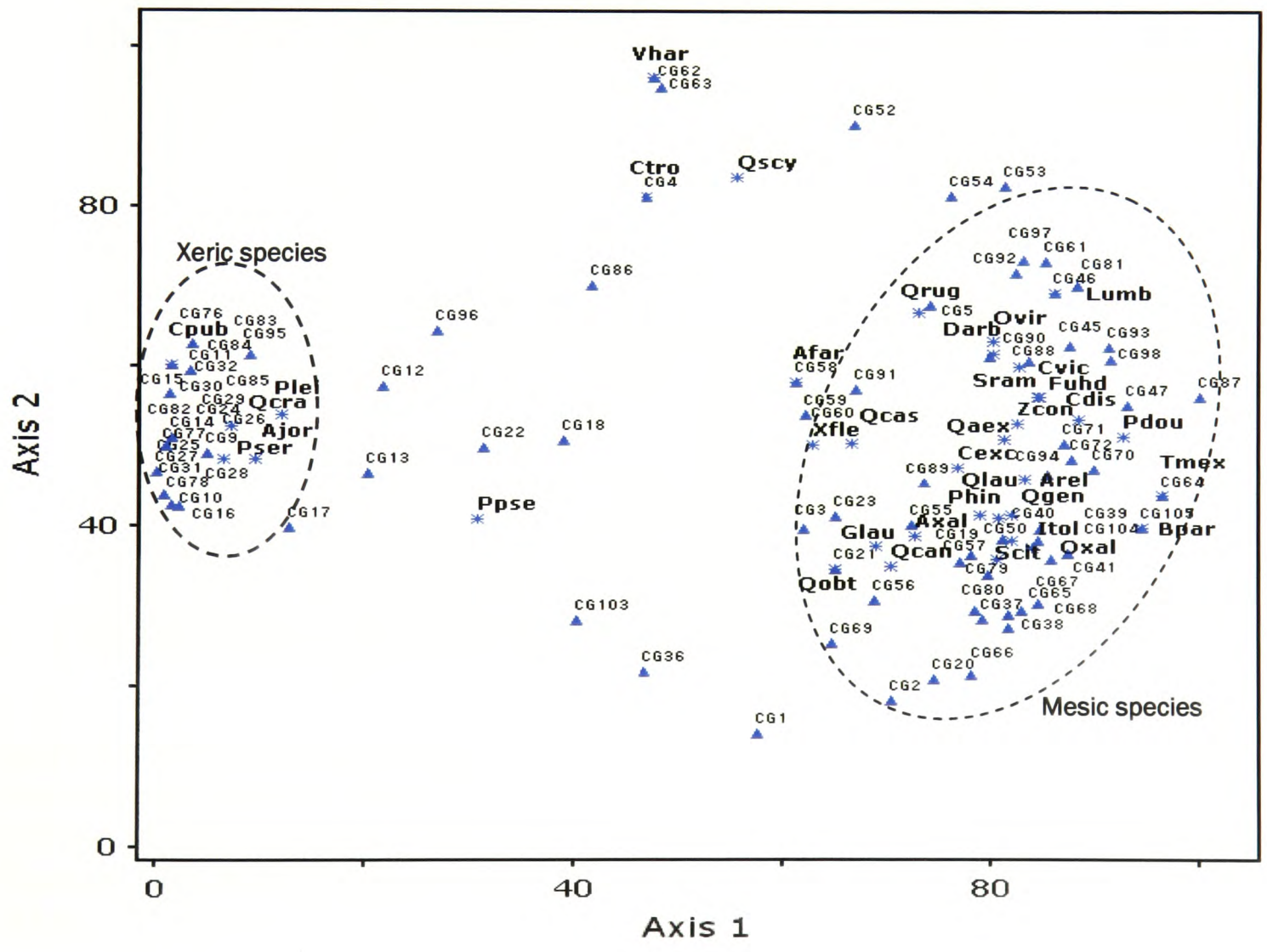


Figure 3.3. NMDS ordination (for the I^P) of the first two axes showing groups of plots and species that share similarities excluding outlier species (*T. lineata*) (*STRESS* 14.9). Asterisks, dark triangles and species names are as in the previous figure.

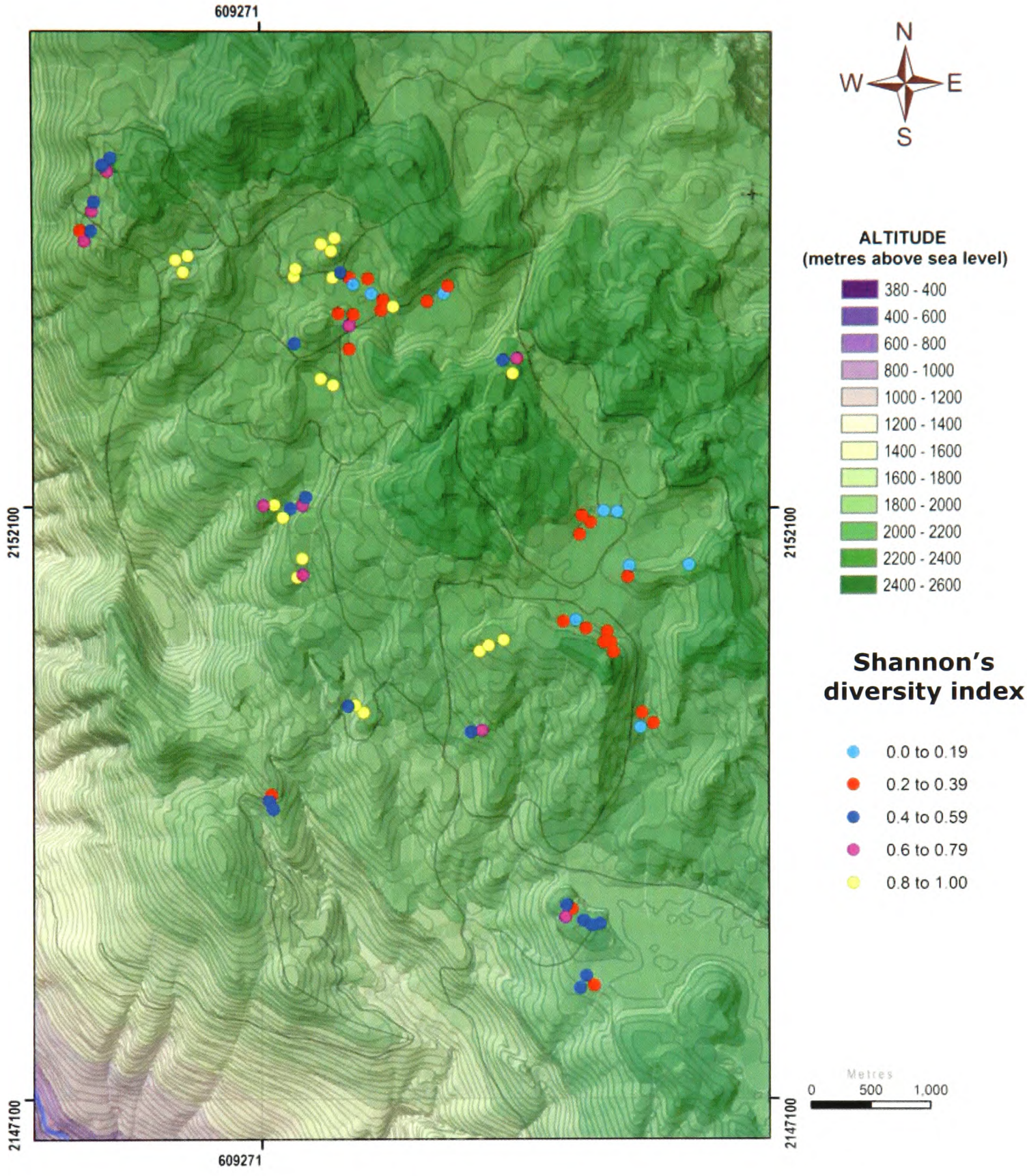


Figure 3.4. Satellite image (Bands 1, 2, and 3 resolution 20 x 20 m dated October 2000) of Cerro Grande, Sierra de Manantlán. Circles indicate GPS-derived permanent sample plot locations. Different colours of the circles correspond to differences in species composition (Shannon's dissimilarity index). Geographical distance between plots ranged from 0.0010-9.5 km.

Because NMDS extracted at least two major floristic gradients, further analyses were carried out with the aim of assessing whether true floristic differences does exist between the mesic and the xeric, the mesic and transition zone, and the xeric and transition zone. For this purpose, Multi-Response Permutation Procedure analyses were carried out to test the null hypothesis of no floristic differences between zones. Multi-Response Permutation Procedure (MRPP) (Stallins & Parker, 2003) is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities (McCune & Mefford, 1999). MRPP is similar to Analysis of Similarity (ANOSIM) in concept but uses a different test of statistics. Unlike equivalent parametric techniques, it makes few assumptions about the distribution structure of the data (Paavola et al., 2003), since it does not require multivariate normality or homogeneity of variances (Zimmerman et al., 1985). MRPP provides a statistic δ, that is the weighted mean within-groups distance and is associated with a *p*-value that indicates the likelihood of getting a δ equal to or smaller than that observed by chance (Biondini et al., 1985). The null distribution of the test statistic is based in the collection of all possible permutations of the objects into groups of a specified size (McCune & Mefford, 1999). The strategy of MRPP is to compare an observed mean within-group distance that would have resulted from all other possible combinations of the group membership. As such, MRPP tests for differences among two or more groups based on the collective variability of the data for each group, rather than their respective means (Stallins & Parker, 2003). This makes it ideal for testing among-group differences in ecological data.

Therefore, to perform the MRPP, based in both their location on the NMDS ordination diagram and species composition, to each psp it was assigned *a priori* as *mesic, xeric or transition* class which was used as the grouping variable and further tested as to whether they differed in position in the multi-dimensional space. This procedure was carried out using a Euclidian distance measure; all permutations were computed in PC-ORD v.4 (McCune & Mefford, 1999).

MRPP showed that there was significant floristic difference ($p = 0.0003$) between the Mesic and Xeric zones (M_E-X_E) but there were not significant differences between the Mesic and the Transition (M_E-T_R; $p = 0.03841$) and the Xeric and the Transition (X_E-T_R; $p = 0.04593$) zones.

In addition to the previous observations it was discovered that a few species, including *Quercus obtusata, Crataegus pubescens* (Figure 3.2) and *Viburnum hartwegii, Carpinus tropicalis,* and *Quercus scytophylla* (Figure 3.3) were not linked to any specific cluster of species or plots and, depending on the degree of orthogonality and on the axes contrasted, this was true for *Pinus pseudostrobus* as well. These species consistently appeared separated from the rest. However, it is worth mentioning that the observed floristic patterns may represent an effect of the sampling scheme implemented in this study, where a number of plots were established over ecotone zones (areas of vegetation change). Infrequent species in the data, or species that were segregated from the main groups such as *Q. scytophylla, Q. obtusata, C. pubescens*, *V. hartwegii* and *C. tropicalis,* were present in some psps but probably they were not sufficiently sampled. This assumption comes from the fact that in the study area there are localities in which *Q. obtusata* is relatively abundant and might constitute moderately large stands. This species mainly occurs in zones of intermediate xeric-mesic environments, mostly located at higher elevations but along ravines of gentle slopes and deep soils (*personal observation*). Nonetheless, the total number of sampling units, the spatial arrangement and the relatively small distance between plots (100-150 m) seems adequate to have captured the overall species variation in the study area, as suggesting by the species-area curve (PC-ORD v.4) in Figure 3.5.

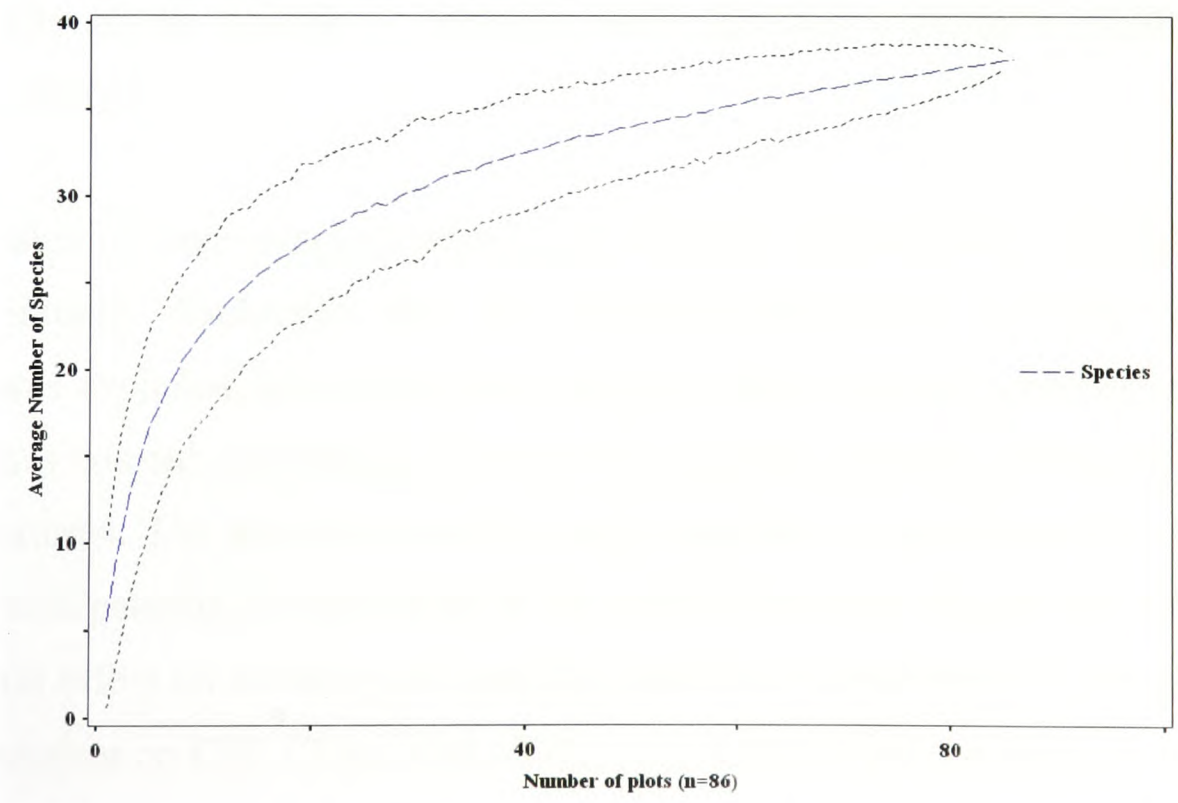


Figure3.5. Species Area curve representing sampling effort, number of graphed plots *n* = 86. Dashed line represents average number of species; dotted lines are confidence distance.

3.4.3 The role of overall environmental heterogeneity

According to Walker & del Moral (2003), biophysical characteristics largely determine which species are established in a particular location. For this reason it is extremely important to collect a wide range of environmental information as this may increase the likelihood of picking up those variables most significantly related to vegetation. When sufficient environmental data are available, direct ordination provides a readily interpretable conceptual framework for vegetation analysis (Peet & Loucks, 1977). Nevertheless, as Jongman et al. (1995) argue to accomplish reasonably trusted ordinations, particularly in CCA, it is of vital significance to use fewer environmental variables than samples, otherwise the model reverts to an unconstrained canonical analysis. In this investigation, because of the high number of environmental variables contained in the data set, some of them were either highly or weakly correlated (*see* Table 3.2). Highly correlated variables were mostly those in the same physical subset; specifically this was apparent with variables describing edaphic properties. Soil erosion for example, was both negatively and positively correlated with a number of variables in its subset. A correlation that called for particular attention was that erosion had a negative association with altitude, indicating that erosion should decrease as altitude increases. However, the intense grazing, logging operations, and overall human impacts mostly through harvesting of non-timber forest products across Cerro Grande, independently of the altitude or location, made the later correlation confusing and difficult to interpret.

With the aim of improving parsimony in the CCA ordinations, apart from those variables initially discharged after the Bonferroni-adjustment, a further group of variables was excluded from subsequent analyses; these included: percentage of twig cover, humus content, percentage of stone cover, grazing intensity, pH and the dummy variable texture4. The first four variables were regarded as superfluous for explaining extant floristic patterns of distribution in the adult community, though they might have an important effect on seedling and saplings patterns of establishment; pH typically is highly dependent on CEC (Brais et al., 1995) and, texture4 was a combined variable of texture1 (sandy soils) and texture3 (clay soils), so that these last variables were deemed redundant for their use in CCA ordinations even though they passed the initial Bonferroni test therefore were not included in further analyses.

3.4.4 Which environmental gradient best explains floristic patterns?

Unconstrained ordination showed that the most strongly weighted explanatory variables with respect to the first two axes (λ_1= 0.444 and λ_2= 0.273), sufficient to explain differences in floristic patterns were elevation (ELEV), mature canopy (Mat3), sun-aspect (ASP), organic matter content (OMC) and terrain of regular topography (Top1) (Table 3.4).

Table 3.4. Canonical correspondence analysis statistics for the I^P. Correlation coefficients (cc) of environmental variables and *t*-values (*t*) are presented for axes 1 and 2; critical value* (df ≥ 18; α = 0.05) =2.1.

	EIGENVALUES	Axis1 0.444		Axis2 0.273	
Variable	**Code**	**cc**	***t***	**cc**	***t***
Sun-aspect	**ASP**	0.195	**2.574**	0.141	**2.166**
One horizontal stratum	**CaLa1**	0.036	0 .499	-0.084	-1.332
Ridge-top	**Cat1**	-0.111	-0.891	-0.089	-0.830
Upper-slope	**Cat2**	0.152	2.009	0.061	0.941
Middle-slope	**Cat3**	0.149	0.964	0.069	0.520
Lower-slope	**Cat4**	-0.120	-0.600	-0.038	-0.222
Base-slope	**Cat5**	-0.066	-0.340	-0.013	-0.078
Gully/ditch	**Cat6**	-0.021	-0.210	-0.036	-0.414
Cation Exchangeable Capacity	**CEC**	-0.106	-1.267	0.026	0.362
Elevation	**ELEV**	0.241	**2.743**	-0.437	**-5.618**
Young reproductive canopy	**Mat2**	0.143	2.003	0.128	2.080
Mature canopy	**Mat3**	0.185	**2.633**	0.233	**3.847**
Old-growth	**Mat4**	-0.030	-0.458	0.071	1.236
Organic Matter Content	**OMC**	0.019	0.263	0.000	0.006
Phosphorous	**P**	-0.142	-1.962	-0.054	-0.877
Slope	**SLO**	-0.157	-1.854	-0.102	-1.402
Sand	**Tex1**	-0.244	-1.000	-0.135	-0.641
Clay	**Tex2**	-0.156	-0.644	-0.079	-0.382
Silt	**Tex3**	-0.120	-1.157	-0.090	-1.013
Regular Topography	**Top1**	-0.183	**-2.489**	-0.070	-1.119

Critical value for a t-test at 5% significance is ca. 2.1, if n-q-1 > 18; n = number of samples, q = number of environmental variables.

The unconstrained biplot of the two first axes (Figure 3.6) shows graphically the importance and the relative contributions of the complete suite of environmental variables in explaining the observed vegetation patterns.

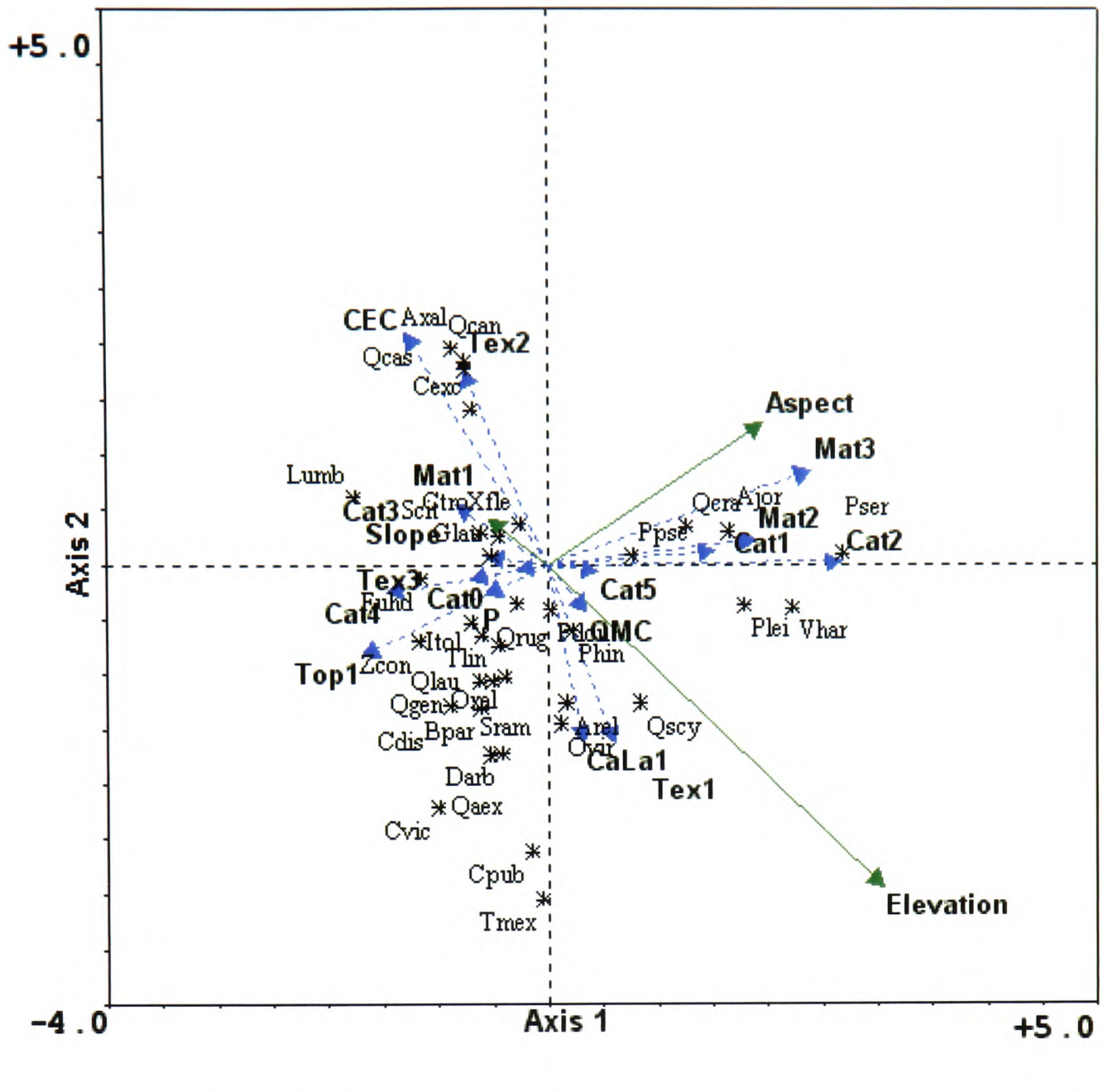


Figure 3.6 Canonical correspondence analysis biplot showing the relationships between species on the measured environmental variables. Dashed and solid arrows indicate the centroids of both interval and nominal variables respectively. The length and direction of the arrows indicate the strength and sign of the correlations. Species acronyms are as indicated in NMDS ordinations.

In figure 3.6 it is worth highlighting the small effect that organic matter content (OMC) had in explaining vegetation patterns as revealed by the length of the arrow (2.5 standard deviations). However, as indicated in Table 3.4 it had one of the lowest *t*-values in both axes. All catenas (Cat) were orthogonal to each other (Figure 3.6) revealing the divergent role of micro-physiographical variations in explaining the floristic patterns observed in the study area. The same can be said for those variables typically considered of importance in explaining vegetation patterns such as soil texture, which were also orthogonal to each other. Slope of the terrain was not as important (2.1 standard deviations) as was expected; however this last result may be attributed to the small range of slope terrain and elevation observed among catenas (*see* Table 2.3

Chapter 2). Another suite of explanatory variables that deserve closer examination are those related to the stand description subset (*e.g.* Mat3 = mature; CaLa1 = one canopy layer 'even-aged') since they exhibited more importance in discriminating vegetation patterns than small-scale physiographical characteristics ($p<0.01$) such as catena, aspect or slope (Figure 3.6 and Table 3.4).

An important result that that should be emphasised is the fact that fairly similar floristic patterns, as described by indirect ordination (NMDS) (Figure 3.3), were extracted by direct ordinations (CCA) (Figure 3.6). For instance, in the upper right corner of the CCA ordination diagram, roughly the same group of species (*Quercus crassipes, Alnus jorullensis, Prunus serotina,* and *Pinus pseudostrobus*) was placed close together as in NMDS. In interpreting unconstrained ordination results, it can be argued that this group of species are more related to differences in aspect, to sites of mature canopies and to sites mostly located from top to middle (Cat1-Cat2) topographical positions (*see* Figure 2.8). Similarly as occurred in NMDS, those classified as mesophytic species (*e.g. Q. candicans, O. xalapensis, O. virginiana,* etc.) were positioned opposite and above previously described group, representing a more widely scattered species distribution over the ordination diagram (Figure 3.6).

As was expected, the most widely distributed and abundant species in the study area were placed nearer to the centre of the CCA ordination diagram (Figure 3.6), revealing more generalist behaviour and, probably, lower susceptibility to habitat variation as compared to the rest of their sympatric and congeneric species. This pattern was evident with *Ternstroemia lineata* and *Quercus crassipes*, which are the two most common species in the dataset. Similarly, those species assumed to have habitat specificity, judged by their reduced distribution and low presence in the data, such as *Tilia mexicana* or *Clethra vicentina,* were placed further from the centre of the CCA diagram (Figure 3.6).

3.4.5 The role of small-scale environmental heterogeneity

To elucidate the relative importance of finer-scale environmental heterogeneity in explaining the floristic distribution patterns in the adult *Quercus* community of Cerro Grande, a number of partial ordinations were carried out. In a first constrained CCA

ordination, altitude (the most statistically significant variable in unconstrained ordination) was set as a covariable. The aim was to reflect the effect of the remaining group of environmental variables on vegetation patterns. This approach revealed a somewhat more heterogeneous set of explanatory variables than in unconstrained ordination, as it was evident by the length and directionality of the vectors shown in Figure 3.7. Accordingly, partial ordination showed that reproductive maturity (Mat3 and Mat4), sun-aspect and regular topography (top1) in Axis 1 and CEC, OMC, P, old-growth (Mat4), one vertical stratum (canopy layers; CaLa1) and middle slope catenas (Cat3) in Axis 2 were amongst the most important variables explaining floristic distribution patterns (Table 3.5 and Figure 3.7).

Table 3.5. Partial ordinations with altitude as a covariable. Correlation coefficients (cc) of environmental variables and *t*-values (*t*) are presented only for axes 1 and 2; critical value* (df ≥ 18; α = 0.05) =2.1. Bold figures are significant results.

		Axis 1		**Axis 2**	
	Eigenvalues	**0.3541**		**0.1255**	
Variable	**Code**	**cc**	***t***	**cc**	***t***
Aspect	**ASP**	0.2477	**2.8676**	-0.0337	-0.6458
One horizontal stratum	**CaLa1**	-0.0375	-0.4478	0.1185	**2.3447**
Ridge-top	**Cat1**	-0.1224	-0.8734	-0.0705	-0.8334
Upper-slope	**Cat2**	0.1570	1.8242	-0.0880	-1.6945
Middle-slope	**Cat3**	0.1404	0.7998	-0.2963	**-2.7961**
Lower-slope	**Cat4**	-0.0668	-0.2974	-0.2624	-1.9359
Base-slope	**Cat5**	-0.1535	-0.6674	-0.4349	**-3.1323**
Gully/ditch	**Cat6**	-0.0466	-0.3991	-0.0684	-0.9712
Cation Exchangeable Cap.	**CEC**	-0.0713	-0.7390	0.1984	**3.4060**
Yong reproductive canopy	**Mat2**	0.0129	0.1695	0.0378	0.8206
Mature canopy	**Mat3**	0.1977	**2.4446**	0.0597	1.2232
Old-growth canopy	**Mat4**	0.2754	**3.3831**	0.1314	**2.6744**
Organic Matter Content	**OMC**	0.0101	0.1223	0.1096	**2.1943**
Phosphorous	**P**	-0.1433	-1.6986	0.1124	**2.2074**
Slope	**SLO**	-0.1586	-1.6388	0.1065	1.8237
Sand	**Tex1**	-0.2838	-1.0031	0.0636	0.3723
Clay	**Tex2**	-0.1884	-0.6751	0.0994	0.5902
Silt	**Tex3**	-0.1503	-1.2159	0.0877	1.1749
Topography	**Top1**	-0.1899	**-2.2538**	0.0322	0.6341

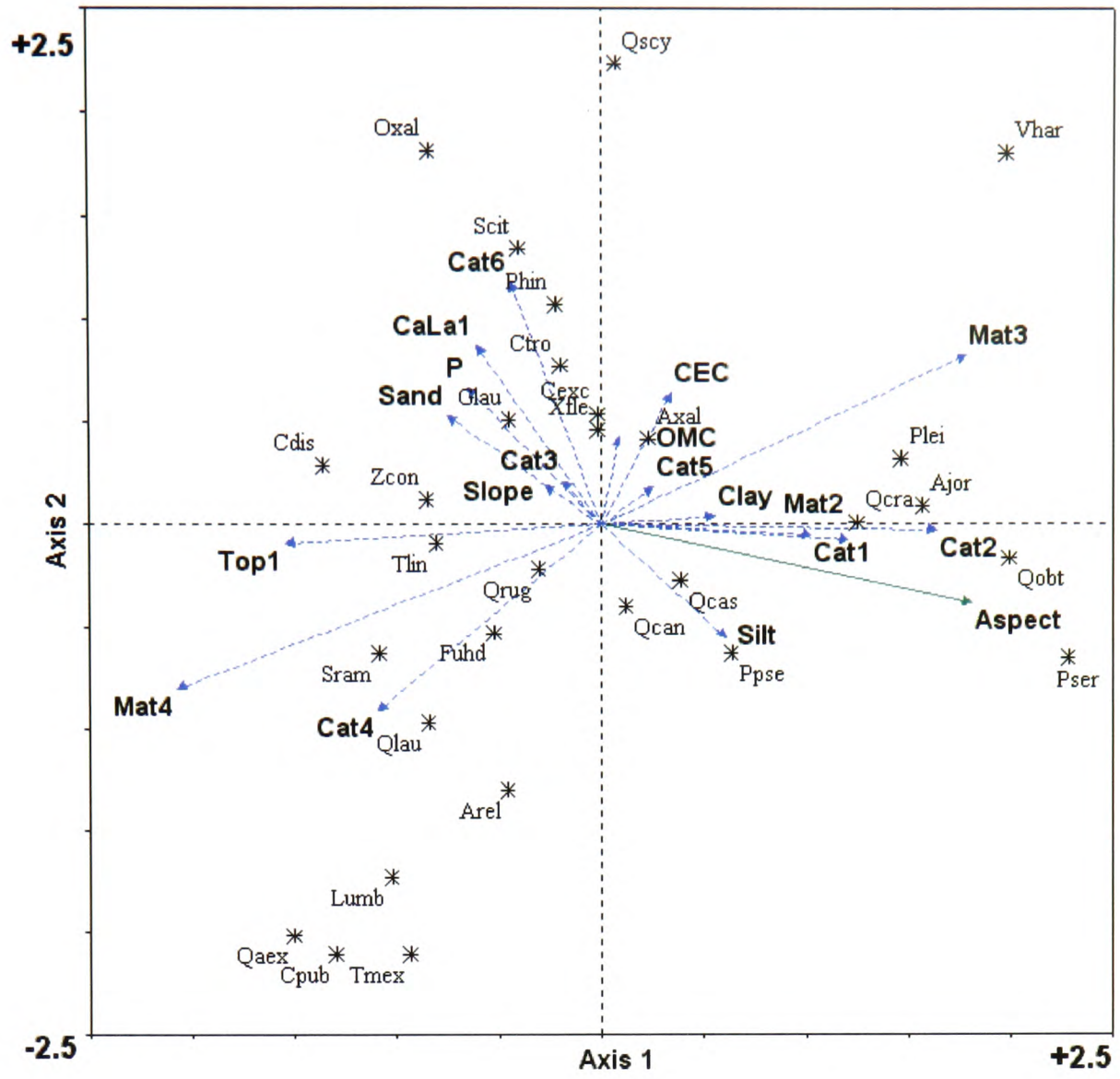


Figure 3.7 Canonical correspondence analysis biplot when altitude is declared a covariable. Dashed and solid arrows indicate the centroids of both interval and nominal variables respectively. The lengths and directions of arrows indicate the strength and sign of the correlations. Species acronyms are as indicated in NMDS ordinations. Acronyms of environmental variables are as indicated in Table 3.1.

The role of a subset of variables in explaining the variance was further explored to uphold the null hypothesis that small-scale environmental heterogeneity better explains community assemblage in *Quercus* species in Cero Grande than elevation. In CCA, the fraction of the variation explained by a set of variables (total variance explained) is the sum of all constrained eigenvalues divided by the total variation (total inertia), which is the sum of all unconstrained eigenvalues (ter Braak & Smilauer, 1998; Palmer, 2000). The results of partial ordinations are shown in Figure 3.8. In this figure, the role of small-scale environmental gradients (the physiographical set) in explaining patterns of species composition is clearly evident. This group of variables accounted for the biggest proportion of the total variance explained, almost twice as much as that explained by elevation.

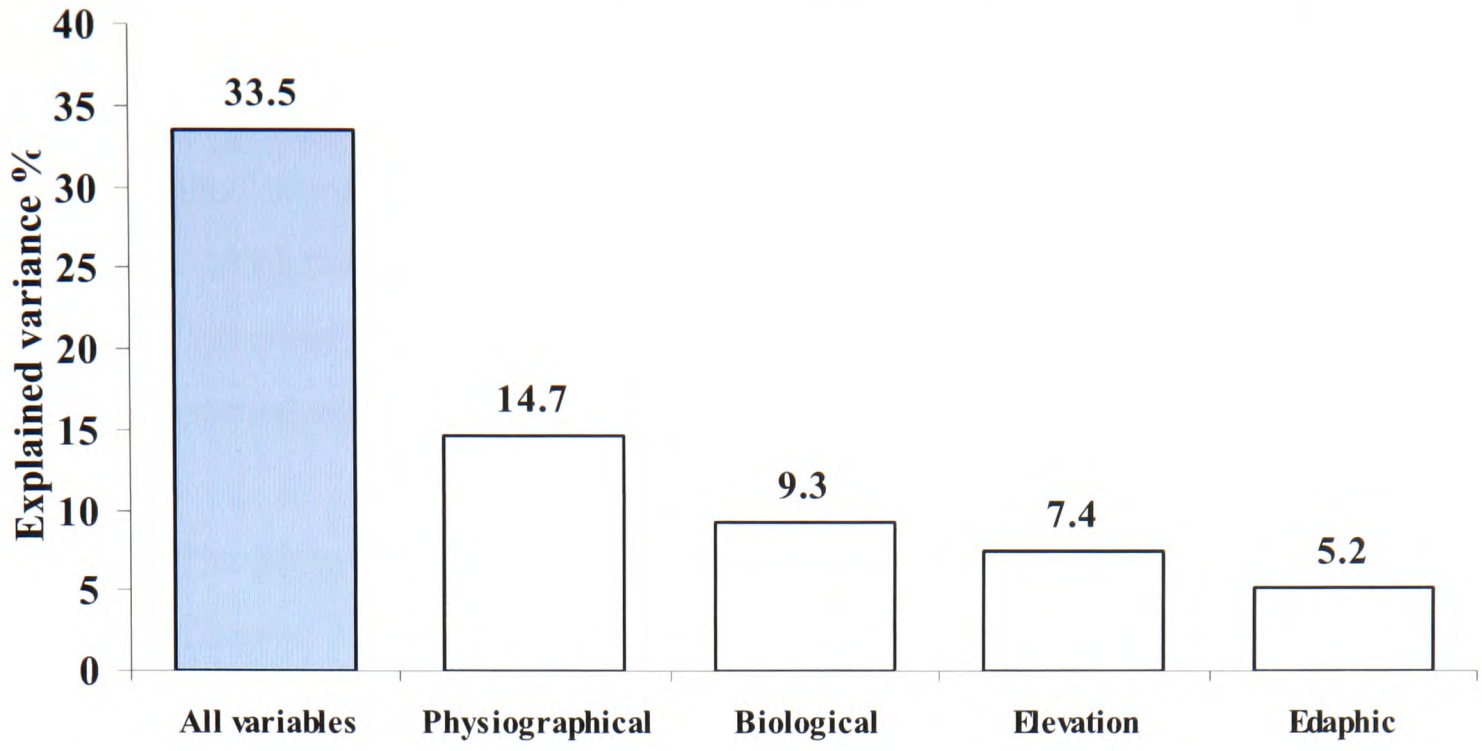


Figure 3.8 Distribution of the proportion of the variation explained by subset of variables in partial CCA ordinations. (For description of variables *see* Table 3.1).

3.5 Discussion

3.5.1 The floristic variation and patterns of species assemblage

The result presented in this chapter relate to an ongoing research project in high altitude sub-tropical mountain forests. Compared with similar investigations carried out in *Quercus* dominated forests in other latitudes Cerro Grande, at the Sierra de Manantlan, is exceptionally species-rich and perhaps unique in the number of sympatric *Quercus* species coexisting as canopy dominants. For example, Kappelle (1995) analysing pattern of distribution in mature montane *Quercus* forests along an altitudinal gradient (2000 – 3200 m a.s.l.) in Costa Rica, which represent a more tropical forest ecosystem than Cerro Grande, reported three species of *Quercus* (*Q. costaricensis, Q. seemanii* and *Q. copeyensis*), however, these group of species are not sympatrically co-occurring in the canopy. Park (2001 and 2003), investigating spatial segregation of oaks under different regimes of fire in northern Mexico also described three species of *Quercus* (*Q. sideroxylla, Q. crassifolia* and *Q. laeta*) and, although according the results of this study, the three species eventually spatially co-occur, this seem not to be common trend across his study area. Similarly, Ramírez-Marcial et al. (1998) and Quintana-Ascencio et al. (1992), in Southern Mexico, reported seven species (*Q.* aff. *acutifolia, Q.*

candicans, Q. crassifolia, Q. crispipilis, Q. laurina, Q. rugosa and *Q. skutchii*), however, the last two investigations represent a wide range of successional communities (from grassland to evergreen cloud forest) than the one in Cerro Grande, no more than two species dominates the canopy sympatrically. An explanation for the striking local diversity of *Quercus* in Cerro Grande is the combined effect of two main geographical and environmental aspects:

i. The geographical location of Cerro Grande, which as previously indicated in Chapter 2, is part of the Mexican Neovolcanic Belt, which is a transitional zone between the Nearctic and Neotropical Realms. Phytogeographical elements of these and other biotas given in Table 3.3 can be deemed as strong evidence to sustain this assumption. Phytogeographical transition zones like the study area are generally acknowledged (Marshall & Liebherr, 2000) to be populated by species that exhibit disparate vegetation patterns as well as by the presence of species unusual to the area. Furthermore, phytogeographic transition zones are thought to have a double effect on the distribution of species; they either act as a barrier to dispersal of many taxa (Aizen & Patterson III, 1990; Kappelle et al., 1992) or function as land bridges for species migration (Qian et al., 1999; Vladimirovitch Wulff, 2004) occurred during the Pleistocene (*see* Chapter 2; section 2.2.3).

ii. The multiplicity of microhabitats or habitat heterogeneity as described by Rees et al. (2000) and Stewart et al. (2000) may be an important parallel component that may foster high species diversity and thus explain *Quercus* species richness and coexistence in Cerro Grande.

A note of clarification should be made with respect to the physical surroundings of the study area. As was described in Chapter 2, the psps' locations span an altitudinal range between ca. 2020 and 2350 m a.s.l. Within this altitudinal range, soil types, micro-climate and topography seem to be relatively similar however, a highly variable micro-heterogeneity does exist, creating complex 'micro-habitats'. Therefore it is common to observe unexpected changes in catenas or aspect at short distances (*personal observation*). Conditions like this have been shown (Beatty, 1984; Sakai & Ohsawa, 1993; Collins & Battaglia, 2002) to play a fundamental role for species coexistence due to the creation of variable niches. Thus, in Cerro Grande, *Quercus* and timber allied

species sub-dividing a seemingly homogeneous area into several micro-niches, each occupied by specialised species in different environmental conditions allowing their coexistence.

Species coexistence in Cerro Grande can occur by mutualism among closely competitive species such as *Ternstroemia lineata* and some of the most abundant *Quercus* species. *T. lineata* can be widely tolerated in most of the stands because at a certain point it does not impose a high competitive cost on sympatric species even though it is a fast-growing sub-canopy species that readily occupies the available spaces in the understory, as it will be described in Chapter 5, *T. lineata* may act as canopy protector for shade-tolerant juvenile tree species, offering suitable environmental conditions for co-occurring species to grow.

3.5.2 Niche partitioning or neutrality processes?

As discussed in this and in Chapter 1, the niche paradigm maintains that species must have their own time and space if several species are to coexist, hence species coexistence is mediated by resource partitioning among highly competitive organisms (Whittaker et al., 1973). The neutral paradigm, as an opposing view, assumes that mere chance processes, along with dispersal limitation, are sufficient elements to explain patterns of floristic composition across a geographical area (Hubbell, 2001). Methodologically, NMDS and CCA are not directly comparable procedures, since the former is not an eigenvalues-based technique whilst the latter is (Palmer, 2000). However, the two approaches produced very similar results in revealing the occurrence of vegetational patterns (NMDS) and identifying those environmental variables (CCA) responsible for such patterns. The spatial distribution of psps and species shown in Figures 3.2 and 3.3, including the Map (Figure 3.4), underpin the prediction made in this chapter that community differentiation, or floristic zonation, rather than compositional drift, best explain floristic patterns and coexistence in *Quercus* forests in the study area. However, the described floristic gradients are not sharply delimited in the field since there are a number of species common to both zones, but also because there are a number of species that are not associated with a particular group, as shown in Figure 3.4. A long-standing tenet in plant ecology maintains that discrete communities exist, at least in the sense that there are areas of relatively uniform vegetation, with

more rapid changes in species composition in zones between them (Bastow & Alessandro, 2000).

Based on the results given in this chapter and supported by both experimental (Eriksson, 1995; Rebollo et al., 2001; Stoll & Prat, 2001) and empirical (Zhang & Lin, 1997; McGill, 2003; Ricklefs, 2003; Tuomisto et al., 2003b) research carried out elsewhere, it is strongly argued that, on base of the results found in this thesis, *Quercus* and allied timber species require niche-differentiation in order to coexist.

3.5.3 Environmental factors explaining patterns in species composition

The initial results suggested that elevation was one of the main factors explaining vegetation patterns. At a finer scale, other micro-environmental characteristics seem to mitigate the effect of elevation and better explain floristic patterns. McNab (1993) argued that landforms, particularly micro-topography, significantly contribute to tree species distribution since they have direct effects on humidity regimes and soil fertility. Collantes et al. (1999) have shown experimentally that variation in micro-topography promoted the establishment of *Quercus michauxxii*, arguing that habitat heterogeneity can be even more important than the surrounding canopy conditions (*e.g.* canopy openness) for seedling establishment. These findings seem to contradict a number of investigations (Wang et al., 1992; Clinton & Boring, 1994; Keller & Hix, 1999; Nagamatsu et al., 2002; Hirayama & Sakimoto, 2003), particularly in Mexican *Quercus* forests (Quintana-Ascencio et al., 1992) stressing the importance of the canopy component on seedling species composition. Based on the results found in this thesis, it is argued that habitat heterogeneity is fundamental for species coexistence as discussed above. Thus, the combined effects of catena variation, aspect and soil fertility in Cerro Grande explain the maintenance of species richness of *Quercus*. It has been widely demonstrated that in mountainous areas vegetation may change with changes slope inclination (Fekedulegn et al., 2003). Thus, the relationship between vegetation and slope position has been attributed to differences in soil fertility and soil moisture (Hirayama & Sakimoto, 2003) which are important elements for species establishment. Nowacki & Abrams (1991) attribute changes in species composition patterns in oak forests to differences in soil-site conditions, but argue that complex gradients typically exist over the landscape making it difficult to determine exactly which factors are the

most important. Hence, the ability to segregate individual environmental gradients and quantify their true influence on plant distribution can be complicated.

There is a good amount of scientific evidence that show that species significantly diverge in habitat requirements which in turn impact the structure and functioning of forest ecosystems. Based on the results found in this thesis the amount of organic matter content (OMC) seems to be an important factor that explain the spatial patterns of floristic distribution in Cerro Grande. OMC is a long-lasting element of edaphic properties and it is directly related to physical-chemical soil properties. It has been observed (Rice & Nagy, 2000; Danner & Knapp, 2001) that OMC has a significant effect on seedling establishment in *Quercus* since it provides nutrients for their establishment and is critical during the early stages of development. Thus, in spite of the results obtained in CCA ordination (Figure 3.6 and 3.7 and Table 3.5) in the long-term, the content of OMC in the soil may have an important effect on species composition, mainly at earlier stages of development; for example Carvell & Tryon (1961) found that litter depth had a strong impact on seedling establishment in *Quercus* since it reduces water losses and equalises soil temperature.

3.6 Conclusions

The data analysed in this chapter support the hypothesis that niche differentiation rather than compositional drift explains species diversity, species coexistence and floristic patterns of assemblage in *Quercus*-dominated forests in Cerro Grande, Sierra de Manantlan.

The floristic patterns extracted by NMDS are, to a certain extent, visible in the field. Xeric gradients of the larger and homogeneous physiographic units, gently sloping terrain and more exposure to solar radiation tend to be less species-rich than those locations that are more humid and have more complex physiography.

The combined results of NMDS and CCA revealed that niche partitioning seems to explain species diversity and coexistence in Cerro Grande and therefore to community differentiation. This seems to contradict a generalised belief that local communities

growing in similar environmental conditions should have similar community composition. Thus, the view that species composition follows compositional drift, as Hubbell (2001) recently implied, does not hold for this group of sympatric species.

As stated previously, at a first level of analysis elevation was one of the main contributing environmental variables in explaining vegetation patterns in Cerro Grande. In this thesis elevation *per se* is regarded an abiotic factor which is insufficient to explain patterns in species distribution as a number of ecological investigations imply. At finer scales within the same altitudinal range micro-environmental gradients such as variations in catena position, sun-aspect or slope may better explain species divergence.

From a methodological point of view, it is common to exclude infrequent species (*e.g.* fewer than 5% of the total in the data) (Acharya et al., 2000; Goodsell & Connell, 2002) in order to perform reliable ordinations. In this thesis, no convincing evidence was found to claim that rare (*C. tropicalis, B. parviflora*, etc.) or abundant (*T. lineata, Q. crassipes*) species had a significant impacted on the statistical or the graphical results of indirect ordinations (NMDS). Furthermore, when analysing the complete data set, this approach provided a better overview of vegetational patterns and thus a better overall understanding of the community assemblage.

CHAPTER 4 - Forest succession and long-term patterns of change

4.1 Introduction

This chapter describes patterns and processes of secondary forest succession in mixed oak forests. To develop this chapter, only the adult communities (individuals ≥ 5 cm dbh and 1.3 m ≥ tall) were taken into account. The chapter is organised as follows: In the first part the dynamics of forest succession is investigated; this includes determining how forest succession unfolds across three relatively different vegetation types and environments and over three time scales. The rate of change at which succession occurs was subsequently investigated. Further analyses concerning the structural modifications that take place during succession are made. The chapter concludes with an analysis of mortality and recruitment and the role of both processes in the dynamics of forest succession.

4.1.1 Background

It has long been recognised that forests are not static, but that their composition and structure is continually changing as a consequence of both natural development as well as a result of forest disturbances such as fire, cattle grazing, windthrow, harvesting and climatic change (Spurr, 1952). Successive changes in vegetation mainly after a major disturbance have long been recognised by ecologists as one of the most important components of forest stand dynamics (Carøe et al., 2000), which has been explained under wide range of perspectives. For instance, early interpretations (Horn, 1975) of stand dynamics processes as a results of natural or human-induced disturbances was that, after a major perturbation one or few species invaded a disturbed area and predominated; as these species once established altered the environment, trigger the opportunity for other species to invade which, in turn, achieve dominance, alter the environment, and allow other species to invade and eventually predominate. This progressive replacement of species has been referred to as *forest succession* which, more recently Oliver & Larson (1996), describes to occur into four stages: (*i*) *Stand initiation stage*: After a disturbance, new individuals and species continue to appear for

several years; (*ii*) *Stem exclusion stage*: After several years, new individuals do not appear and some of the existing ones die. The surviving ones grow larger and express differences in height and diameter; first one species and then another may appear to dominate the stand; (*iii*) *Understory reinitiation stage*: Later, forest floor herbs and shrubs and advance regeneration again appear and survive in the understory, although they grow very little; (*iv*) *Old growth stage*: Much latter, overstory trees die in an irregular fashion, and some of the understory trees begin growing to the overstory.

Succession, a synonym for community change in composition and structure (Horn, 1975; Myster & Pickett, 1994; Oliver & Larson, 1996), is a central issue in forest ecology and silviculture as it represents patterns of replacement of species over time (Walker & del Moral, 2003). Odum (1969) summarised successional processes in terms of three parameters: (*i*) It is an orderly process of community development that is reasonably directional and predictable; (*ii*) It results from modification of the physical environment by the community; that is succession is community-controlled even though the physical environment determines the pattern, the rate of change, and often sets limits as to how far development can go; (*iii*) It culminates in a stable ecosystem in which maximum biomass and symbiotic functions between organisms are maintained per unit of available energy flow.

Alternatively, a cyclic model of succession was first proposed by Watt (1947) for describing a plant community as a working mechanism that upholds and regenerates itself with a predictable end phase. Recent models not only accept that successional processes are stochastic (Wilson et al., 1996; Battles et al., 2003) but strongly maintain that they are unstable and dependent on both internal and external modifying factors such as competition and disturbance (Rogers & Hartnett, 2001; Jentsch & Beyschlag, 2003), which can eventually alter the course of a successional trend.

The dynamics of succession therefore, should be understood so that these processes can be adequately considered in the management of forest ecosystems (Guariguata & Ostertag, 2001), particularly in the design of silvicultural alternatives of management. Despite the fact that past as well as contemporary ideas of forest succession can be extrapolated to describe general processes that occur in forest ecosystems, particular situations of many local forest communities that contain unique species associations still

need to be explained. In western Mexico the mechanisms of successional processes are still poorly understood in most *Quercus* forest and almost no long-term studies have been carried out in them.

The objectives of this chapter were: (**1**) to investigate the dynamics of successional trends. The rate at which this event occurs across three relatively different vegetation types using data collected over periods of 4, 8 and 11 years; (**2**) to investigate whether changes in each type of vegetation are accompanied by changes in species abundance, dominance or by changes in structure and; (**3**) to identify patterns of mortality and recruitment and their roles in the successional dynamics of *Quercus*-dominated forest ecosystems.

4.1.2 Hypotheses to be tested

Ho_1. A steady and unidirectional successional trend occurs over time in *Quercus*-dominated forest communities.

Ho_2. Successional trends are determined by the canopy dominant *Quercus* species.

Ho_3. Species dominance rather than abundance promotes the most obvious structural modifications.

Ho_4. There is a balance between the processes of mortality and recruitment and hence these are not sources of community modification or successional processes.

4.2 Research methods

4.2.1 Data description and processing

Because the sampling design (described in Chapter 2) aimed to capture the whole range of floristic variation, sampling periods and the number of plots established and re-measured varied. As a result, the database is fragmentary and had to be handled carefully for statistical analyses. Since one of the main objectives of this chapter is to investigate stand dynamics, successional processes and rates of successional change over time, paired records were necessary for making comparisons from an initial to a later condition. This approach, permits the drawing of conclusions for equal time-scales,

and also allows description of forest dynamics and successional processes over relatively contrasting vegetation types. Thus, the database used in this Chapter was partitioned into three floristic groups as shown in Table 4.1. The plot grouping presented in this table, apart from representing the successive times of measurement also show the spatial and, more importantly, the floristic, ecological and environmental differences of the places where they were established.

As describe in Chapter 2, the three groups of plots differ from each other as follows: One group was established across a relatively species-poor and xeric zone. Stands in it are represented by three or four different species at most, but most are dominated by *Quercus crassipes.* This group was called *Quercus crassipes* (Qc). The species contained in it are of lower stature and smaller diameters than those growing in the wet zone. In general, the physiography is gentle, soil are shallow and the relative humidity is low. The second group was established across the most species-rich areas (*see* Chapter 2 for sampling design methodology). They contain to mountainous mesophytic (Mm) vegetation (*sensu* Rzedowski, 1978), floristically representing the most heterogeneous stands and contain the biggest proportion of shade tolerant species. These are stands of irregular diameter structures and have trees with the biggest mean diameters and heights. Environmentally, this is the wettest zone across Cerro Grande with the most complex physiography and includes deepest organic soils. Most of the plots were established within one of the core zones of the SMBR. Finally, a third group was established across a zone that had intermediate floristic and environmental characteristics and was considered to be a intermediate (It) between the other two vegetation zones. The idea of establishing the psps across environmentally distinct vegetational zones was aiming at capturing the complete range of floristic and environmental variation found in the study area.

Not all the permanent sample plots were re-measured over the various sampling periods (*see* Chapter 2: section 2.3.1), so that for some plots in each zonwe data is missing. To avoid confusion between the initial number of plots established in each period and the number of plots inventoried or established at different times, they are referred to henceforth by the names of the; *Quercus crassipes* zone (Qc), Mountain mesophytic zone (Mm), and Intermediate zone (It) corresponding to periods of 11 (1991-2002), 8 (1994-2002) and 4 (1998-2002) years since establishment respectively.

Table 4.1. Floristic and chronosequence-based data structure in relation to number of plots per group, number of inventories in each group and years since establishment. (.) Indicates continuity of data available; (-) indicates data not available; **Nt** indicates number of trees in the plot; **Ni** indicates number of inventories in each plot.

Plot	Nt	Year of Forest Inventory				Ni.	Time scale(yrs)
		1991	1994	1998	2002		
		Mean diameter (cm)					
1	**46**	**33.5**	**35.6**	**-**	**39.1**	**3**	**11**
2	**66**	26.6	27.7	-	29.8	3	11
3	82	15.6	16.1	-	18.3	3	11
.	.	.	.	-	.	.	.
.	.	.	.	-	.	.	.
.	.	.	.	-	.	.	.
31	.	66.7	68.9	-	70.1	3	11
32	**39**	**45.6**	**47.1**	**-**	**49.4**	**3**	**11**
33	**75**	**-**	**23.4**	**-**	**25.5**	**2**	**8**
34	69	-	18.7	-	19.5	2	8
34	87	-	33.4	-	35.4	2	8
.	.	-	.	-	.	.	.
.	.	-	.	-	.	.	.
.	.	-	.	-	.	.	.
59	71	-	23.4	-	24.8	2	8
60	**40**	**-**	**60.6**	**-**	**61.9**	**2**	**8**
61	**58**	**-**	**-**	**56.7**	**58.0**	**2**	**4**
62	91	-	-	46.4	46.9	2	4
63	70	-	-	65.1	66.0	2	4
.	.	-	-	.	.	.	.
.	.	-	-	.	.	.	.
.	.	-	-	.	.	.	.
104	75.	-	-	35.6	38.6	2	4
105	**88**	**-**	**-**	**17.5**	**18.1**	**2**	**4**

Quercus crassipes Zone ***n* = 32** plots

Mountain mesophytic Zone ***n* = 28** plots

Intermediate Zone ***n* = 45** plots

Definitions

Because of the continual use of the terms "successional trends" and "turnover" in this chapter it was thought important to put them into context. The terms can be confusing since they are frequently used to describe different aspects in community ecology (Van Andel et al., 1993). Turnover is perhaps the more widely used of the two expressions. For example, Kneeshaw & Bergeron (1998) and Berlin et al. (2000) use 'turnover' to describe patterns of change in species composition across gradients. Whittaker (1972) named this 'beta diversity' defining it as 'the extent of differentiation of communities along habitat gradients'. In contrast Phillips & Gentry (1994); Sheil (1995) and more recently Condit et al. (1999) apply the term 'turnover' to assess the dynamics of mortality and recruitment (ingrowth), but not necessarily for describing patterns of beta diversity. Furthermore, it would be most useful to distinguish between turnover of

species and turnover of individuals. 'Species turnover' occurs when one species replaces another. This could either be at a single site, over time or along a gradient at a single time. 'Individual turnover' occurs when one individual replaces another. The extent of individual turnover can be calculated from mortality and recruitment data, and this can only be at a single site over time (N. Brown, *per. com.*). Throughout this thesis, 'successional trends' is used when describing changes or patterns of change in vegetation over time; while 'individual turnover' is used to depict the dynamics of mortality and recruitment.

4.3 Data analyses

4.3.1 Successional trends and rates of change

Detrended Correspondence Analysis

Detrended Correspondence Analysis (DCA) provides an explicit approach for developing a 'best-fit' model of composition successional trends (Sheil, 1999a) and for portraying directional trends in forest succession (Halpern, 1988). DCA is an indirect, eigenanalysis-based ordination method that uses reciprocal averaging or correspondence analysis (Hill & Gauch, 1980). In general, DCA is used to assist in organising samples in multidimensional space on the basis of differences in species composition or any other attribute derived from vegetation data (*see for instance*: Woods, 1984; Kearseley, 1999; Ewing, 2000; Martens et al., 2001). Therefore, when DCA is used as a measure of floristic changes over time, the location of samples from the same geographical site but collected on different occasions can be compared graphically by drawing time-line trajectories of the sample's change in position between periods, or by drawing envelope lines that enclose a group of samples from the same observational period. Such diagrams give an impression of the relative rate of, for instance, species migration or sample displacement over the ordination diagram that can be due to changes in species composition or due to an increase or decrease in individual species' abundance or dominance (Cramer & Hytteborn, 1987). Since the lengths of the axes produced by DCA are a direct measure of variation, this is one of the most widely used multivariate methods for the estimation of changes in vegetation. The technique is fundamentally

different from any other indirect ordination method, such as non-metric multidimensional scaling (NMDS), because in DCA the magnitude of change is a direct measure, in standard deviation units, given by the relative position of the samples in the ordination space. Hence, in DCA the axes can be divided into segments of equal beta diversity and the average importance of each species along each segment is thus calculated. The fixed beta diversity of each segment allows for comparison between gradients and between data sets (Økland, 1986a).

Successional trends

Under the hypothesis that successional dynamics, including the trend and rate of change, are a function of canopy dominant species in mixed-oak forests in Cerro Grande, then psps with analogous floristic structures should migrate in the same direction and at similar rates across the DCA ordination diagram. Therefore, to describe the trajectory followed by psps over time (convergence or divergence) as a measure of successional trends, a number of DCA ordinations were run on abundance and dominance data. The goal for using two different measures of ecological similarity was to capture different perspectives of vegetation change and thus discover which parameter revealed the most change.

To carry out the DCA ordinations a single data matrix was produced by groups of psps (It, Mm and Qc respectively) in which all the psps and periods of observation within groups were simultaneously analysed (*e.g.* 1991→1994 →2002; 1994→2002 and 1998→2002). The object was to track the development of psps over time (Whittaker, 1991) as well as to discover whether comparable successional trends occur in floristically similar plots. This approach generated sample scores for each re-sampling period. The scores were then used to calculate the rate of change in individual psps. Numerically, the sample scores assisted in ascertaining the magnitude of change of each psp as well as in discovering the direction of succession over the range of forest conditions sampled.

While computing the DCA ordinations all species found within the plots were included, but standard procedures of down-weighting infrequent species and detrending by segments (Palmer, 2000) (both options available in CANOCO v.4) were implemented.

To minimise the effects of abundant species, all data matrixes were log-transformed as recommended by ter Braak (1995). To test for DCA sample score differences between time intervals, the non-parametric Wilcoxon's test (Sokal & Rohlf, 1981) using SPSS v.12 was performed. This test resembles the *t*-test for paired samples, but it is used with non-parametric data such as the sample scores produced by DCA.

Rate of change

According to Whittaker (1991) the simplest expression of change in ordination space is the individual site movement within a DCA-biplot. Thus, to calculate the magnitude of vegetation change in abundance and dominance by a psp, its net movement was estimated by subtracting the sample score produced at time t_0 (the initial time) from that at t_{+1} (the final time). This estimate was undertaken using the sample scores of the first two axes, providing a direct measure of the rate of change over time. Then, 95% confidence intervals were calculated (SPSS, 2003) to give an estimate of the mean rate of change in standard units.

4.3.2 Community and population structural differentiation

In community ecology three statistics are commonly used as diameter size-structure descriptors: 1) the coefficient of variation, 2) the skewness coefficient and 3) the Gini coefficient (Arenas & Fernández, 2000). Weiner & Solbring (1984) and Bendel et al. (1989) reviewed the effectiveness of these estimators as measures of size-structure in biological communities concluding that the Gini coefficient is the least biased and most sensitive for detecting subtle structural changes. The Gini coefficient, *G*, is an index often used by economists to describe the inequality in the distribution of wealth in human societies (Gastwirth, 1972) but it has recently gained an important place in plant ecology. Mathematically, *G* is based on the Lorenz curve, a cumulative frequency curve that compares the distribution of a specific variable with the uniform distribution that represents equality (Weiner & Thomas, 1986).

G ranges from 0 to 1; 0 represents perfect equality and 1 total inequality. There are several ways to compute *G*; in this thesis *G* was calculated using individual tree diameter data at both community and populations levels (Dixon, 2001):

$$G = \frac{\sum_{i=1}^{n}(2i - n - 1)X_i}{(n-1)\sum_{i=1}^{n} X_i} \qquad 4.1$$

Where: n = number of individual trees in the sample; X_i is the size (diameter) of the ith tree, when trees are sorted from smallest to largest, $X_1 \leq X_2 \leq ....\leq X_n$; i represents the diameter of an individual tree.

The skewness coefficient (Sk) was computed following the standard procedures included in SPSS v12. The coefficient of variation was not calculated since it is an inappropriate statistic to measure the relative structural variation of ecological communities (Weiner & Thomas, 1986).

4.3.3 Turnover patterns

Mortality

To determine the role that tree mortality plays in the successional dynamics of *Quercus* communities in Cerro Grande, first a straightforward count of dead stems, by plot, species and sampling period, was carried out. Then, to establish whether there is a consistent pattern of mortality by species and diameter class, a cross-tabulation contingency table was produced (SPSS, 2003). A Pearson chi-squared test of independence (Krebs, 1999) was subsequently performed to test the null hypothesis that tree species mortality follows a random path and hence is independent of diameter class. The Pearson chi-squared test of homogeneity of distribution tests the null hypothesis that there is no difference in the proportions of individuals in a set of mutually exclusive categories between two or more populations (Garson & Moser, 1995).

Then, absolute mortality counts were converted into annual rates using a logarithmic model (Sheil et al., 1995b):

$$m = (\log_e No - \log_e Ni)/t \qquad 4.2$$

Where: *m* is the mortality rate, No is the number of living trees at time 0 - first forest inventory -, Ni is the number of survivors at time t_{+1} - a subsequent forest inventory - *t* is the time interval between two surveys (years).

The use of this equation minimises bias derived from dissimilar re-sampling periods and ultimately allows direct comparisons of rates of mortality amongst species, across periods of sampling.

Recruitment

To investigate the relative contribution of the patterns of recruitment by the different species in the successional dynamics of *Quercus* communities, a similar approach was used to that followed for mortality. Thus, a direct count of absolute recruitment by plot and species across sampling periods was first carried out. Then, in order to relate patterns of recruitment to patterns of mortality, a logarithmic model (Condit et al., 1999) was used to extrapolate the absolute recruitment counts into annual rates:

$$r = \frac{\ln n_t - \ln S_t}{t} \qquad 4.3$$

Where: *r* is the recruitment rate, n_t is the population at time t, S_t is the number of survivors at time t_{+1}.

Mortality-Recruitment cross-comparisons

The resulting annualised rate of mortality was plotted against the annualised rate of recruitment, by species and by chronosequence-based groups of plots (It, Mm and Qc) in order to determine whether there is a balance between these two processes. For this purpose, an *x-y* diagram similar to that produced by Swaine et al. (1987) was plotted. The annualised rate of mortality (on the *x* axis) was compared with the annualised rate of recruitment (on the *y* axis). Then, the overall mean mortality was calculated and represented by a dashed line on the *x-y* diagram. In the same graph, starting from the origin, a solid line was plotted assuming that both mortality and recruitment are equal, so that all those species along the solid line represented a balance.

4.4 Results

4.4.1 The dynamics of successional trends

Tables 4.2 and 4.3 and Figure 4.1a-f illustrate the DCA ordination results for the time-series data summarised in Table 4.1. To carry out a more pragmatic description of the results and at the same time to facilitate their further discussion, the dynamics of succession and the extent to which this mechanism develops over time in mixed-oak forests in Cerro Grande are described at two organizational levels: a) successional changes that occur at community level, defined as the vegetational changes derived from the same group (It, Mm, and Qc) and; b) within group, floristic changes that occur at plot level.

Judged by the extent an individual plot was displaced over the ordination diagram between two sampling periods, it was found that at least three major successional patterns are evident: *i*) a dynamic successional tendency of change exhibited by plots that had a striking degree of separation between periods of observation, accompanied by a stochastic migration over the ordination diagram; *ii*) plots that revealed a modest rate of change and uniform movement across the ordination space and; *iii*) a small number of plots that changed very little over time which seemingly followed the same route of migration. A few of them showed no changes over time.

Community successional trends

The scaling of the DCA units is such that 4.0 standard deviations (std) correspond approximately to the distance over which a species appears, rises to its mode, and disappears again. Thus, two psps at the extremes of the axes each with separation greater than 4.0 std deviations will, theoretically, have no species in common (Whittaker, 1991). It follows that a plot in which there is a gradual vegetational change should display an ongoing displacement over the ordination diagram or stay in the same position over time as long as no floristic changes had occurred over time. DCA results for the two "importance" indices (abundance and dominance) and the three groups (It, Mm and Qc) showed that most of the gradient lengths on axis-1 were nearly 4.0 std units, except for Group It which exceeded this value. Likewise, along axis-2 most of the

gradient lengths were greater than 2.5 std units with eigenvalues from 0.1811 to 0.3376 (Table 4.2). These results correspond to a nearly entire beta-diversity range embodied across both ordination axes (Økland, 1986c; Kent & Coker, 1998).

The eigenvalues and total inertia by group of years (plots) and type of data showed little variation (Table 4.2) between periods of observation, suggesting that modest overall community changes had occurred over time. These results were, to a certain extent, expected since the time-span of observation was relatively short, particularly for the It group. Besides, the three groups of psps are floristically very similar (H' 1.406 for the Qc group; H' 1.516 for the Mm group and H' 1.702 for the It group) (H' - Shannon's diversity index $H' = - \Sigma_{Pi} * \ln_{Pi}$ (McCune & Mefford, 1999)) most are composed of slow-growth species expressing little variation in either abundance or dominance data.

Table 4.2. DCA eigenvalues for abundance and dominance data for the three time-scales analysed.

Group	Variable	Eigenvalues Axes 1	2	3	4	Total Inertia
Qc						
	Abundance	0.6925	0.1871	0.1067	0.0553	2.072
	Dominance	0.6582	0.1811	0.1171	0.0608	2.113
Mm						
	Abundance	0.5987	0.2478	0.0739	0.0359	2.054
	Dominance	0.5480	0.2838	0.1003	0.0434	2.088
It						
	Abundance	0.8099	0.3376	0.2436	0.1556	2.098
	Dominance	0.7696	0.3098	0.1992	0.1517	2.095

Within groups, the Wilcoxon's signed-rank test indicated no significant differences in the sample scores, except for the Mm group for both types of data analysed and, for the Qc group in axis 2 for the dominance data (Table 4.3). These results are interpreted as a strong indication that non-significant successional changes at community level had occurred since 1991, when the first group of plots was established.

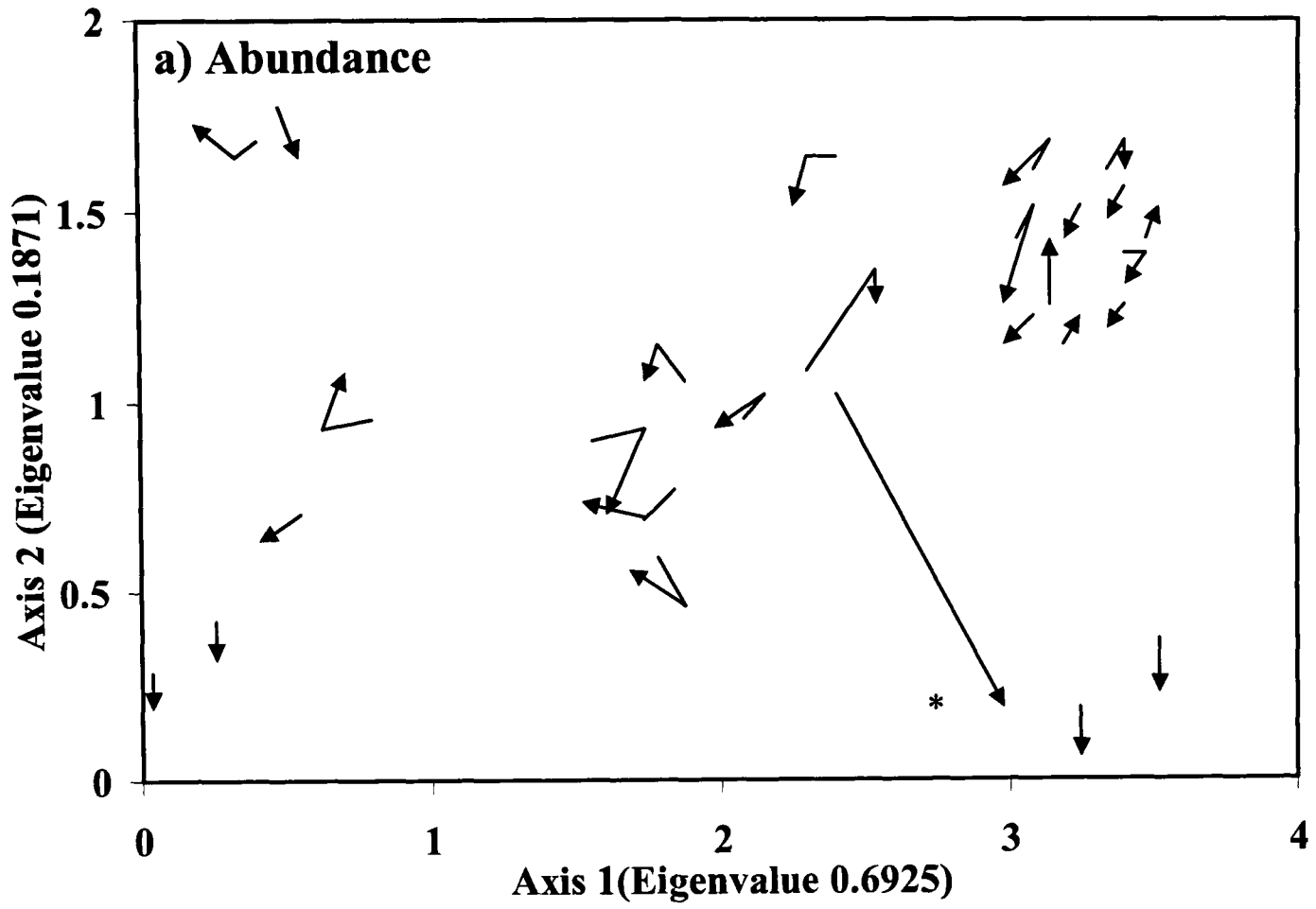
Table 4.3. Wilcoxon's signed-ranks test of DCA sample scores contrasting two consecutive observations (p <0.05). Bold figure indicate significant differences between periods.

			Axis-1		Axis-2	
Group	Variable	Period	*z*	*p*	*z*	*p*
Qc						
	Abundance	1991-1994	-1.057	0.290	-0.730	0.465
		1991-2002	-1.249	0.212	-1.946	0.052
	Dominance	1991-1994	-0.432	0.665	-2.511	**0.012**
		1991-2002	-0.841	0.400	-0.408	0.683
Mm						
	Abundance	1994-2002	-2.817	**0.005**	-2.911	**0.004**
	Dominance	1994-2002	-1.965	**0.049**	-2.462	**0.014**
It						
	Abundance	1998-2002	-1.411	0.158	-0.566	0.572
	Dominance	1998-2002	-0.203	0.839	-1.893	0.058

The fact that the Mm group was statistically different in both abundance and dominance is attributed to its greater variation in species composition. Therefore, potentially, it should vary more for these two parameters than the Qc year group. If contrasted to the It group, which was the richest in terms of species, it was assumed to be an effect of the longer observational period (8 versus 4 years) and the relatively small differences in species richness between these two groups.

Within-group successional trends

In Figures 4.1a-f, the direction of a vector symbolises an individual plot's migration over the DCA ordination diagram according to successional changes in either abundance or dominance, the length is proportional to the rate of change over time (described in the next section of this chapter). In this group of figures it is clearly evident that not all the psps follow a neither unidirectional successional trajectory, nor do they have equivalent rates of change as was hypothesised (Ho_1) earlier. Stochastic successional pathways accompanied by variable rates of change are rather noticeable in the three groups of plots analysed. This pattern is most evident in the Qc group (Figure 4.1a), which has three periods of observation and had the longest observational time-span. Most discernibly in the It and Qc groups, a number of plots have similar alignments to each other, but point in opposite directions. Vector lengths are about the same in size, suggesting that in this group of plots the dynamic of successional processes are explainable by contrasting mechanisms, in which alternate patterns of either abundance or dominance may be the responsible factors of such alignment and pointing directions.



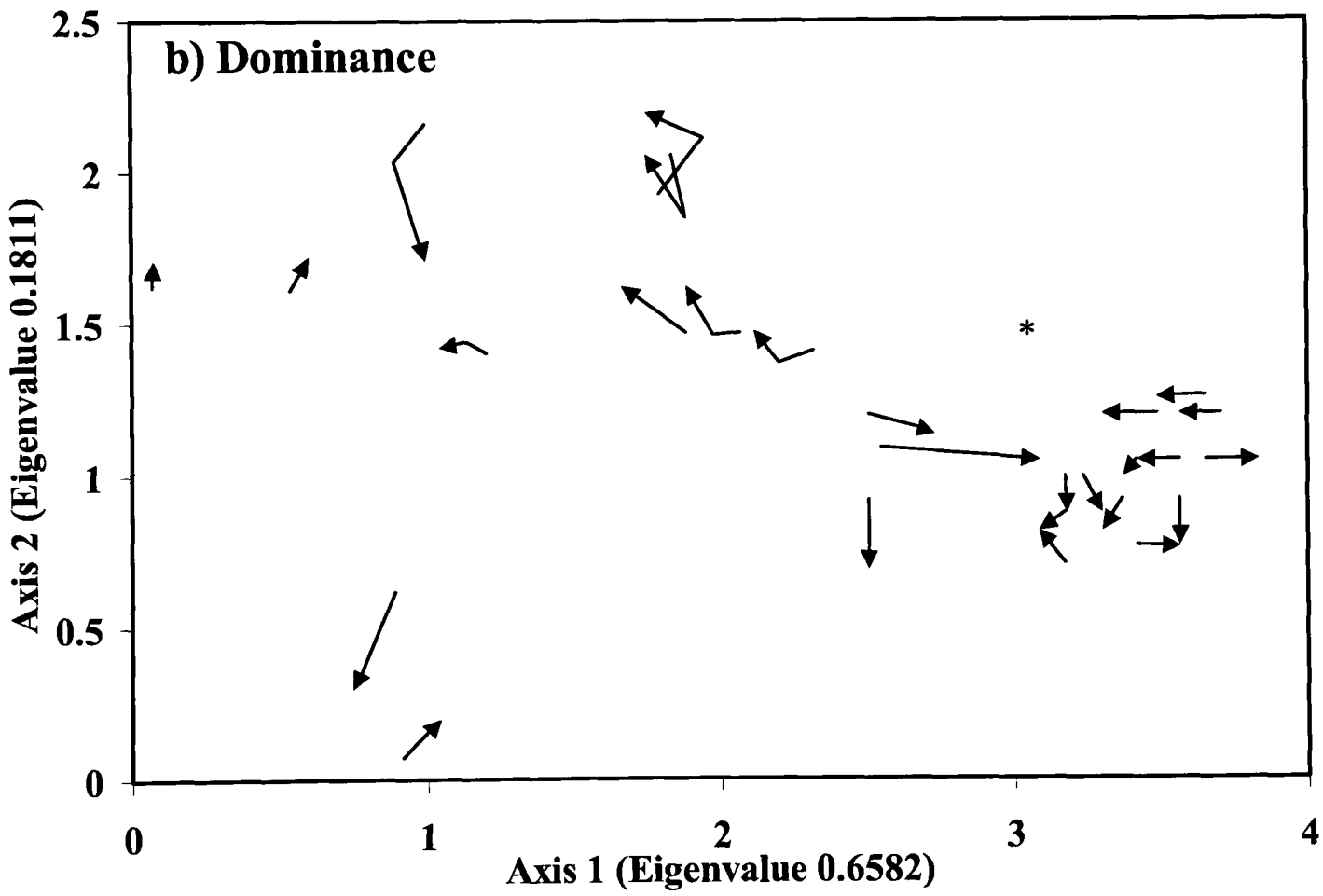
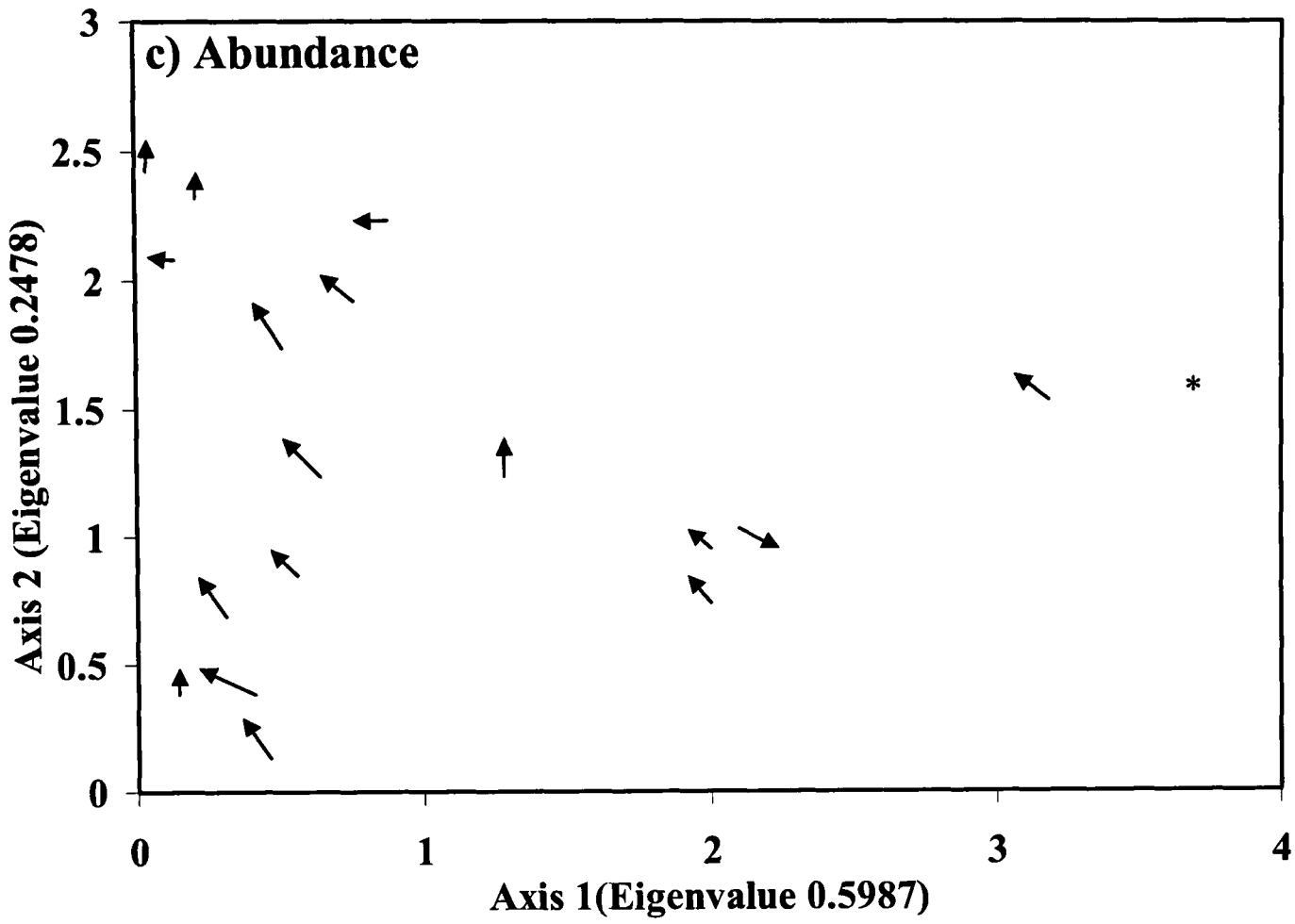


Figure 4.1. Plot trajectories as described by Detrended Correspondence Analyses for the: **a-b**) Group Qc-11 years; (next pages) **c-d**) Group Mm-8 years and **e-f**) Group It-4 years psps respectively. Lines connect initial to final plot position for successive sequences. Arrow directions and their lengths indicate plot migrations and the rate of change respectively. Asterisks indicate plots that did not change over time. Species composition, dominance and H' of the plots are given in appendix 4.2.



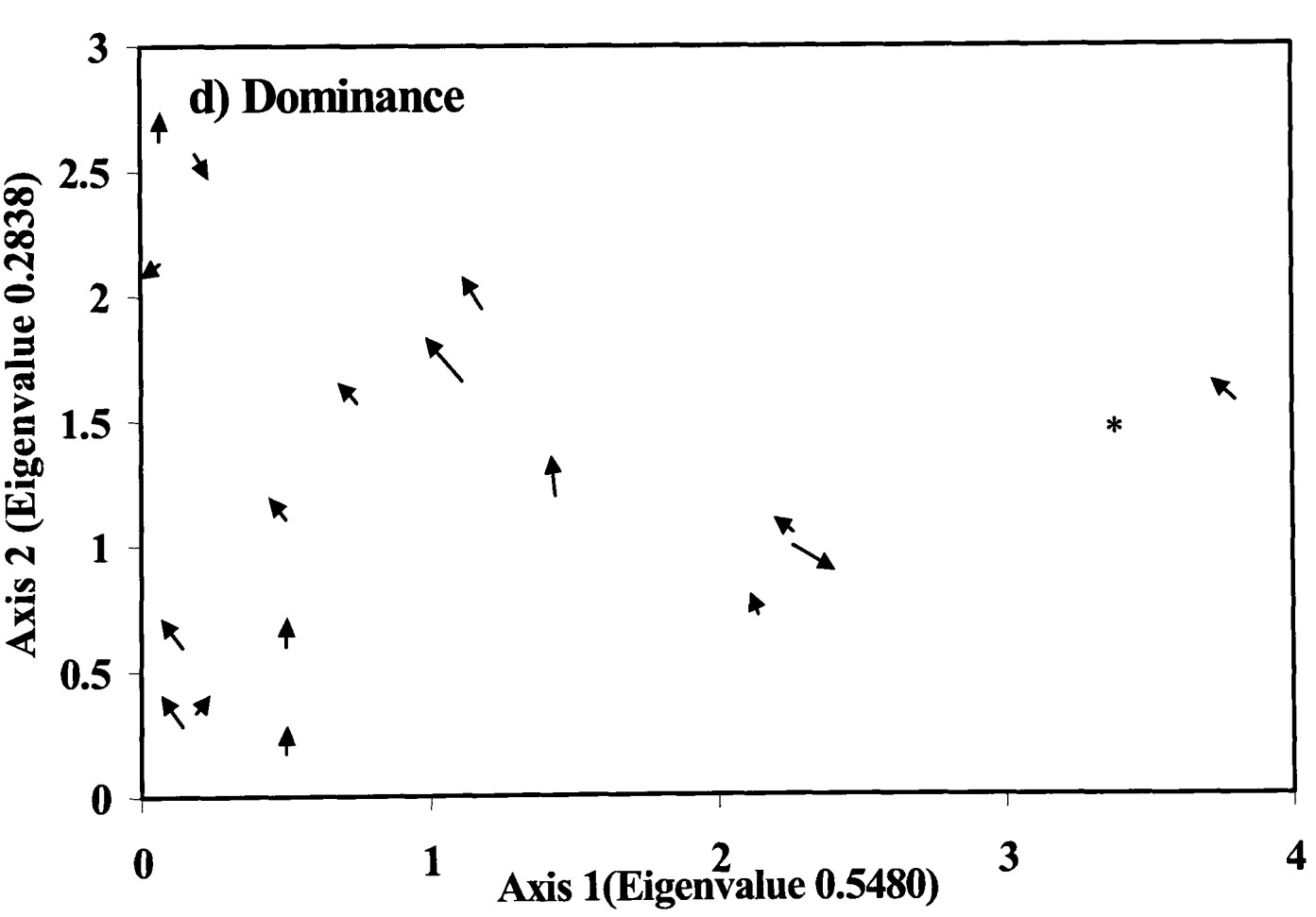
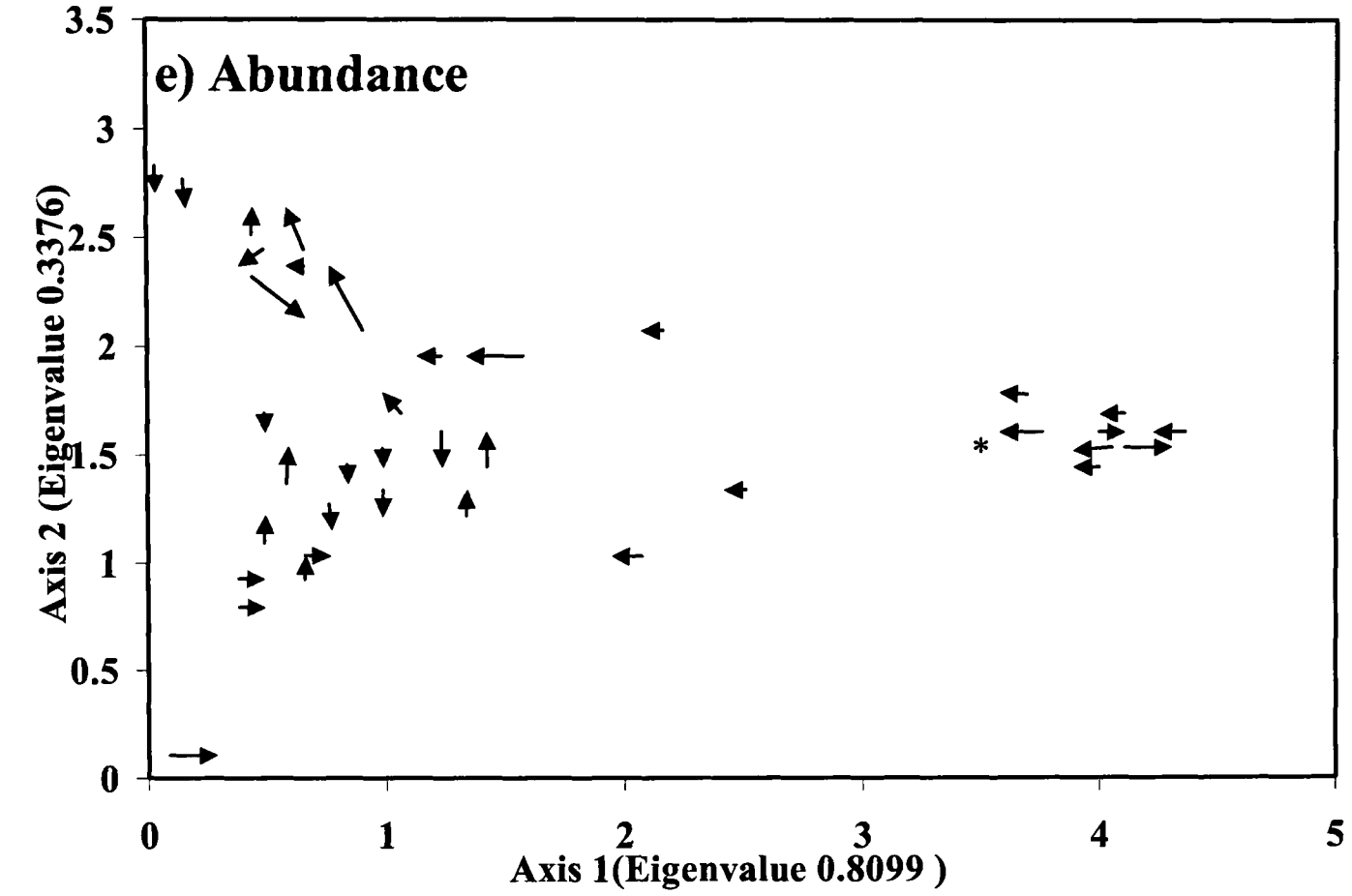


Figure 4.1c-d (*Continued*).



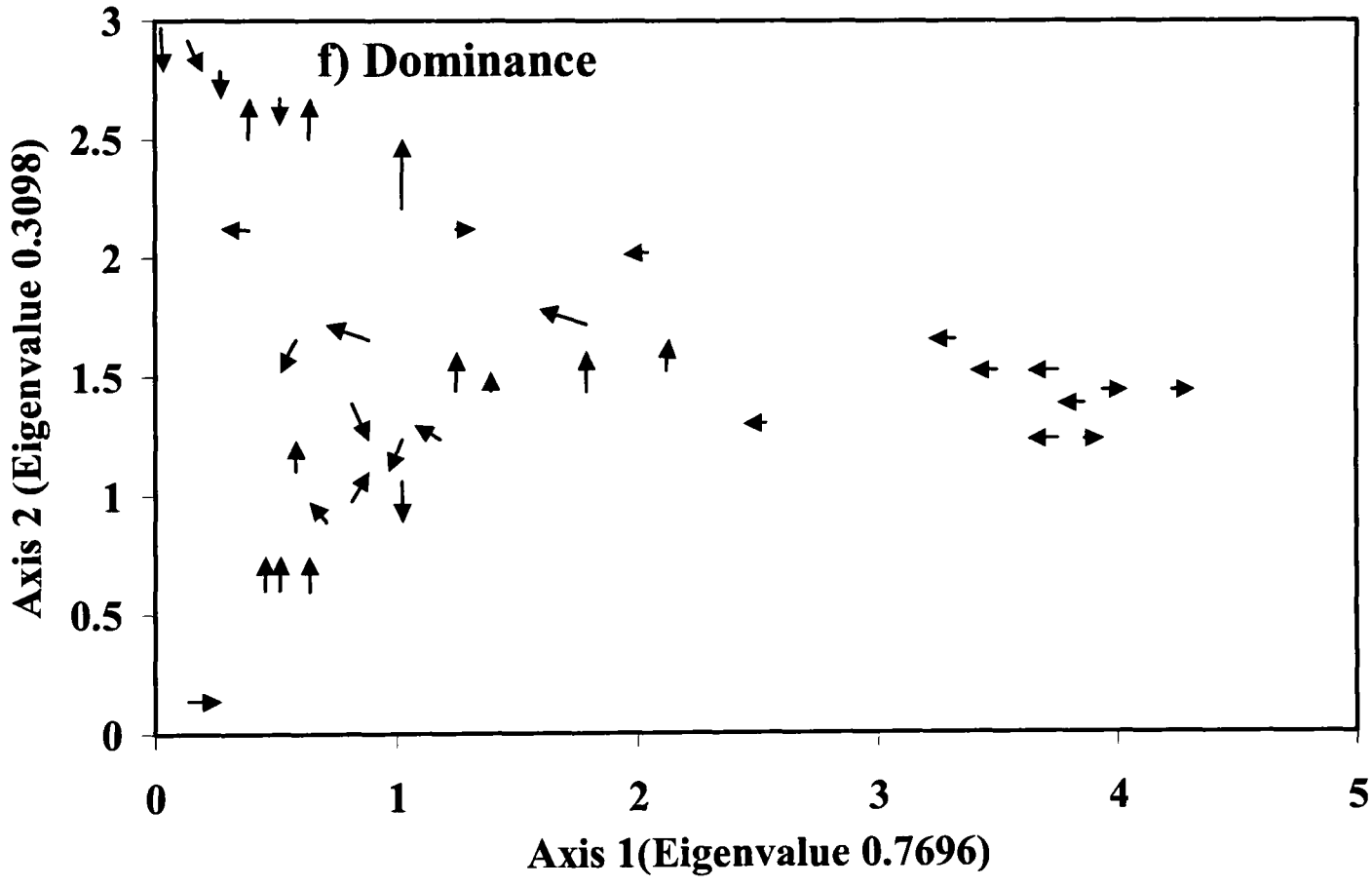


Figure 4.1e-f (*Continued*).

Theoretically, given the relatively similar micro-environmental conditions in the study area, mainly in terms of aspect, slope and catenas (Table 4.4), successional trends and the rate at which this process occurs should be relatively similar among psps. This ought to hold, at least in all those plots that are floristically similar and located in analogous environmental conditions. Fulton & Harcombe (2002) argued that community changes may be visualised as a vector field in a space, where each vector points from an initial to a final community composition after a fixed time period. If community changes are predictable, then any pair of vegetation patches with similar species compositions and located in comparable environments should follow analogous trajectories and magnitudes of successional change (McCune & Allen, 1984). Interestingly, the results in this thesis showed that in spite of the fact that a number of plots had comparable movements, suggested by the length and direction of the arrows, (especially in the It and Mm group, Figures 4.1c-f), the overall within-group trajectories show that most plots experience a rather stochastic migration in the DCA ordination diagram.

Furthermore, the spatial distribution of most of the psps gave the appearance of being randomly distributed over the DCA ordination diagram. This was particularly evident in the Mm group particularly when analysing the dominance data (Figure 4.1d). In the It and Qc groups some slight patterns were evident. For example, a closer look at the Qc group shows that a number of psps are positioned on the upper right side of the DCA diagram along axis 1 (Fig. 4.1a). Another group of plots are randomly positioned along axis 2; but a small number tends to overlap as indicated by the small arrows in these figures. The data for the It group (Figure 4.1e) repeated a similar pattern. Overall results showed in Figures 4.1a-f could be an indication that in spite of the similitude in species composition and environmental characteristics distinct successional processes seem to be occurring in Cerro Grande.

In most of the psps there was a consistent canopy dominance by Holarctic species such as *Quercus*, commonly associated with *Oreopanax xalapensis*, a Neotropical genus and; in the middle stratum by Pantropical (*Ternstroemia lineata*) or eventually Cosmopolitan (*Ilex tolucana*) elements (*see* Appendix 4.2). The phytogeographical affinity, or at least the dominant species in the plots, offered little information to sustain the hypothesis that the canopy dominant species determine the direction of succession (Ho_3).

Table 4.4 Descriptive statistics for both **a)** continuous and **b)** categorical environmental variables recorded in the plots (n=105). **ELEV** = elevation (m a.s.l.); **SLO** = Slope terrain (%); **ASP** = sun-aspect; **A_0** = hums layer (cm); **LTDP** = Litter depth (cm); **OMC** = Organic matter content; **CEC** = Cation Exchange Capacity; **Ca** = Calcium; **K** = Potassium; **Mg** = Magnesium; **Mn** = Manganese; **N** = Nitrogen; **P** = Phosphorous; **CAOP** = Canopy openness; **CAHE** = Canopy height; **CRLE** = Crown length; **CAT** = Catena; **TOP** = Topography; **RCK** = rocks; **STO** = stones; **CALA** = Canopy layers; **MAT** = Maturity; **GRA** = Grazing; **ERO** = Erosion. (For variable description see Chapter 2).

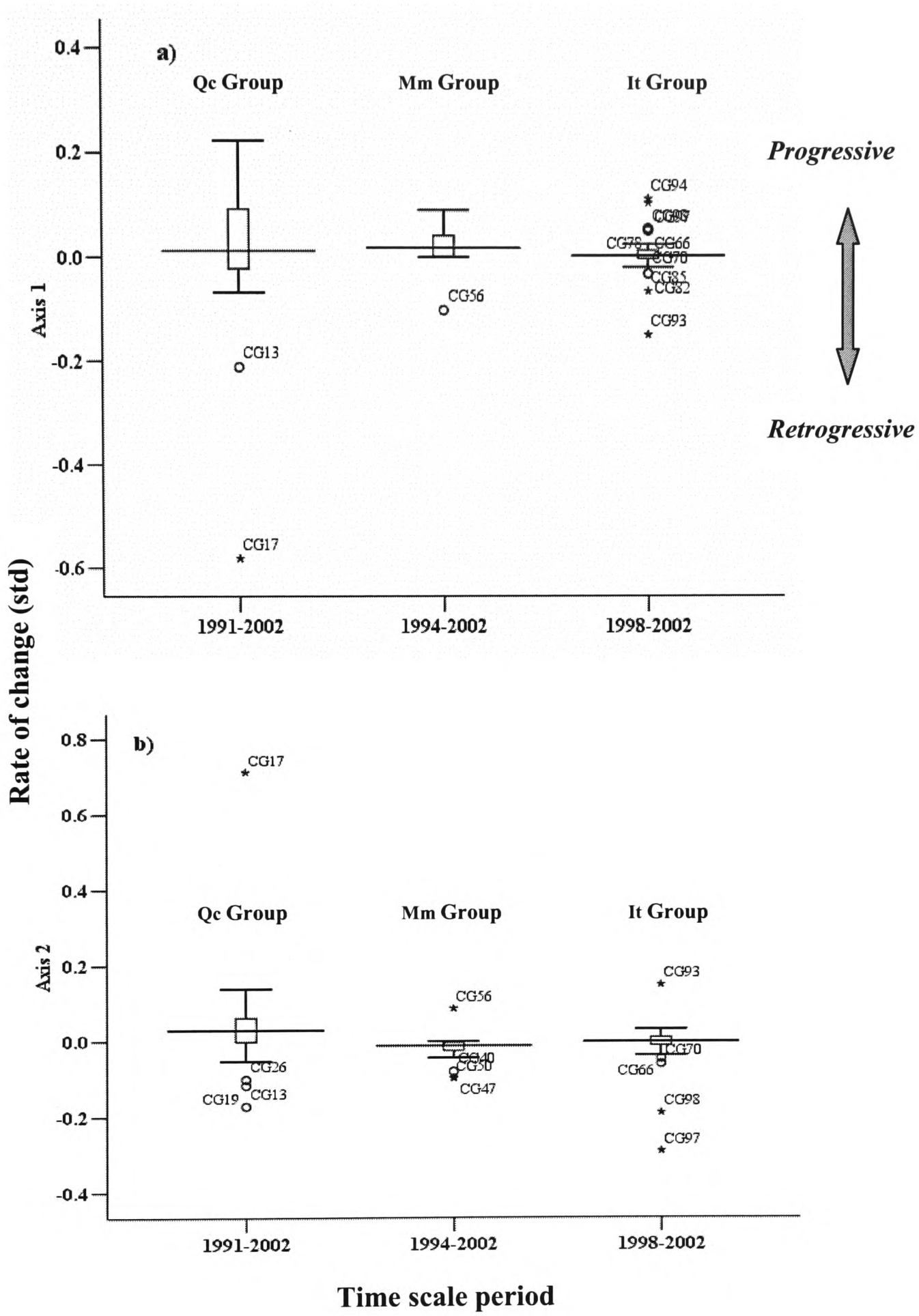
a)	ELE	SLO	ASP	A_0	LTDP	OMC	pH	CEC	Sand	Clay	Silt	Ca	K	Mg	Mn	N	P	CAOP	CAHE	CRLE
Mean	2243	32	1.08	2.3	5.3	9.68	6.58	31.3	62.07	3.83	34.14	998.6	297.8	434.3	14.83	26.64	17.74	12.18	13.44	24.90
Std. Error	9	1	0.07	0.1	0.2	0.28	0.04	0.5	0.60	0.27	0.74	50.2	10.9	15.8	0.14	0.68	0.43	0.95	0.21	1.00
Std. Dev.	80	14	0.68	1.4	2.3	2.62	0.41	5.0	5.53	2.47	6.89	465.1	100.6	146.1	1.33	6.35	3.98	8.78	1.98	9.28
Range	330	75	2.00	9.0	11.1	12.91	1.86	18.0	26.00	9.28	37.28	2174	390	410	4.90	25.10	16.80	51.76	11.72	43.40
Minimum	2020	0	0.00	0.0	1.0	3.79	5.88	22.0	45.32	0.12	15.28	88	170	210	12.30	12.30	13.20	1.62	9.38	11.81
Maximum	2350	75	2.00	9.0	12.1	16.70	7.74	40.0	71.32	9.40	52.56	2262.0	560.0	620.0	17.20	37.40	30.00	53.38	21.10	55.21
CV	**0.04**	**0.42**	**0.63**	**0.58**	**0.43**	**0.27**	**0.06**	**0.16**	**0.09**	**0.64**	**0.20**	**0.47**	**0.34**	**0.34**	**0.09**	**0.24**	**0.22**	**0.72**	**0.15**	**0.37**

b)	CAT	TOP	RCK	STO	CALA	MAT	GRA	ERO
Mode	3	2	0	0	2	3	0	0

Rate of change

Whittaker (1989) indicates that in successional terminology the interpretation of change in DCA-ordination space can be of two types: *i*) negative movement along axis 1 indicates a *progressive* successional change towards a dominance by species of specific habitats; in his case these were species of drier conditions; *ii*) while positive movement would be indicative of a *retrogressive* change and a trend of dominance by species of wetter environments. Similarly, Bakker (1985) defined 'progressive' changes in vegetation if there is an increase in structural complexity (*e.g.* an increase in density or in number of species) while 'retrogressive' changes will be when there is a reduction in any or in both of these parameters. Donnegan & Rebertus (1999) considered succession to be 'progressive' when there is an increase in relative dominance rather than species replacement. In this thesis, a combined criterion of these approaches was followed for considering whether successional changes are 'progressive' or 'retrogressive'. Hence, *progressive* change is considered to occur in situations in which there is an increase in either dominance or abundance, while *retrogressive* is if the contrary took place: a decrease in abundance or dominance in the plot.

Figures 4.2a-d show the rate of change, in standard deviations (std), for the type of data and the three chronosequences analysed. In these figures, negative numbers along the 'y' axis indicate *retrogressive* changes, while the positive ones on the same axis indicate *progressive* changes. In Table 4.5 the absolute psps movements are given along axis one and two on the DCA space (total amount of movement). As Figures 4.2a-d and 4.3a-b show, the rate of change within groups was highly variable. It is clear from these figures, however, that change increases as the time-scale becomes longer. Figure 4.3 also shows that more plots experience retrogressive than progressive changes; and a few remain unchanged. Except for the Qc group (Figure 4.3a), more changes occurred in abundance than in dominance data.



Figures 4.2. Box plots of direction and strength of change for: **a**) and **b**) abundance data and; **c**) and **d**) for dominance data (next page). Axes 1 and 2 display mean, maximum and minimum standard deviation units (95%) Open circles and asterisks represent outliers. The boundary of the box indicates the 25th and 75th percentiles; the line within the box marks the mean.

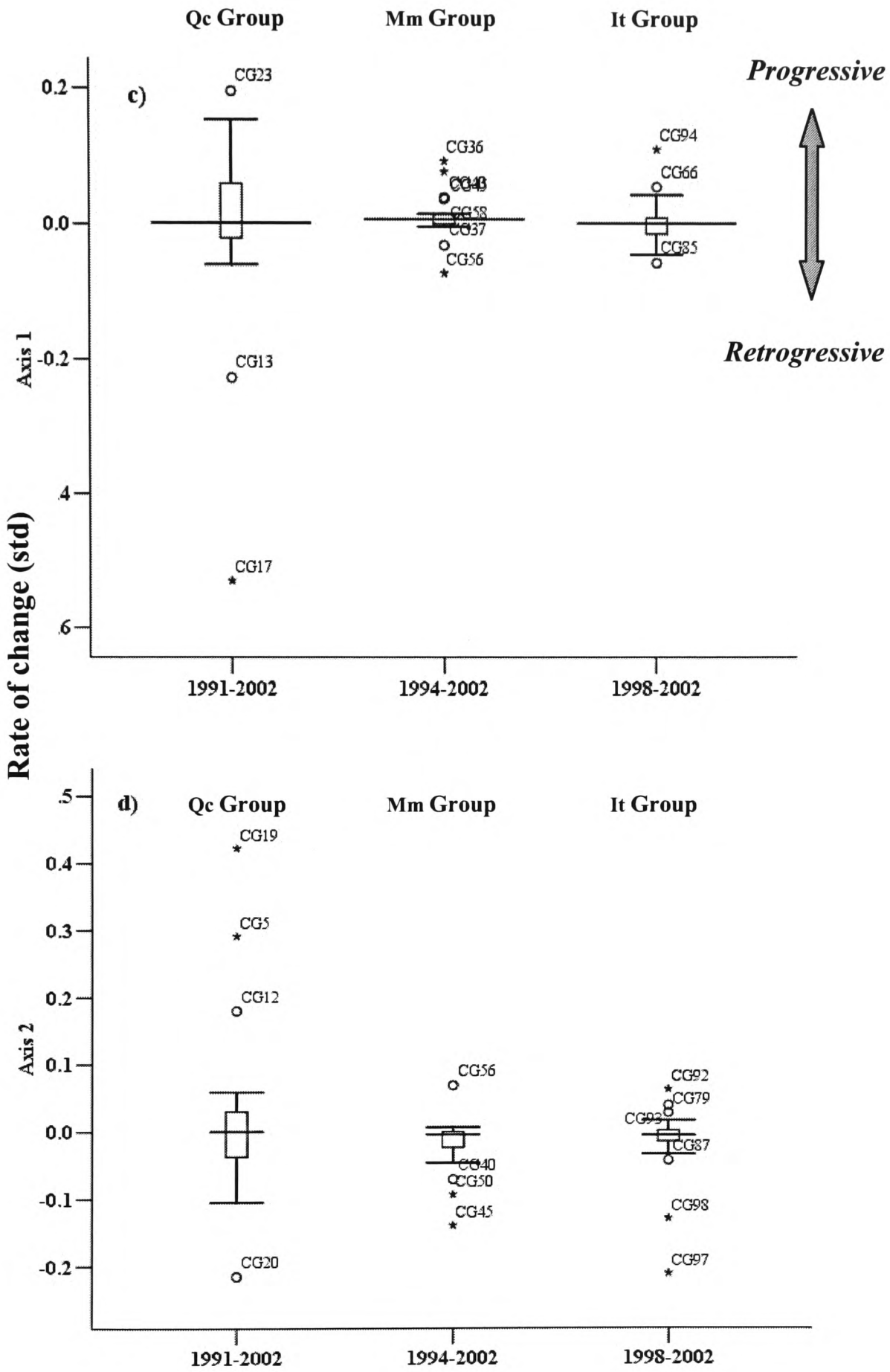


Figure 4.2**c-d** (*Continued*)

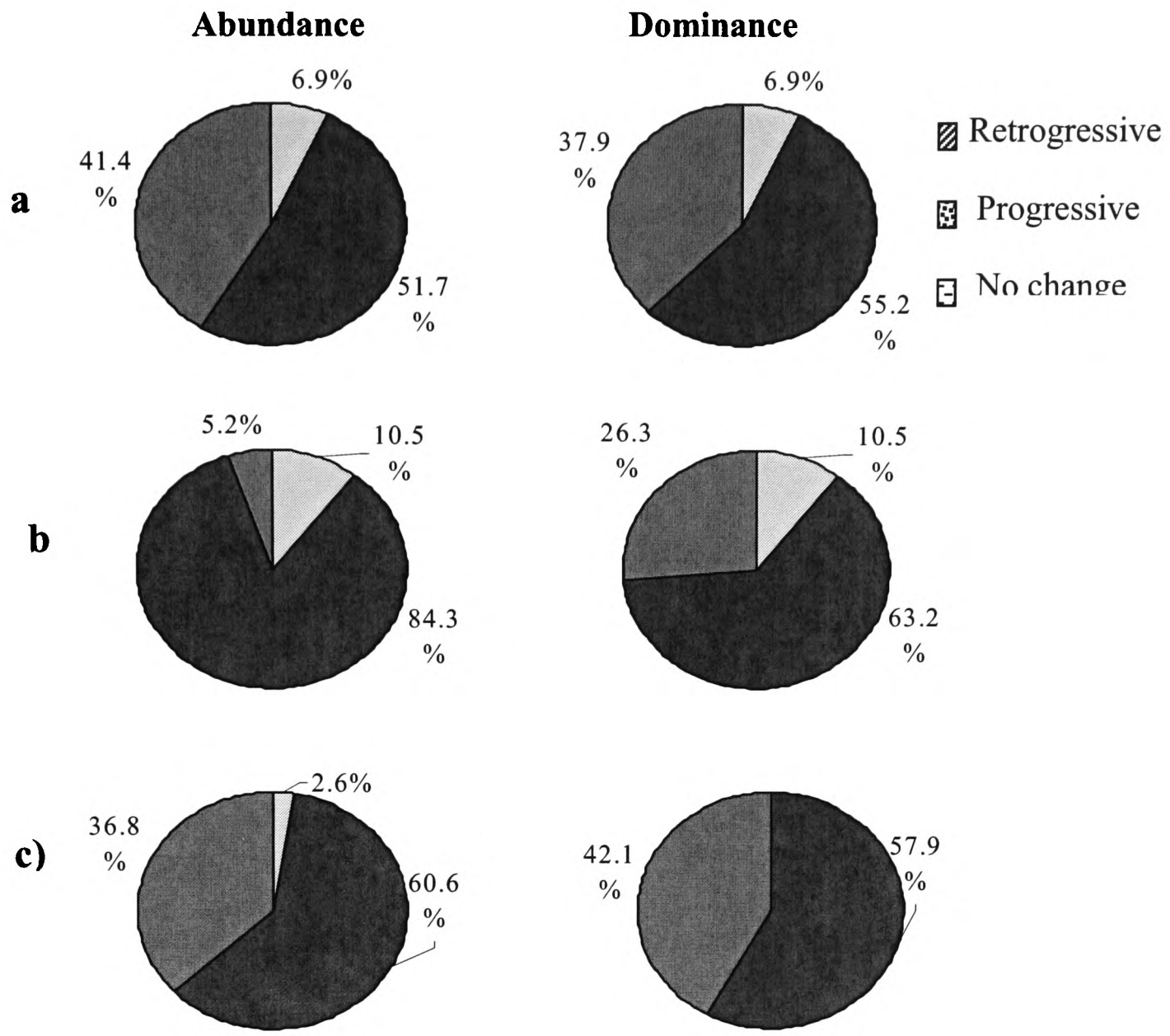


Figure 4.3 Proportions in type of rate changes for: **a**) Group Qc; **b**) Group Mm and **c**) Group It

An extreme case of retrogressive change arose in plot 17 in both types of data. The length of the vector (longest arrow in Figure 4.1a) on axis 1 was 0.7128 std; 80% higher than the average for the group. This result seems to be a combined effect of a substantial density reduction (due to silvicultural cuttings within the plot) and therefore in dominance, accompanied by relatively high proportion of trees that died (possibly before the silvicultural interventions) and no recruitment.

Table 4.5. Absolute psps movement in axis space (total amount of movement, positive or negative for all plots by group and by period).

		Axis 1				Axis 2			
		Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Group	**Abundance**								
Qc	1991-2002	0.081	0.114	0.0000	0.581	0.074	0.130	0.0000	0.712
Mm	1994-2002	0.030	0.032	0.0000	0.102	0.029	0.034	0.0000	0.099
It	1998-2002	0.023	0.034	0.0000	0.149	0.028	0.057	0.0000	0.290
	Dominance								
Qc	1991-2002	0.072	0.104	0.0000	0.529	0.062	0.096	0.0000	0.422
Mm	1994-2002	0.022	0.028	0.0000	0.092	0.027	0.039	0.0000	0.138
It	1998-2002	0.017	0.021	0.0003	0.110	0.022	0.038	0.0004	0.210

A closer look at some of the psps shows that one of the main causes of retrogressive change was due to species turnover. For example, in plot 93 (in the It group) only one individual of *Monnina ciliolata* was recorded in the first census (1998). When this plot was re-measured in 2002 the species was not found so that it was assumed to have died. In addition, there was no recruitment between 1998 and 2002 (It Group) and as a result *M. ciliolata* was no longer represented in the plot. These results suggest that tree mortality, if it has a direct impact on species richness, may have an important effect on the plot's successional dynamics.

An interesting dynamic can be seen in Figures 4.4a-c as well. These histograms represent the internal floristic structure of a number of plots that showed different magnitudes (rates) of change as judged by the lengths of the arrows on the DCA ordination diagrams for the three groups of psps (Figures 4.1a-f). The patterns observed across this group of histograms were very consistent. All successional changes that occurred in the plots were an outcome of linked effects of individual turnover (mortality of individuals of the same species) and changes in patterns of dominance-abundance with time. For example, a careful examination of the diameter-class frequency distributions of plots 13 and 17 (Figure 4.4a-b) shows clearly that there were floristic variations in the Qc group, even though the species richness in the plots was not affected. These circumstances are believed to be the main reason behind the inconsistent directionality of the arrows in Figures 4.1a-b, which suggest that there might be a pattern of alternating species' dominance over time. Yoshida & Kamitani (2000) in a study carried out in Niigata, Central Japan investigating the effect of interspecific competition in a *Quercus-Fagus-Magnolia* canopy dominated forest, observed that

mixtures of different species may result in concomitant differences in stem size and growth of each species and thus in alternate patterns of dominance. They conclude that their results explain the conventional model of stand dynamics in which patterns of dominance eventually shift between species, having a profound impact on successional mechanisms.

In plot 17, an important point to note which could support the dynamics described above, is that this plot had the biggest rate of change of all psps. In addition, it followed a constant successional trajectory across the entire observation period (Qc Group). However, all trees that died in plot 17 were of the same species (*Q. crassipes*), so that in spite of high mortality it kept their representativeness in the plot across sampling periods therefore there were not over time floristic changes (*Quercus crassipes, Pinus leiophylla, Garrya laurifolia* and *Alnus jorullensis*, given in order of dominance). Thus, mortality, which was believed to have triggered the rate of change in plot 17 did not have any effect on species turnover and thus, in a retrogressive change if following the Baker and Donnegan-Rebertus approaches. The variation in rates of change observed to occur at plot level suggest that local processes, mainly represented by individual losses either by density-derived competition and/or by harvesting, partially could explain that despite no substantial changes seem to occur at community level, at small scales changes may arise due to local dynamic process.

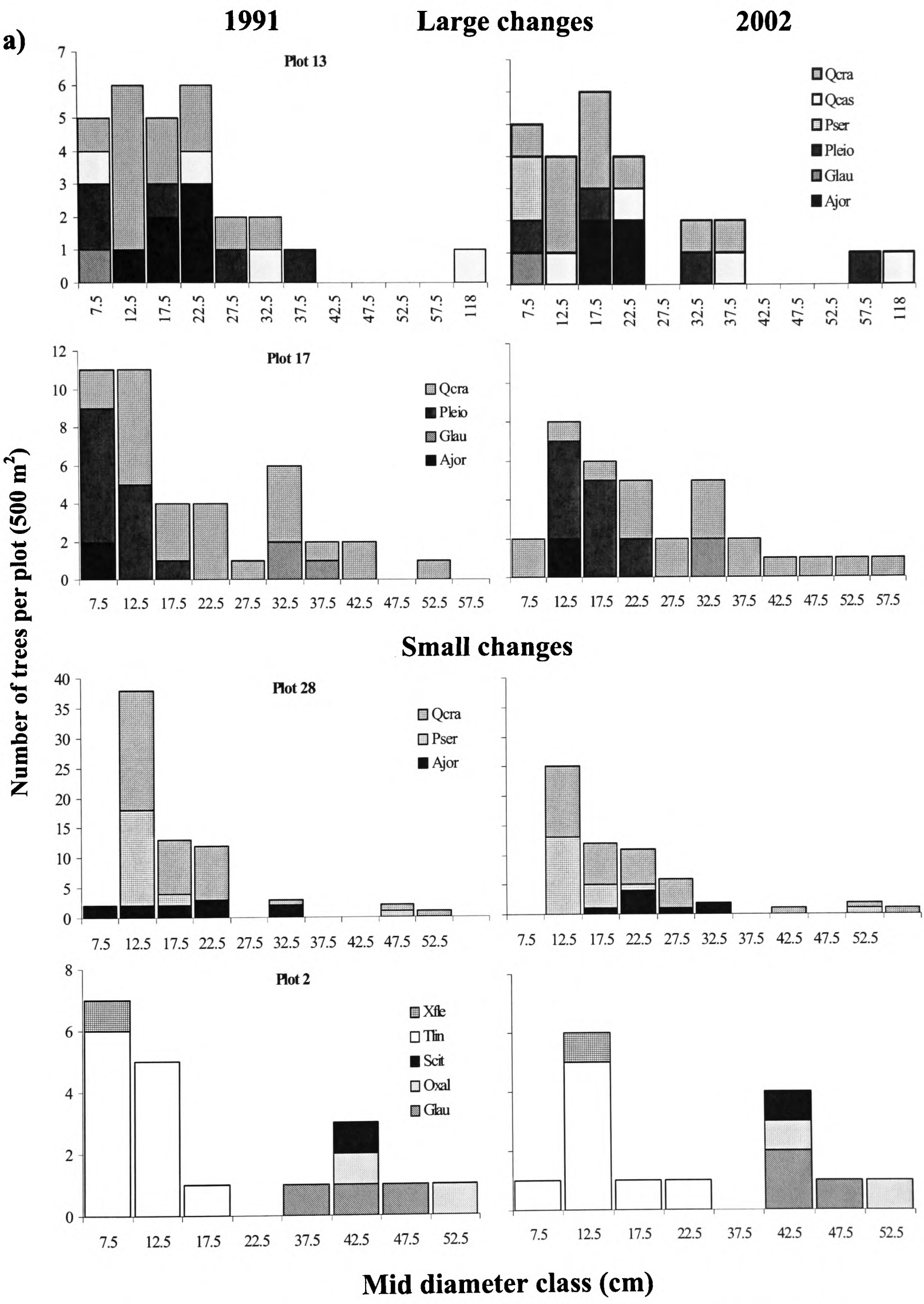


Figure 4.4. Diameter class distributions of plots with large and small changes. **a)** Qc; **b)** Mm and **c)** It.

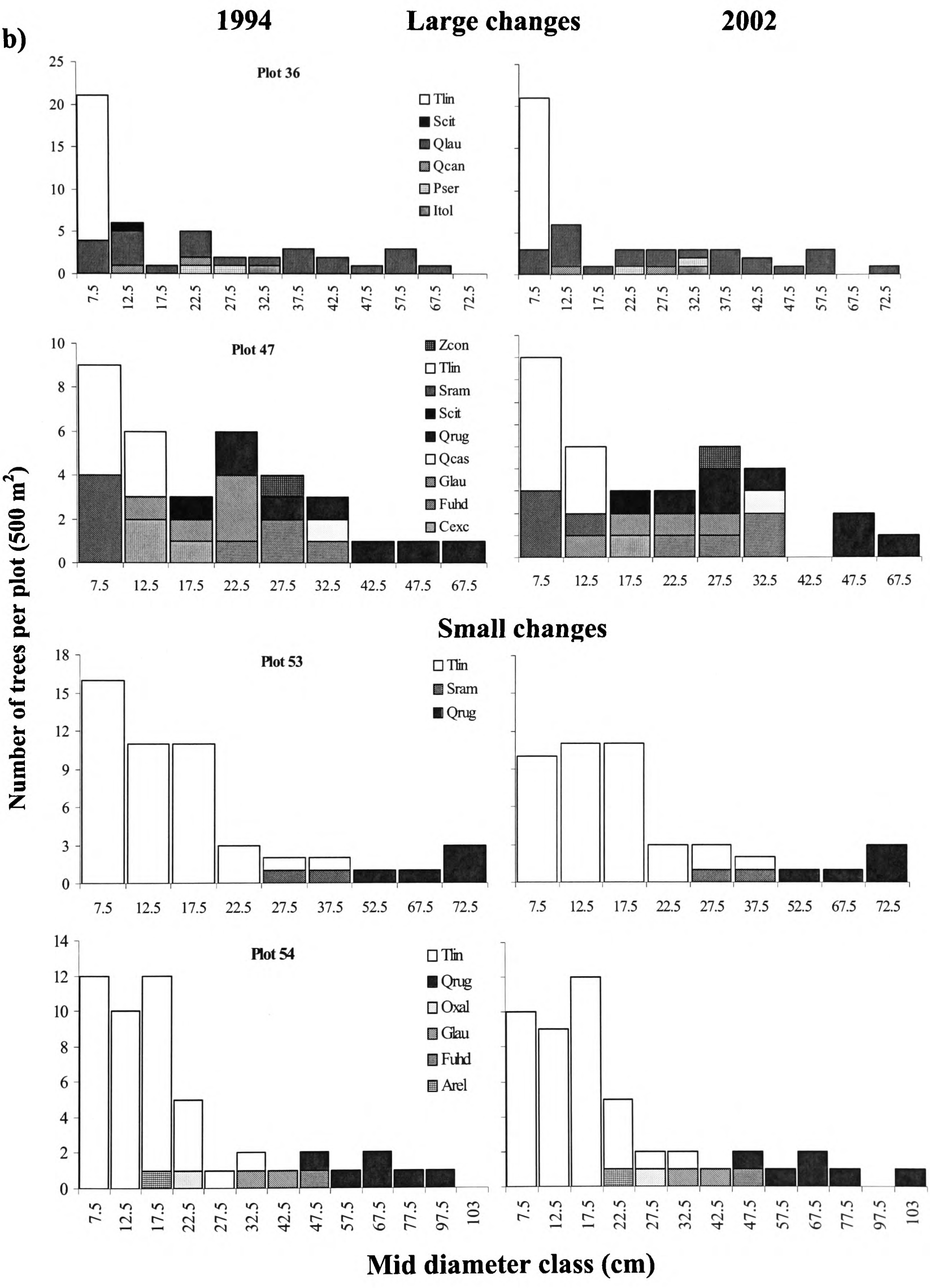


Figure **4.4b** (*Continued*).

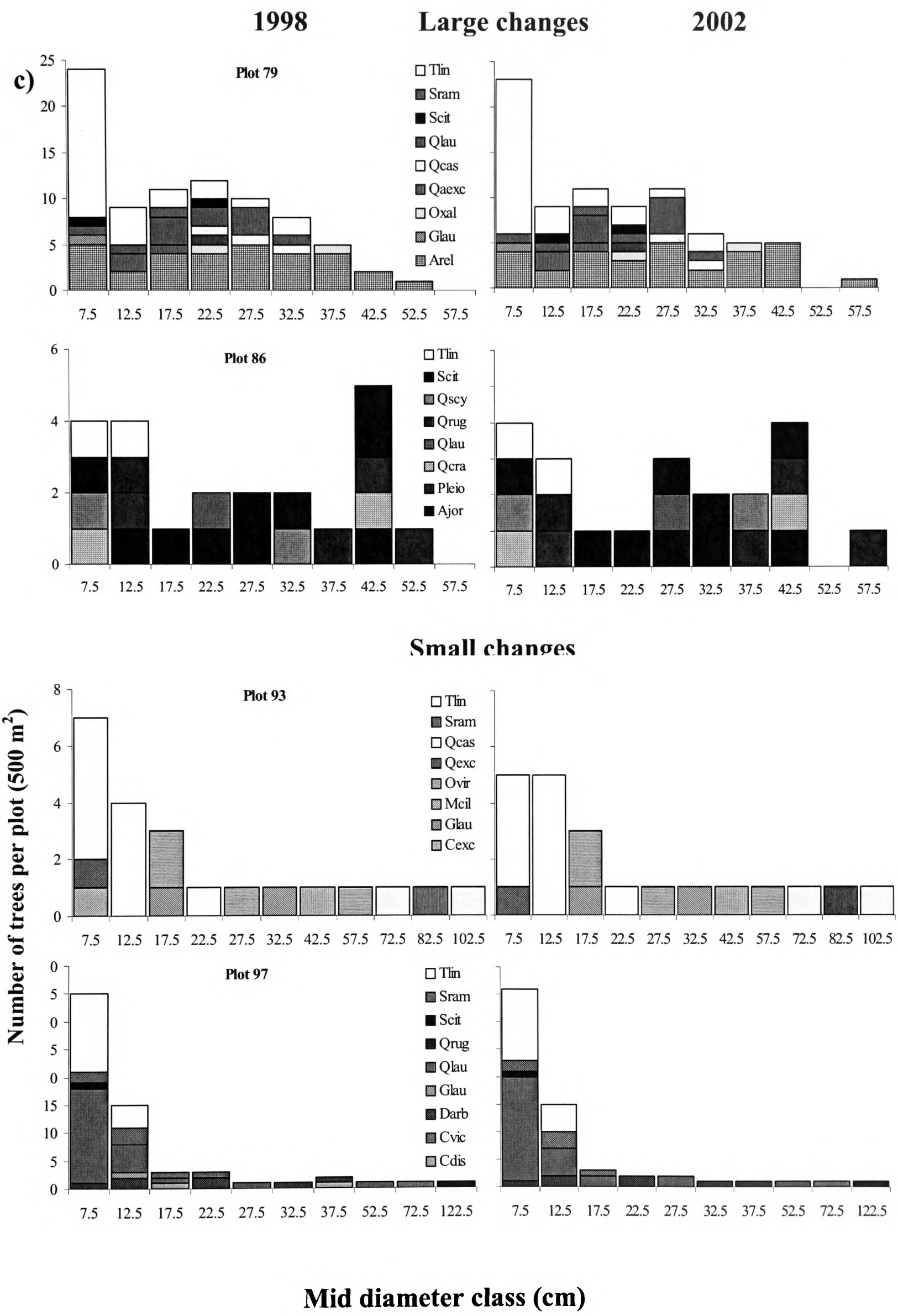


Figure **4.4c** (*Continued*).

4.4.2 Community and population structural dynamics

Community structural dynamics

Figures 4.5**a-c** show the community diameter-class frequency distributions, the estimated Gini coefficients (*G*) and Coefficient of skewness (Sk) for the Qc, Mm and It groups. The three groups exhibited characteristic reverse-*j* shaped diameter distributions, portrayed by forest communities constituted by semi-tolerant to shade-tolerant species. Swaine et al. (1987) describe this pattern as typical of natural forest regenerating from seed, with high numbers in the smaller size classes and a more or less logarithmic decline in number of individuals as diameters increase.

The horizontal structural analysis in the three communities revealed two main aspects; first, the diameter-size class distributions for the three communities varied to some extent, but in all three the maximum diameter-size class exceeded 100 cm. Comparing the structural changes that occurred within communities between consecutive measurement periods, showed that there was a slight increase in the number of individuals larger than 22.5 cm diameter. This does not necessarely imply that there was an overall rise in the number of trees in each diameter class, but an increase in diameter size in almost all the diameter classes.

The Sk in the three communities was positive, irrespective of the variation in species composition and very similar for the It and Qc groups. However, comparing consecutive periods within communities showed that there is a gradual diminution in the Sk. This confirms that there was a general increase in diameter as previously described. The results also show that *G* did not change for the It and Qc group. For the Mm group, although *G* changed suggesting structural changes between periods of observation, such a changes seem not to be substantial since the value of *G* was about the same between the two sampling periods (Figure 4.5b). The combined results indicate that the three communities have comparable structural dynamics. The *G* coefficient indicates, in particular, that in none of the three groups of plots did structural changes represent an important source of structural differentiation between periods of observation.

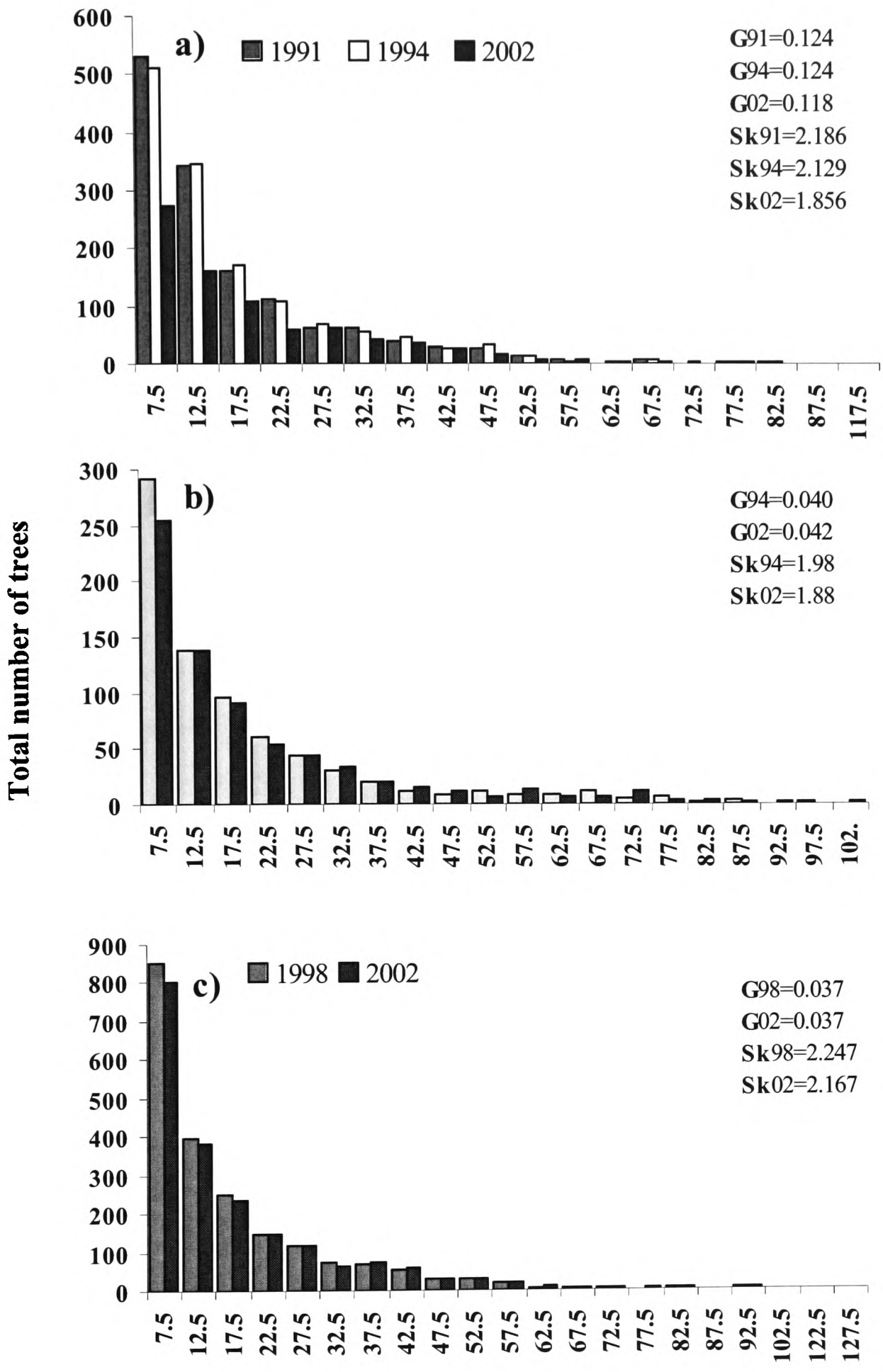


Figure 4.5. Community diameter-class frequency distributions, combining all psps and species by inventory. The Gini coefficient (*G*) and the coefficient of skewness (Sk) are given in order of chronosequence: **a)** 1991-2002 (Qc Group); **b)** 1994-2002 (Mm Group) and **c)** 1998-2002 (It Group). *x*-axis values are mid points of diameter classes of 5 cm. (Note the difference in the *y*-axis range value).

Population structural dynamics

Three general patterns of diameter frequency-class distribution were observed, representing the various populations that integrate the mixed oak communities of Cerro Grande; Group Qc is taken as an example (Figure 4.6): *i*) one was roughly consistent with the reverse-*j* shaped curve observed at community level (*e.g. Quercus crassipes, Prunus serotina*); *ii*) a second group with a bell-shaped distribution (*e.g. Cornus excelsa, Pinus pseudostrobus*) and *iii*) a third group exhibited a rather irregular frequency distribution pattern (*e.g. Quercus candicans, P. leiophylla*). Apart from that shown by *Q. crassipes*, most of the *Quercus* species exhibited rather irregular diameter frequency distributions and, in general *Quercus* species had the widest diameter-class range of which *Q. laurina, Q. candicans* and *Q. rugosa* had the most persistent populations in the community. This was judged by the proportions of trees in the different diameter classes, irrespective of the pattern of diameter frequency distribution. All populations also showed unimportant structural changes over time (Appendices 4.1a-c).

No evidence was found to support the contention that a particular population was either declining or increasing in the different sampling periods. Apart from *Q. crassipes, Q. castanea* and *A. xalapensis* in the Qc year group; and *Q. crassipes, Q. laurina,* and *O. xalapensis* for the It group (whose *G* coefficients were unchanged over time, suggesting a structural stability); the most noticeable changes occurred in the most abundant species including *Q. crassipes, Q. castanea, Q. candicans* and *T. lineata*. The modest rightward increase in the frequency distributions of these species may be an indication of future canopy dominance (except for *T. lineata* that is a mid-story canopy species which seldom reaches the upper canopy) (Appendix 4.1a-c).

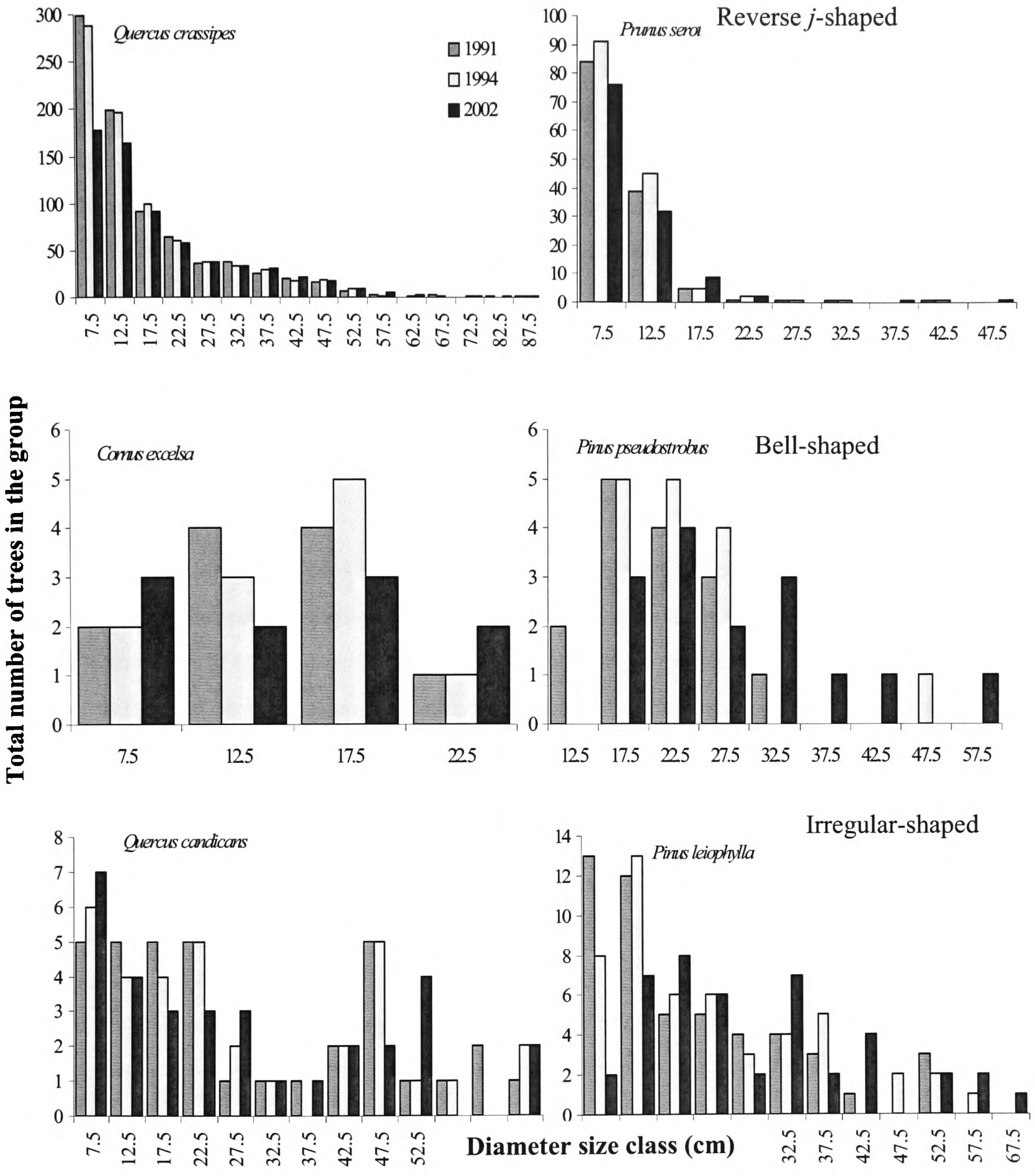


Figure 4.6 Representative population structures in *Quercus crassipes* Group (Qc). The proportions of individuals in each of the diameter class are those calculated from the total number of individuals in the community; x-axis values are mid points of diameter classes of 5 cm.

An unexpected result was that some infrequent species such as *Buddleia parviflora* and *Carpinus tropicalis* are very persistent in the community. Both species survived under the canopy as suppressed individuals, with less than 10% crown length and no recruitment since the psps were established. Kunin & Gaston (1993) point out that there is a growing body of evidence to suggest that locally rare and geographically restricted species may have characteristics that differ from the most common taxa and that this may be why such species thrive. These results merit further investigation but they are beyond the scope of this research.

4.4.3 Turnover patterns

Mortality

The cross-tabulation analyses showed that there were generalised patterns of mortality in which the greatest proportion of trees that die belong to the smaller diameter classes. The diameter-size of the tress that die in the three groups spanned from 7.5 to 52.5 cm dbh but the highest proportion was concentrated at the lower diameter categories for all species and groups (Table 4.6). However, except for the most recently established plots (the It group) in which, for most species, mortality was dependent on diameter, the Pearson chi-square goodness-of-fit test indicated that there was no direct relationship between mortality and diameter (Table 4.6). These results may appear contradictory and should be interpreted cautiously. For example; during the last forest inventory in the It group (Table 4.6c) only one individual each of *Clethra vicentina, Dendropanax arboreous, Monnina ciliolata* and *Quercus castanea* was dead, hence mortality for these species was represented in just one diameter class. This is thought to have obscured the real effect of species on mortality since there were too few individuals to allow a more formal statistical test.

Table 4.6. Absolute mortality by species and diameter class for: **a**) Qc; **b**); Mm and; **c**) It. T_D = total deaths by species. Bold numbers in the ***p*** ($p<0.05$) column indicate that mortality is dependent on diameter class by species (Pearson chi-square goodness-of-fit).

	Mid point of diameter classes										
a) Qc group	**7.5**	**12.5**	**17.5**	**22.5**	**27.5**	**32.5**	**52.5**		T_D	x^2	***p***
Alnus jorullensis	15	9	7	5	2	1			39	0.00	1.00
Arbutus xalapensis	4								4	3.57	0.06
Cornus excelsa		1	1						2	1.29	0.26
Pinus leiophylla	1								1	3.57	0.06
Quercus castanea	2	1	1						4	2.00	0.37
Quercus crassipes	66	20	3	4	1	1	1		96	2.29	0.68
Symplocos citrea				1					1	3.57	0.06
Ternstroemia lineata	1								1	3.57	0.06
b) Mm group	**7.5**	**12.5**	**17.5**	**22.5**	**27.5**	**37.5**	**42.5**				
Acacia farnesiana			3						3	3.57	0.06
Alnus jorullensis			1						1	3.57	0.06
Cornus excelsa		3							3	3.57	0.06
Garrya laurifolia		1							1	3.57	0.06
Lippia umbellata		1							1	3.57	0.06
Pinus leiophylla			1						1	3.57	0.06
Quercus candicans	1						1		2	1.29	0.26
Quercus castanea	2	3		2	1				8	1.57	0.67
Quercus crassipes	1	2							3	4.57	0.10
Symplocos citrea	3	3	1			1			8	0.29	0.87
Styrax ramirezii	1								1	3.57	0.06
Ternstroemia lineata	7	3	3						13	2.00	0.37
Xilosma flexuosum	1								1	3.57	0.06
c) It group	**7.5**	**12.5**	**17.5**	**22.5**	**27.5**	**32.5**	**37.5**	**47.5**			
Alnus jorullensis		1	2						3	6.25	**0.04**
Abies religiosa	3		1						4	6.25	**0.04**
Arbutus xalapensis		2							2	4.5	**0.03**
Cornus excelsa	3	1	1				1		6	1.75	0.42
Clethra vicentina							1		1	4.5	**0.03**
Dendropanax arboreus	1								1	4.5	**0.03**
E. aff. maritenianum	2								2	4.5	**0.03**
Garrya laurifolia	2	1							3	6.25	**0.04**
Ilex tolucana	1		1					1	3	0.5	0.48
Monnina ciliolata	1								1	4.5	**0.03**
Oreopanax xalapensis		1	1		1				3	0.5	0.48
Quercus aff excelsa	3	1							4	6.25	**0.04**
Quercus castanea				1					1	4.5	**0.03**
Quercus crassipes	4	1	1	1			1		8	1.75	0.42
Quercus laurina	18	5		1					24	6	0.Qc
Quercus scytophylla	1	1							2	2	0.16
Symplocos citrea	7	2							9	6.25	**0.04**
Styrax ramirezii	1		1	1					3	0.5	0.48
Ternstroemia lineata	7	3	1	2					13	4.5	0.34
Tilia mexicana						1			1	4.5	**0.03**

Mortality-recruitment relationships

The mortality-recruitment relationships across sampling periods are presented in Figure 4.7a-c. In these figures it is evident that a number of species such as *Garrya laurifolia, Quercus rugosa* and *Ternstroemia lineata* (Figure 4.7a), *Ilex tolucana* and *Styrax ramirezzi* (Figure 4.7b) and *Ostrya virginiana* and *Q. rugosa* (Figure 4.7c) were 'self-replaced' i.e. losses (mortality) and gains (recruitment) were balanced. However, this 1:1 balance between mortality and recruitment was not taking place for many species in the study area. In most the mean annual mortality exceeded mean annual recruitment, so that the null hypothesis (Ho_3) of a compensatory balance between these two demographic processes was not supported.

In addition, across all species the results indicate that *T. lineata* had not only an exceptional demographic balance, but also that this species had the highest rate of mortality and recruitment over all observational periods (Figure 4.7a-c) showing it to be one of the most dynamic species in Cerro Grande.

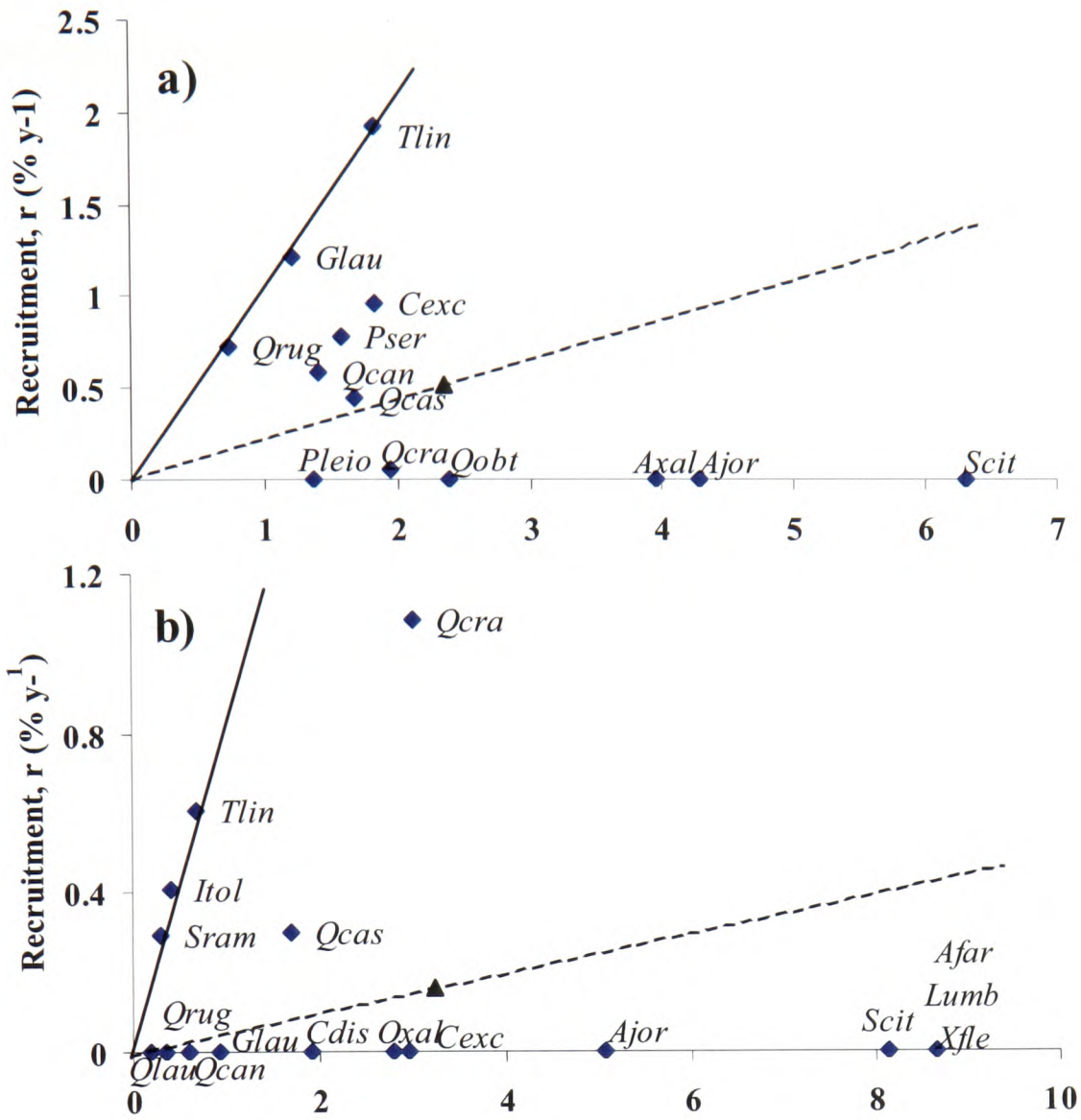


Figure 4.7a-c. Scattergrams showing the relationship between annualised rates of mortality (*m*) and recruitment (*r*) for the periods of: **a)** Qc; **b)** Mm and **c)** It. Dashed lines indicate overall inter-group mean mortality and ingrowth. Solid lines indicate equality (*after* (Sheil, 2003) ($x = y$). It is prudent to indicate that the three graphs have dissimilar scale axes as explained in the main text. Species codes are given in table 3.4.

4.5 Discussion

4.5.1 The dynamics of successional trends

Overall the results show that several successional pathways are unfolding in the *Quercus* forests of Cerro Grande indicating successional trends that depend upon a number of interrelated factors. The general structural characteristics of the adult vegetation such as species composition, stand density, developmental stage, patterns of recruitment and mortality etc., suggest that most of the stands in the study area are in an *old growth stage* (overstory trees die in an irregular fashion, and some of the understory trees begin growing to the overstory) as described by Oliver & Larson (1996). Old growth stage characterise most of the stands in Cerro Grande although, it seems to be most well typically represented across the stands that constitute the mesic zone (Chapter 3) which eventually may reflect a combination of environmental factors and the traits of the species on there present. On mesic sites, trees form mixed and dense stands with scatter occurrence of old-growth trees (Mat3), mostly *Quercus* species. These are strongly associate to species of the middle story (*e.g. Cornus excelsa, Ternstroemia lineata*) but that the eventually can reach the upper canopy such as *Oreopanax xalapensis, Ilex tolucana, Garrya laurifolia,* these species eventually undergo mortality (*see* Table 4.6) at higher rates that *Quercus* species (Figure 4.7a-c). The later species, in general terms, grow faster than most of the *Quercus* species in Cerro Grande (*per. obs.*), thus represent the understory trees that begin growing to the overstory considering the 'old growth stage as described by Oliver and Larson (*op. cit.*).

Furthermore, the data also suggest that even subtle changes in species composition within a plot, such as that which occurred with *Monnina ciliolata* in plot 93 (Figure 4.4c), or a severe reduction in either dominance or abundance, although not necessarily in species richness (as in plot 17; Figure 4.4a), appear to be sufficient to alter the trajectory of a succession.

Because there were just two periods of observation and only one plot in which a true reduction in species composition was found, it cannot be argued strongly that reducing the number of species within a plot will result in retrogressive successional changes

(Bakker, 1985) or provoke a substantial change in the direction of succession. Walker & del Moral (2003) argue that successional trajectories in plant communities can follow several alternative routes ranging from definitive pathways, moving through well-defined stages leading to a predictable and stable association. In this scenario, multiple starting points (different ranges of species composition) converge into a single point in terms of dominant species composition. Thus, the same suite of species found in spots of mature vegetation eventually dominates vegetation that initially varies or has different species compositions. Alternatively, in an extreme situation successional trajectories may follow less predictable patterns without convergence. Such extreme situations are mainly attributable to fluctuations in dominance by different groups of species over time. The results in this thesis are very much in accordance with the second alternative, the results in Figures 4.1a-f clearly shows the stochastic patterns manifest by the psps independently of the time span of observation, however, the successional patterns followed by plot 17 in the same group give a signal of caution, since even when it was the most changed plot, caused either by competition-derived mortality or by harvesting, this plot followed an unidirectional successional trajectory across the observational period.

Patterns of species dominance and change in stand structures are not the result of obligatory laws which species must follow. While changes in species dominance or structure can be anticipated these are simple the result of interactions of plants (Oliver & Larson, 1996). There are compelling evidences in the scientific literature indicating that the co-occurrence of species of different temperament to light or of reproductive strategies can cause several microsuccessional dynamics with a relatively geographic area. Forcier (1975) observed that, depending on the species composition and reproductive strategy the dynamics of forest succession may follow several alternative routes and may vary in rate over time. He describes a cyclic successional process in which the canopy dominance by the species may be temporary process. This cyclic succession would assure the co-occurrence of several species in a community through times of infrequently occurring exogenous disturbances.

A fundamental assumption of gradient analysis theory is that a single species generally responds in the same manner to the same environmental gradient (Ejrnæs, 2000). This statement can be interpreted as referring to the classical 'unimodal' species response to

a single gradient suggested by ter Braak (1994). Hence, the psps in Cerro Grande have great ecological similarity among the mainly dominant species (*Quercus*) and high sympatricity with allied timber species. These provide strong reasons to hypothesise that if potential successional changes were to take place they should precede at similar rates and ultimately converge towards a similar successional condition. This was intuitively thought to be true, at least for those psps consisting of comparable suites of species, similar developmental stages and similar environmental gradients. The DCA results nonetheless indicated that this does not necessarely take place in the study area since a considerable number of psps not only experience a rather stochastic migration, but also many of them show different magnitudes of change over time. These circumstances were particularly evident in the Qc group, in which it was difficult to elucidate the true mechanism that lead to the observed successional trends. Fulton & Harcombe (2002) claim that the working of processes in forest succession takes place at several different scales. Concluding that this is largely what makes forest dynamics complex, and therefore difficult to predict.

Among the most significant contributions of this research to the general understanding of the mechanisms that contribute to the forest dynamics in Cerro Grande, were the successional trends observed in each group of plots. For example, from an ecological point of view it was discovered that the temporal and spatial contexts could be of fundamental importance to judging whether floristic changes are taking place. In this context, when all psps (by group) were analysed, relatively unimportant floristic and structural changes occurred in the *Quercus* communities of Cerro Grande. From a methodological point of view in the Qc group, it was also discovered that the time interval and the number of repeat observations can play a fundamental role in judging whether successional processes, independently of the vegetation type, are unidirectional or indeed vary over time. Investigating successional processes in grasses, Collins (1990) concluded that the distinction between directional and non-directional change depends largely on the scale of observation in time and space, a view that coincides with the results found in this study.

Foster & Tilman (2000) established that forest succession is a time-decline process. In their study, the authors found that after 14 years of succession at Cedar Creek Natural History Area, in Minnesota USA, successional rates declined over time. They argued

that the overall rate of compositional change decelerates, eventually reaching a point of stabilization. The results in this thesis, in contrast, show that in *Quercus* forest at Cerro Grande successional trends are more notable in the Qc group than in the Mm and It groups. One of the likely reasons of contrasting patterns observed between Foster and Tilman and this thesis may be fact that they carried out their investigation in temperate forests, which in general terms are less diverse, and of lower dynamics than sub-tropical forests.

Because successional processes have been intensively studied over a wide spectrum of conditions (*e.g.* under anthropogenic and non-anthropogenic disturbances, experimental versus observational, forest plantation versus naturally regenerated forests etc.) and vegetation types, including *Quercus* ecosystems (Abrams & Downs, 1990; Rousset & Lepart, 2000) the underlying successional patterns observed in *Quercus* at Cerro Grande can be placed in a wider context. For instance, Higgins et al. (1999); Chase (2003) and Kneitel & Chase (2004), in a slightly different approach, agree that successional trends in forest communities can follow unpredictable patterns and that forest succession is time-scale dependent. In general, the above investigations reveal that factors such as soil nutrients, organic matter in the soil, species composition, and type of disturbance, amongst others, are fundamental for promoting successional processes. However, it has been reported (McCune & Allen, 1984) that forest communities are systems whereby species replacement follows a deterministic mode and therefore forest succession is a highly predictable event. For example, Hunt et al. (2003) in a 20-year study of succession in forest plantations, report that all stands migrated roughly towards the same direction within the DCA ordination space. Because Hunt's collaborator results were derived from data obtained from a forest plantation in which just two tree species were involved (*Pinus banksiana* Lamb. and *Picea mariana* (Mill.) BSP) and the site conditions varied little over time, this can be taken as an indication that, other factors being equal, as explained above in the Foster and Tilman case, monospecific stands tend to be highly stable and hence ecological succession predictable, evidence that seems not to apply in the *Quercus* communities of Cerro Grande due to the local species richness.

4.5.2 Rate of change

Analysis of the rate of change indicated that different patterns of change are occurring in the three groups of plots. However, if successional rates of change are analysed with longest temporal resolution, the Qc group, different patterns and stochastic trajectories were evident, as described in the results section. The trends in the rates of change were characterised by: *i*) plots that had a relatively unidirectional and uniform rate of change, judged by the length and direction of the arrows, *ii*) plots that had a relatively slow and then rapid rate of change in an unpredictable direction and; *iii*) plots that exhibited insignificant rates of change over time.

The apparent greater rate of change in abundance in comparison with dominance deserves a closer examination, mainly because for such a relatively short scale time (Qc years for the longest period), it would be expected that community changes are more likely to occur in dominance rather than in abundance. These assumptions are derived from the fact that species with very low representativeness such as *Buddleia parviflora*, *Crataegus pubescens* and *Carpinus tropicalis* (*see* Figure 3.2, Chapter 3) were very persistent over time and also that no new species 'entered' the psps within the time-span that this investigation covered, so that species composition in all the psps did not suffer major compositional changes.

4.5.3 Community and population structural dynamics

As expected, the most relevant issues that informed the diameter frequency distributions presented in Figures 4.4a-c and Appendices 4.1a-c was that, at the community level there was a consistent decrease in the number of trees as the diameter increases. Variation of diameters ranged from 5 cm to 110 cm. Also, stem density consistently fell after the 22.5 or 27.5 dbh-classes (Figures 4.4a-c), maintaining about the same proportions in terms of number of trees for each diameter class over the range sampled. These structural patterns are an indication that density-dependent processes such as a constant mortality rate over the various diameter classes regulate the community (Crawley, 1990). However, the results showed (Table 4.7) that mortality occurred predominantly in the smaller diameter classes.

The fact that density declines over time in forest communities is not an unusual discovery. It is the typical diameter distribution pattern of shade-tolerant to semi-tolerant species. Classical investigations (Reineke, 1933; Yoda et al., 1963) have described similar processes. It is well-established in the ecological literature that dense stands with high species richness often suffer from resource competition between individuals, which leads to a decline in diversity and/or productivity due to the elimination of the less competitive individuals, thus producing structural configurations represented by many small individuals and a reduced number of big ones. Nonetheless, it is evident that the degree of structural differentiation increases with time.

4.5.4 The dynamics of turnover

Even though significant statistical differences were found in mortality rates, this process impacted only upon the absolute number of individuals, not in a reduction in the total species number except for *Monnina ciliolata* in plot 93 for the It group. The same pattern occurred with recruitment. Newly recruited individuals always belonged to the same species pool that was already represented in the psps, so species richness remained the same between 1991 and 2002.

Sheil (1999a), using long-term data, reported a consistent pattern of recruitment and mortality where most species have higher recruitment rates than mortality. The results in this thesis showed the opposite trend since always there was more mortality than ingrowth. The lack of dependency between mortality and tree size by species is thought to be a combined effect of the number of individuals found dead in each diameter class, the time-interval considered and the rigour (significance) of the statistical test, rather than a real pattern. For example, in the groups where mortality was not dependent on diameter by species, a high percentage of species (50% and 61% respectively) were quite close to being significant (0.06) (Table 4.6). A number of investigations (*e.g.* Harcombe & Marks, 1978; Davies, 2001; Lorimer et al., 2001; Antos & Parish, 2002) have demonstrated that there is a high correlation between patterns of mortality and tree diameter in which the causes of death have been attributed to asymmetric competition. In this respect, the imbalance observed between mortality and recruitment amongst the species in the *Quercus* forests in Cerro Grande, may be a result of competition both, intra- and interspecific, leading to community modification.

4.6 Conclusions

Considering, the stand structure characteristics, the species composition and, overall the dynamics (structural changes, patterns of recruitment and mortality and successional trends) of most the stands that constitute the vegetation of Cerro Grande, are in an 'old-growth strange' of development (*sensu* Oliver & Larson, 1996).

The results in this chapter also suggest that the three groups of plots analysed (It, Mm and Qc) are undergoing contrasting stand dynamics and successional trends. Within groups of plots (*e.g.* It, Mm and Qc), the stochastic distribution and different pointing direction of the arrows on the DCA diagrams suggest that the dynamic of forest succession may vary from plot to plot. Therefore, the results in this Chapter do not provide convincing evidence for sustaining the predictions that, a consistent and unidirectional successional trajectory led by the canopy-dominant *Quercus* species, is taking place in the study area.

Because DCA ordinations showed that there is great variation in successional trends (Figures 4.1a-f), it is assumed that this process occurs at fine spatial-temporal scales. This might occur within patches of forest across Cerro Grande in which species composition and site conditions closely interact in defining individual pathways.

Although the unchanged *G* values, as well as the small differences in Sk over time by the communities, seem to contradict the previous conclusion, it is important to stress that *G* and Sk are both measures of differentiation between consecutive periods (Bendel et al., 1989; Damgaard & Weiner, 2000).

The hypothesis that processes of mortality and recruitment are not sources of community modification can partially be accepted. The general structure of both communities and populations suggest that there are no substantial changes in the vegetation of Cerro Grande. However, there were also good indications that, if mortality has a direct impact on species richness, eventually it can become an origin of structural modification. Although it may be difficult to separate the true underlying causes of mortality a probable mechanism is intra- and inter-specific competition since as

explained in previous Chapters in this thesis no catastrophic events such as intense forest fires, pest attack, etc. have occurred in or nearby the psps since their establishment

CHAPTER 5 - Oak forest regeneration dynamics: the role of spatio-temporal filters

5.1 Introduction

One important factor that often determines the presence of a plant on a site is propagule availability. Subsequently, abiotic and biotic factors act as a series of filters operating sequentially from seed to adult stage, determining the pattern of recruitment (Houle, 1995). This chapter investigates the spatio-temporal dynamics underlying juvenile individuals in *Quercus*-dominated forest communities by: *i*) describing the floristic heterogeneity in seedlings and saplings and how they are spatially structured; *ii*) looking at links between the spatial patterns of floristic variation with micro-environmental heterogeneity and; *iii*) analysing the temporal dynamics of both vegetation categories.

5.1.1 Background

Species-rich forest communities have long been the focus of hypotheses about the processes that produce such high diversity and how coexistence occurs (Morgan, 2001). Different processes can induce variation in species diversity and spatio-temporal floristic variations (Hou et al., 2004). In Chapter 3 it was discussed that in current ecological literature, there are essentially two main competing hypotheses on the ecological mechanisms that structure species-rich communities: strict local determinism and neutral ecological drift. It is generally agreed by supporters of local determinism that plants react differently to variations in environmental conditions and because of this, woody plants depict characteristic vegetational patterns across the landscape. For instance, greater similarity is expected to arise between communities that are close together than between communities that are widely separated (Spencer et al., 2002). This is because adjacent physiographical areas tend to have similar environmental characteristics, which allows the establishment of individuals that have similar habitat requirements (Rees et al., 2000; Svenning, 2001). Many studies have also established that the causative forces that determine the distribution, coexistence and variation of neighbouring plant species across the landscape are a combined effect of multiple factors such as restricted seed dispersal, environmental determinism and inter- and

intraspecific competition. These processes often have local, temporal and species-specific impacts (Schurr et al., 2004). In a spatial context, the importance of seed dispersal has been suggested (Janzen, 1970; Clark et al., 1999; Howe & Miriti, 2000; Shea et al., 2004) as one of the main contributing mechanisms for species variation across the landscape. In a temporal context, exogenous events such as grazing, fire or human-induced impacts commonly have adverse effects on the establishment and persistence of juvenile individuals in many forest communities (Runkle, 1989). Therefore, understanding the patterns and processes that produce fluctuations in vegetation is an important goal in plant ecology.

A commonly cited hypothesis is that community members participate at different temporal and spatial scales. This alone suggests that there is a range of circumstances that eventually cause variations in the abundance and distribution of plants across the landscape. These can be classified into three broad categories (*cf.* Dale, 2000):

i. Morphological factors, based on the size and growth pattern of the plants.

ii. Environmental factors that are themselves spatially heterogeneous and;

iii. Phytosociological factors, whereby the spatial arrangement of one species affects the occurrence of another species through their interaction.

The above processes result in a considerable range of differentiation in frequency, intensity and magnitude of associations and hence in species composition assemblages over time and space (Parker, 2004). Traditionally, as discussed in Chapter 1, the theory for explaining patterns and processes of species diversity and their coexistence have been based on work in lowland tropical rain forests. In contrast sub-tropical, species-rich, forests growing at high altitudes have only been recently studied. As a result their structure and functioning remain little understood.

The ecology of oak regeneration

Among timber trees, oak is an outstanding genus. It is widespread across Northern Hemisphere although the biggest concentration of species is found in the mountainous areas of Mexico. Biogeographical theories consider its origin as in the context of past tectonic movements, climatic fluctuations, patterns of expansion and contraction; species isolation and connections that occurred during the Pleistocene (*see* Chapter 2 for additional information). *Quercus* species differ widely in distribution because of water availability, but most are well adapted to grow on dry sites (Abrams, 1996). A number of studies also have indicated that the presence of many oak species is inversely correlated to soil fertility (Gordon & Rice, 2000; Danner & Knapp, 2001; Bigelow & Canham, 2002; Meisel et al., 2002) and exhibit conspicuous morphological changes on dry sites. Mineral nutrition appears not to be limiting to many oaks except on very sandy soils where moisture is also a limiting factor (Johnson et al., 2002). Several studies have identified the depth of the A, and A2 horizons and the percent clay in the surface soils with successful establishment. The major environmental constraint influencing the growth and establishment of *Quercus* are latitude, aspect, and topography. The environmental heterogeneity is also the cause of the large number of oak species (31) in Manantlan. Responses to seasonality in both temperate and subtropical oaks, including those of North America and Europe, results in relatively consistent patterns of flowering and fruit production. Most temperate species have a characteristic flowering time in spring and a fruit production period in autumn. This is true throughout much of montane of Mexico as well (Nixon, 2006). The same flowering and fruiting pattern is followed by a number of species (*e.g. Quercus crassipes* and *Q. castanea*) in the Sierra de Manantlan (Olvera Vargas et al., 1998) where masting years are synchronous among oak species, allowing an array of different species to co-exist in the same habitat (Olvera Vargas et al., 1998). In contrast, the tropical and montane tropical oaks that extend from southern Mexico to Colombia, have a less predictable pattern of flowering and fruit production (Nixon, 2006). Basic ecological research on most species is lacking, and only a few studies have addressed the regeneration and management from an ecological perspective. For instance, seed predation, seed germination, and seedling survival and growth are processes crucial for regeneration but seldom investigated, at least for the Mexican forests (Bonfil, 2006).

Regeneration processes have a pivotal role in the ecology of woody plants. They link events such as seed dispersal and germination, and seedling growth and establishment. Tree regeneration encompasses a sequence of coordinated events, each requiring specific environmental conditions and time intervals to survive. At any time the regeneration process may be interrupted for any one of numerous reasons and can eventually cause a species to become locally extinction.

Natural regeneration is crucial if a species is to maintain a viable population in the forest community. It involves the establishment and survival of juvenile individuals in the forest. The site requirements for a tree's regeneration depend on tree's temperament (Grubb, 1977). The sites themselves are regulated by many abiotic (*e.g.* light, soil water, nutrients, etc.) and biotic factors (*e.g.* competition, grazing, predation, etc.) and their interactions (Oliver & Larson, 1996). In turn, these are largely affected by species composition and the architecture of the forest via shading, and competition (Kun-Fang, 1995).

The regeneration of oak (*Quercus* spp.) forests involves time frames related to stages of stand development. It can be viewed as a multifaceted ecological process which includes flowering, fruiting and acorn dispersal from mature trees as well as acorn germination, seedling establishment and growth (Johnson et al., 2002). Oak forests can be successfully regenerated by sexual or asexual means including from seed or from root or stump shoots but the relative importance of these modes of reproduction differ between species (Johnson & Krinard, 1983; Larsen & Johnson, 1998). It is difficult to establish a comparison among the alternatives for regeneration of oak forests mainly because their methods of establishment, and the physiological processes including photosynthesis as well as their range of tolerance to stress varies between species and developmental stage (Hodges & Gardiner, 1993). Even though coppice is extremely important source of regeneration, due to the growth and persistence of shoots after disturbances, including fire and flood (Bond & Midgley, 2001; Johnson et al., 2002), the commonest way to naturally regenerate oak forests is from seed. Seed provides the most effective means of securing a stand of seedlings (Griffin, 1971; Hannah, 1987). Seedling mortality is normally very high (Collins & Good, 1987; Callaway, 1992a) and because there are numerous potentially biological and environmental factors that can prevent their successful establishment (Buckley et al., 1998; Löf et al., 1998). Their

establishment is therefore a critical and uncertain step in securing successful regeneration.

There are a number of interrelated ecological issues involved in regenerating oak forest ecosystems. This is one of the reasons it has been claimed (*see* Loftis & McGee, 1993 *and references therein*) that regenerating oak forests represent a significant problem. Prime causes that impede a satisfactory regeneration include erratic acorn production, acorns being unable to reach the mineral soil due to litter accumulation, acorn predation by insects, rodents, and mammals, including defoliation and browsing of established seedlings and saplings and seedling mortality due to environmental stresses (Lorimer, 1993; Harmer, 1994a; Aizen & Woodcock, 1996; Leiva & Fernández-Alés, 2003). In Mexican oak forest ecosystems, the same range of problems exists (Bonfil, 2006). The current intensity and pattern of land-use in many montane forests in southern Mexico has been also cited (Quintana-Ascencio et al., 1992; Ramírez-Marcial et al., 2006) as a factor that obstructs the successful establishment of *Quercus* species.

Oak seedlings grow slowly, and another important cause of the lack of success in achieving regeneration in Mexican is caused by competition with more tolerant and faster-growing woody species and herbaceous vegetation (Ramírez-Marcial et al., 1996). Hix & Lorimer, (1991) argue that most oaks have a conservative growth strategy in which photosynthate resources of young seedlings are devoted first to build a root system. If seedlings do not develop large and adequate root systems quickly they will stagnate and eventually die if they are not released from competitive vegetation.

Abiotic factors

Water availability is one of the most crucial and limiting factors linked to failure of oak regeneration, which is consequently most successful on moist well-drained soils and in mid-slope position (Danner & Knapp, 2001). Sufficient water promotes germination, survival and successful establishment (Bonner, 1968; Anderson et al., 2001). However, other studies carried out in North America have shown that on some moist sites it can be more difficult to achieve successful regeneration than on drier ones because of under storey competition with both faster-growing woody species and herbs (Carvell & Tryon, 1961).

In dry habitats the two important factors that limit the establishment and growth of seedlings are excessive radiation and reduced water availability. The ease with which certain species of oaks can be regenerated on dry sites appears to be a function of differences in morphology and physiology between oaks and their competitors. The theory suggests that in several species of Mexican oak there are marked intraspecific differences in physiology which are likely to influence patterns of regeneration in mixed stands (Luna-Vega et al., 2006; Meave et al., 2006).

Morphological adaptations that account for the success of some oak species on dry sites include deep roots, xeromorphic leaves, and an effective xylem transport system (Abrams, 1990). Thus, for *Quercus* seedlings to persist in dry habitats they must produce long taproots. These are needed to access underground water before the surface soil dries excessively. This is behaviour is evident in several species of oak but it is apparently quite rare in many other woody species (Battaglia et al., 2000). Compared with co-occurring species in dry habitats oaks show: (1) higher rates of photosynthesis and less decrease in photosynthesis with increasing soil and atmospheric drought, (2) higher water-use efficiency, (3) slower stomatal closure as drought progress and higher leaf conductance, (4) lower water potential for stomatal closure, and (5) greater osmotic and elastic adjustments in leaves (Hodges & Gardiner, 1993; Gardiner et al., 2001).

In addition, there is evidence to suggest that soil fertility is an important contributory factor for seedling establishment. Research has shown that the presence of most oak species on a site is inversely correlated to soil fertility, although most species are adapted to grow in a wide range of fertility conditions (Gordon & Rice, 2000; Danner & Knapp, 2001; Bigelow & Canham, 2002; Meisel et al., 2002).

Acorn germination is usually good in uncompacted, moist and well-drained mineral soils. This allows a penetration by the developing radicle. Because radicles are unable to penetrate soil that has been compacted at the surface, soil disturbance can also enhance the establishment of oak regeneration; as a result soil scarification is often suggested to improve initial and possible long-term survival of seedlings (Gribko et al., 2002).

Light availability is important for successful oak regeneration. Juvenile oaks are usually considered to be somewhat intolerant to shade and they eventually need full light and

release from competition to become properly established (Rzedowski, 1978). However, the interaction between canopy species composition and sizes of the canopy openings with species regenerating beneath and their respective establishment success has not yet been extensively studied and still not well understood. Research in the Sierra de Manantlan has suggested that oaks are moderately tolerant or shade-intolerant (Figueroa-Rangel & Olvera Vargas, 2000b; Olvera Vargas et al., 2000b; Olvera Vargas et al., 2006) making them unlikely to thrive beneath the canopy of their own parents and thus to facilitate their replacement by shade-tolerant species. This has particularly been observed on mesic sites.

Biotic factors

The management implications of fluctuations in acorn crop size underscore the desirability of understanding their patterns of production and the factors that cause the variability, and whether acorn crops can be predicted (both within a year and long term) (Greenberg, 2000). In oaks, natural regeneration can be limited by the quantity of seed produced, by the effectiveness of dispersers, by the availability of microsites for germination and establishment and the activity of herbivores feeding on acorns, seedlings and juveniles. However, one of the most obvious reasons for limited natural regeneration is the wide range in acorn crop size from year to year, which characterises the concept of "mast seeding" or "masting" behaviour. Acorn crop variation is also significant at several others levels, including from individual to individual, population to population, and species to species (Koenig & Knops, 2002).

Masting is the synchronised, episodic production of acorns by one or more tree species in one year, followed by widespread crop failure in others (Steele et al., 2004). The irregular production of large crops is assumed to satiate populations of acorn predators. In years of low or average production, many vertebrates act as predators, whereas in years of high production, they function as dispersal agents when hoarding and then fail to use excess acorns (Janzen, 1971).

Masting is considered by many as a genetically influenced factor affecting acorn dispersal and seedling establishment. In a recent review Koenig & Knops (2002) concluded that masting in oaks is an adaptive response that is best explained by the

predator station hypothesis. This argues that mast failures serve to decrease seed predators, whilst good crop years result in satiation of seed predators and seedling establishment.

Acorn predation can hinder recruitment indirectly by specifically affecting the few seeds dispersed to high-quality microsites. When the activity of acorn predators varies between microhabitats, the spatial distribution of acorns and seedlings can alter their own probability of survival and passage to the next demographic stage (Janzen, 1971; Sork et al., 1993; Leiva & Fernández-Alés, 2003; Sun et al., 2004). Mortality due to acorn predation and herbivory is usually high in oaks. Research confirms that acorn predation and herbivory present a significant bottleneck to oak seedling recruitment. In areas with poor oak regeneration the evidence points to lack of acorn production, an event that is strongly linked to animal predation.

Another important cause of a lack of success in regenerating oak forests is competition with more tolerant and faster-growing woody species and herbaceous vegetation, a process that is frequently associated with the slow growth of oak seedlings. Hix & Lorimer (1991) argue that most oaks have a conservative growth strategy in which photosynthate resources of young seedlings are devoted initially to building a root system. If seedlings do not develop large and adequate root systems quickly they will stagnate and eventually die if they are not released from competing vegetation.

Anthropogenic factors

Fire and disturbance by logging favour oak regeneration (Crow, 1988). This seems to be the reason why successful regeneration in the Sierra de Manantlan appears to depend upon some sort of low-impact disturbance that eventually involves the creation of gaps (Figueroa-Rangel & Olvera Vargas, 2000b). The same is true for oak in Chiapas, southern Mexico where undisturbed successional paths following the abandonment of agricultural fields is *Quercus*-dominated pine-oak forest (Ramírez-Marcial et al., 2001).

In some oak forest ecosystems around the world, severe regeneration problems have occurred due to the lack of large scale fires that favoured the spread of several oak species during the last century (Abrams & Downs, 1990; Abrams & Nowacki, 1992;

Crow et al., 1994). Crow (1988) provides an excellent review and bibliography on the ecology and regeneration of oak forests. He cites numerous authors to show how fire and logging favour oak regeneration.

In this context, the specific objectives of this chapter are: (1) to determine whether the juvenile forest communities at Cerro Grande show detectable spatial patterns of floristic variation; (2) to discover the extent to which micro-environmental heterogeneity correlates to observed patterns of floristic variation and (3) to investigate the temporal dynamics of seedlings and saplings across the *Quercus*-dominated forests.

5.1.2 Hypotheses to be tested

Based on the literature reviewed and the objectives proposed in this chapter, the following hypotheses are tested:

- **Ho_1.** Seedlings and sapling of the various species are not randomly distributed across the study area.
- **Ho_2.** Environmental heterogeneity does not promote discrete assemblages of floristic distribution in either seedlings or saplings.
- **Ho_3.** The abundances of the different species of seedlings and saplings do not vary over time.

5.2 Research methods

5.2.1 Data description and processing

In this chapter, only juvenile trees within the 500 m^2 plots (seedlings -individuals $\leq$ 1.30 m tall- and; saplings -individuals > 1.30 tall and < 5 cm dbh) were included in the analysis. Data collected during the 2002 forest inventory were analysed to describe spatial patterns of floristic variation across the study area in seedlings and saplings (objective **1**), along with their micro-environmental characteristics (objective **2**). A similar pair-wise data structure by floristic zone as the one generated for the adult community in Chapter 4 (Table 4.1) (*e.g.* 1991→1994→2002; 1994→2002 and

1998→2002) was built for both seedlings and saplings using absolute density data to investigate the dynamics of temporal floristic changes (objective **3**).

5.3 Data analyses

Analytical approaches

In this section a brief theoretical review of the statistical methods used in this chapter is presented. The generalities of non-metric multidimensional scaling (NMDS), multi-response permutation procedure (MRPP) and canonical correspondence analysis (CCA) were described in Chapter 3 and are not described here.

The Mantel test

The Mantel (Mantel, 1967) test is a non-parametric randomisation statistical method based on similarity distance matrices that evaluates the significance of relationships between matrices by a permutation approach (Fortin & Gurevitch, 2001; Sokal et al., 2004). The Mantel test was originally designed for applications in medical science research to test the independence of the elements contained in two distance matrices considering that, within each matrix, the coefficients are not independent (Raufaste & Rousset, 2001). Therefore, the Mantel test evaluates the null hypothesis of no association between each pair of similarity matrices obtained independently, and describes the relationships among the same sample stations (Legendre & Fortin, 1989; Legendre & Legendre, 1998). There are two extensions of the Mantel test: the simple and the partial Mantel test. The *simple* Mantel test assesses the correlation between two distance matrices. In this, the statistic used to gauge the correlation between them is the classical Pearson-*r* correlation coefficient so it is subject to the same statistical assumptions (Smouse et al., 1986). However, in the simple Mantel test two variables may appear to be correlated simply because they are both linked to a third common variable. This fact may obscure underlying true associations, so that it is necessary to remove this effect before concluding that the original two variables are indeed correlated. This can be done with the partial Mantel test. Thus, the *partial* Mantel test investigates the existing correlation between two matrices while controlling the effect of

a third one, seeking to remove spurious correlations (Fortin & Gurevitch, 2001). The partial Mantel test extends the analysis to linear models with one dependent distance matrix and two or more independent matrices (Reynolds & Houle, 2002). Therefore standardised multiple regression coefficients are calculated between the elements of the dependent and independent matrices as a measure of correlation (Castellano & Balletto, 2002). Two of the most helpful features of the Mantel test are (1) the possibility of using a large number of distance measures, both Euclidean and non-Euclidean distances and; (2) any type of data can be used to construct the association matrices (*e.g.* continuous, ordinal or binary) (Peres-Neto & Jackson, 2001). King et al. (2004) also claim that because the Mantel test uses distance matrices, this approach allows the extraction of variation caused by spatial autocorrelation as well as other environmental variables to yield pure-partial correlation-relationships representing variables that can not be explained by all other variables included in the analysis.

A classic example of the application of the Mantel test in forest ecology relating environmental, geographical and floristic distances is shown in Figure 5.1. Stands that are in close proximity tend to have similar biophysical environments (*e.g.* similar soil fertility or type, micro-climate, topography, etc.) and hence a positive correlation between environmental and geographical distances. Such stands will also be likely to share similar species so that floristic distances will also be positively correlated with spatial distances. The consequence is that an observed positive association between floristic and environmental distances may simply be due to a spatial effect and not a true association between environment and species. This is an effect that can be untangled with the partial Mantel test.

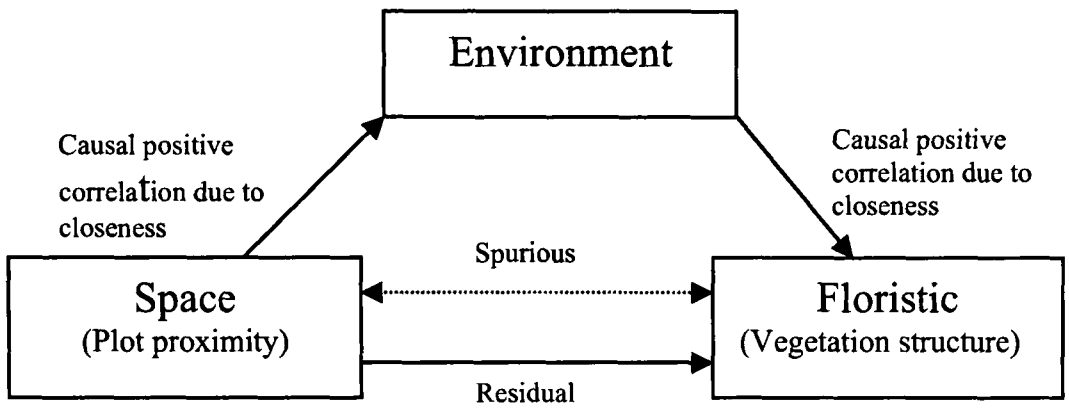


Figure 5.1. Diagram representing the interrelationship between the environment, the floristic variation and the geographic separation as assessed by the Mantel test (*modified from* Legendre & Fortin, 1989).

Repeated measure analyses of variance

Typically, ecological experiments involve repeated measurements over time on groups of organisms or samples subjected to different treatments (Gurevitch & Chester, 1986). Repeated measures analysis (RMA) can be defined as measurements made in time or space on the same experimental unit, such as a tree or a plot. RMA is therefore the investigation of the repeated measures factors, the treatment factors, and their interactions (Moser & Saxton, 1990). RAM designs have been used in psychology and agriculture research for some time but they have received the explicit attention of ecologists only relatively recently (Von Ende, 2001). For example, Potvin et al. (1990) used RMA to analyse the CO_2 dependence of photosynthesis in the ecophysiological response curves derived by repeated measurements in C_{14} grass; Funk (1979) studied the impact of various intensities of pruning on *Juglans nigra* L., taking repeated measurements of total height and bole diameter at the end of each growing season; and Baker et al. (2003) recently used RMA to test for differences between species sites and years in annual diameter increment of tropical tree species in a Ghanaian rain forest.

RAM designs are generally analysed by parametric methods using either univariate or multivariate approaches. The univariate analyses are ANOVA designs (randomised block, split-plot design) that involve blocking. MANOVA is used for multivariate analyses. Although the univariate approach is computationally simpler and generally

considered to be more powerful than MANOVA, it also has more restrictive assumptions (Von Ende, 2001).

5.3.1 The spatial pattern of floristic variation

The spatial patterns of floristic variation of juvenile trees were extracted with Non-metric Multidimensional Scaling (NMDS) (Kruskal, 1964) to test the hypothesis that species are randomly distributed across the study area (Ho_1). All NMDS ordinations were carried out separately on seedlings and saplings following an equivalent protocol to the one used for the adult community (*see* section 3.3.3; Chapter 3 and Appendix 3.1). However, in both seedlings and saplings instead of using I^P as the quantitative parameter, transformed plot-by-species absolute density data matrices (Binary Relativization with respect to the Mean; PC-ORD v.4; (McCune & Mefford, 1999)) were used for each vegetational category. The number of dimensions with the lowest *STRESS* on each matrix was determined by running at least five slow and thorough autopilot ordinations, and then NMDS was carried out by manually stepping down from six to one dimension.

From the above procedure it was found that three dimensions for seedlings and two dimensions for saplings gave the best fits since it was observed that there was no reduction in *STRESS* if additional axes were added. Therefore, to run NMDS the general settings were as follows: number of dimensions (axes) = 3 (for seedlings) and 2 (for saplings); number of runs with real data = 40; stability criterion 0.0005; interactions to evaluate stability = 500; maximum number of interactions = 400; initial step length = 0.2 and the staring coordinate file produced in autopilot with the lowest *STRESS*. Similarly, the Sørensen's (Bray-Curtis) index was used as a measure of dissimilarity between plots.

5.3.2. The role of micro-environmental heterogeneity

Environmental variable selection

In ecological investigations the number of variables on hand for measurement is generally large (≥ 20). This particularly situation arises with environmental information, and as a result, a number of parameters contained in the data set may be redundant (King & Jackson, 1999). When there are a large number of highly correlated variables the results are often little changed if only a subset is used (Jolliffe, 1972). Principal Components Analysis (PCA) is a popular ordination method in community ecology used for analysing the structure of vegetation; however this technique is also employed for several other purposes such as data reduction. It is beyond the scope of this chapter to describe PCA in detail but a brief outline of how it was used in this study is given.

PCA is an indirect ordination method involving a mathematical procedure that transforms a number of correlated variables (X's) into a smaller number of uncorrelated variables (Y's) called principal components. Each Y is a linear combination of the original variables X. Each new Y*i* variable is derived in decreasing order of importance, that is, the principal component (Y_1) accounts for as much as possible of the variation in the original data, then a second component (Y_2) and so on. PCA creates new orthogonal axes that are linear combinations of the original variables that explain, as much as possible, of the total variance (Dale, 2000) of the data and thus parsimoniously simplify its structure.

In this chapter, as a means of eliminating redundant environmental variables two steps were followed. First, out of the total number of environmental variables recorded in the 500 m^2 psps ($n = 38$; *see* Chapter 2) a sub-group of 28 were subjectively selected (Table 5.1). This sub-group was intuitively hypothesized to be the most likely to explain spatio-temporal patterns of floristic variation in seedlings and saplings. Information contained in the original data set such as bark thickness, damage on tree stem, biological condition etc. (*see* Table 2.1; Chapter 2) were deemed unimportant factors for explaining the dynamics of the juvenile communities. Secondly, the subjectively selected sub-group of variables was subject to PCA ordinations based on a correlation matrix. The ultimate goal of running PCA prior to any further analysis was to reduce the

number of explanatory variables by creating X composite variables (one by principal component), and thus avoiding misleading results due to highly correlated data.

PCA is one of the few ordination methods allowing the use of variables measured in different scale units (*e.g.* elevation, concentration of nutrients, canopy openness, pH, etc.) (Palmer, 2000). However, in this thesis, prior to running PCA the data was transformed in order to approximate normality as well as to give each variable equal weight for the analyses as recommended by (Jackson, 1993). For soil-related variables (except for pH; *see* Peres-Neto et al., 2003) log_{10} transformations were performed. Sun-aspect recorded as degrees of azimuth was converted into a liner scale (Beers' transformation; *see* Chapter 2). The remaining variables were power transformed (Seaby et al., 2004).

Table 5.1 Descriptive environmental variables thought to correlate with the juvenile communities in *Quercus*-dominated forests. I = interval; N = nominal (see also Table 2.1 and Table 2.2; Chapter 2 for variable description). Trans. = Transformation applied to the data.

Code	Variable	Type	Units	Trans.	Min.	Max.	Mean	Std.
	Physiographic							
ELE	Elevation	I	Metres	Power	2020	2350	2243.43	79.55
SLO	Slope terrain	I	Percentage	Power	0	75	31.94	13.52
ASP	Aspect*	I	Degrees	Beer's*	$1.5x10^{-4}$	1.99	1.08	0.68
CAT	Catena$^{\ell}$	N	1-6	Power				
TOP	Topography	N	1-2	Power				
RCK	Rocks ≥1 m ø	N	Percentage	Power	0	20		
STO	Stones ≥5cm< 1m ø	N	Percentage	Power	1	40		
	Edaphic							
LTD	Litter	I	Centimetres	$\log_{10}$	0	12.1	5.35	2.35
A	A_0	I	Centimetres	$\log_{10}$	0	9.0	2.4	1.39
OMC	Organic Matter Content	I	Percentage	$\log_{10}$	3.96	18.45	9.63	3.35
PH	Ph	I			5.2	6.8	6.2	0.34
CEC	Cation Exchangeable Cap	I	mmol g^{-1}	$\log_{10}$	31.0	90.0	63.77	12.48
Sand	Sand	I	Percentage	$\log_{10}$				
Clay	Clay	I	Percentage	$\log_{10}$				
Silt	Silt	I	Percentage	$\log_{10}$				
Ca	Calcium^{+}	I	Kg.ha^{-1}	$\log_{10}$	560	2200	913.02	386.53
K	Potassium^{+}	I	Kg.ha^{-1}	$\log_{10}$	170	560	456.35	123.46
Mg	Magnesium^{+}	I	Kg.ha^{-1}	$\log_{10}$	12	25	14.27	4.9
Mn	Magnesium $^{+}$	I	Kg.ha^{-1}	$\log_{10}$	5	12	5.1	0.88
N	Nitrogenous $^{+}$	I	Kg.ha^{-1}	$\log_{10}$	3	25	9.16	5.3
P	Phosphorous $^{+}$	I	Kg.ha^{-1}	$\log_{10}$	12	25	15.92	6.01
	Biological							
CAOP	Canopy openness	I	Percentage	Power	1.61	67.32	13.15	10.92
CAHI	Canopy height	I	Metres	Power	2	40	13.56	8.00
CELH	Crown length	I	Percentage	Power	3	95	23.95	13.24
CALA	Canopy layers	N	1-3	Power				
MAT	Maturity	N	1-4	Power				
	Disturbance							
GRZ	Grazing	N		Power				
ERO	Erosion	N		Power				

* Beer's transformation and $^{\ell}$ Terrain shape index are described in Chapter 2. + Exchangeable. Ø = diameter.

Determining the number of components: the Broken-stick method

PCA produces as many axes (principal components) as variables in the data set. Thus it is necessary to choose those worth interpreting. Furthermore, within a given principal component, it is necessary to decide which variable(s) should be considered in further analysis. There are several methods for this endeavour (Franklin et al., 1995; Robertson et al., 2001; and Peres-Neto et al., 2003). In this thesis, in order to determine how many principal components to use in subsequent analyses, the 'Broken-stick' stopping rule for PCA (Jolliffe, 1972; Jackson, 1993) was applied. In a review of stopping rules Jackson (1993) found that the broken-stick method was the most reliable of a range of methods for deciding how many principal components to include. The rationale of the method assumes that if the broken stick eigenvalue is less in magnitude than the actual eigenvalue for an axis, then that axis contains more information than expected by chance and therefore should be considered for interpretation. The Broken Stick method was then calculated as (Jackson, 1993):

$$b_k = \sum_{i=k}^{p} \frac{1}{i}, \qquad 5.1$$

Where: p is number of variables (or components) and b_k is the expected proportion of variance that the k^{th} component summarises for any particular variable under the broken stick model.

Interpretation of the PCA-Broken-stick method results

As previously described in this chapter, PCA was not performed for interpreting environment gradients. Instead it was used to identify a subset of uncorrelated variables that accounted for the largest proportion of variation contained in the environmental data set. Therefore, after submitting the 28 variables to PCA, 13 of them captured the biggest amount of the explained variation (Table 5.2). Within the 13 principal components starting with the first component, all those variables with the highest loadings onto each PCA axis were kept for further analyses; all the remaining K-p variables were not taken into account.

Table 5.2. Summary of the Principal Component Analysis (PCA) based on a correlation matrix of the 28 environmental variables. Bold figures represent the significant components after the Broken-stick method.

Component (Axis)	Eigenvalues	Cumulative Total	Total Variance (Percentage)	Total Variance (Cum. %)	Broken-stick Eigenvalue
1	**4.765045**	4.765045	17.01802	17.01802	**3.927171**
2	2.60422	7.369265	9.300786	26.31881	2.927171
3	2.35656	9.724921	8.416288	34.73509	2.427171
4	**2.130955**	11.85587	7.610555	42.34565	**2.093838**
5	1.800861	13.65673	6.431648	48.77737	1.843838
6	**1.644391**	15.30112	5.872826	54.65012	**1.643838**
7	**1.486225**	16.78738	5.307947	59.95807	**1.477171**
8	**1.337278**	18.12465	4.775993	64.73406	**1.334314**
9	**1.237281**	19.36193	4.41886	69.15292	**1.209314**
10	1.074456	20.43727	3.837343	72.99026	1.098203
11	0.911249	21.34852	3.254462	76.24472	0.998203
12	0.801707	22.15023	2.863239	79.10796	0.907294
13	0.751441	22.90167	2.683719	81.79168	0.823961
14	0.695551	23.59722	2.484113	84.27579	0.747037
15	0.603418	24.20064	2.155065	86.43086	0.675609
16	0.550957	24.75159	1.967702	88.39856	0.608942
17	0.506484	25.25808	1.808871	90.20743	0.546442
18	0.468103	25.72618	1.671796	91.87922	0.487619
19	0.417453	26.14363	1.490905	93.37013	0.432063
20	**0.392293**	26.53593	1.401045	94.77117	**0.379431**
21	**0.333021**	26.86895	1.189361	95.96054	**0.329431**
22	0.271952	27.39445	0.905536	97.83733	0.281812
23	**0.253557**	27.14092	0.971257	96.93179	**0.236358**
24	**0.221384**	27.61583	0.790657	98.62798	**0.192885**
25	0.141231	27.75706	0.504397	99.13238	0.151213
26	**0.111431**	27.86855	0.397965	99.53035	**0.110213**
27	0.069287	27.93778	0.247454	99.7778	0.072751
28	**0.062216**	28	0.222245	100	**0.035714**

Canonical correspondence analysis ordinations

The importance of the measured micro-environmental heterogeneity on the spatial patterns of floristic variation in seedlings and saplings was assessed running separated Canonical Correspondence analysis (CCA) (performed with CANOCO v.4) (ter Braak, 1986) following a similar protocol as the one described in Chapter 3 (section 3.3.5) for the adult community. Therefore, using the micro-environmental data after the PCA-broken stick method for variable selection (Table 5.2), CCA ordinations were computed with forward selection ($\alpha = 0.005$) of independent variables and an unrestricted Monte Carlo Permutation test (ter Braak & Smilauer, 1998) using 499 permutations. In

addition, to comply with statistical assumptions and with the aim of excluding the effect of species with low frequencies the downweighting procedure, available in CANOCO v.4, was performed. This approach should reveal the strength and direction (significance) of each contributing environmental variable in explaining the observed patterns of floristic variation.

5.3.3. Is the floristic variation spatially autocorrelated to the environmental heterogeneity?

To discover whether the floristic variation was correlated to micro-environmental heterogeneity irrespective of their geographic separation, the simple and the partial Mantel tests (performed with zt v.1) (Bonnet & Van der Peer, 2002) were further carried out on separate data matrices for seedlings (n = 85 psps) and saplings (n = 54 psps) as a measure of partial correlation (Smouse et al., 1986; Fortin & Gurevitch, 2001). For this purpose three dissimilarity distance matrices derived from data on species composition, environmental variation and psps' geographic location were produced. The first matrix should reflect the ecological distance between each pair of psps; and the other two matrices should reveal respectively, the environmental and the geographical distances among/between psps (Legendre, 2000). The dissimilarity matrices were calculated as follows:

Ecological distance: The floristic differences between a given pair of plots were constructed on the basis of their differences in species composition. This differentiation was estimated as a percentage of dissimilarity (compositional dissimilarity *sensu* Faith et al., 1987 and De' Ath, 1999) using the Sørensen index as a measure. The Sørensen similarity is annotated as $2A/(2A+B+C)$; *where*: A is the number of species shared between plots and B and C are the number of species unique to each plot. This is a robust dissimilarity measure commonly used in community ecology when looking for unbiased quantitative estimations of floristic difference between two or more sample observations (Boyce & Ellison, 2001).

Environmental distance: The environmental dissimilarity matrix was built considering the 13 environmental variables with the biggest loadings on each PC judged to be a significant component after the Broken-stick method for variable selection.

Subsequently, a Euclidean distance matrix was calculated between each pair of plots after all environmental variables were standardised.

Geographic distance: The last matrix contained the geographic linear separation between all pairs of plots. This information was produced from the UTM (Universal Trans-Mercator) coordinates obtained with the GPS-derived geographical psps' location. The purpose was to test for a dissimilar species composition between every pair of psps, as they tend to be geographically far apart.

The size of the environmental and the geographic distance matrices were both in agreement with the size of the ecological distance matrix for each vegetational category analysed. For seedlings it consisted of 85 rows and columns, while for saplings it encompassed 54 rows and columns that corresponded to the number of psps where seedlings and saplings respectively were found. The linear distance between the psps for both vegetational categories ranged from 0.0010 to 9.5 km.

Mantel calculations

After matrix construction, the simple and partial Mantel tests were performed. In the simple Mantel test, pairs of matrices were evaluated so that the correlation between the species composition and the environment was first tested. Then the correlation between species composition and geographic separation was tested. This analytical approach should reveal whether the psps tend to be floristically dissimilar as their environmental differentiation and geographical separation increase. In subsequent partial Mantel tests the existing correlation between two matrices was evaluated while controlling for the effect of a third one. While computing the Mantel tests, all correlations were statistically tested at $p>0.0001$ using a Monte Carlo permutation with 10,000 randomisations.

5.3.4. Assessing the spatio-temporal abundance fluctuations

To test the hypothesis that patterns of recruitment by the different species in the psps do not vary spatially and temporally (Ho_3), absolute density histograms of species by plot and period of observation (*e.g.* 1991→1994→2002; 1994→2002 and 1998→2002) were first built, separately, for seedlings and saplings. This initial operation should

reveal graphically whether patterns of variation in species abundance are taking place over time and space. Then, Repeated-Measures Analysis of Variance (Gurevitch & Chester, 1986) (a GLM procedure fitted in SPSS v.12) was conducted, to test for statistical differences in density amongst the different species and along time; the analyses were conducted separately for seedlings and saplings. The records on species density taken during the periods of 1991→1994→2002; 1994→2002 and 1998→2002 were used as the repeated measures. The dependent variable was the number of individuals by species (density). The effect of time (year) was incorporated into the analysis as the (within-subjects) treatment factor and the different species in each psps, as the between-subject factors according to the following model (Von Ende, 2001):

$$X_{ijk} = \mu + V_i + \psi_{k(i)} + \tau_j + V\tau_{ij} + \psi\tau_{jk(i)} = \varepsilon_{m(ijk)} \qquad 5.2$$

Where: **X** = density, **i** = species, **j** = time, **k** = plot (subject*), **μ** = population mean, $\mathbf{V_i}$ = effect of the of different species (in k -plot-) on density, $\boldsymbol{\psi_{k(i)}}$ = subject effect nested within the respective species, $\boldsymbol{\tau_j}$ time effect, $\mathbf{V\tau_{ij}}$ time x species interaction, $\boldsymbol{\psi\tau_{jk(i)}}$ = subject interaction, $\boldsymbol{\varepsilon_{m(ijk)}}$ = source of error term; **m** = is a dummy variable to indicate that the experimental error is nested within individual observations.

The effect of time on the fluctuation in species densities (temporal fluctuations as the response variable) was evaluated for 11 (n=3), 8 (n=2) and 4 (n=2) years separately corresponding to the Qc, Mm and It groups respectively already considered in Chapter 4. Mauchly's test for the compound symmetry of the variance-covariance matrix was obtained together with the corrected significance levels (Greenhouse-Geisser and Huynh-Feldt) in case of rejection of the symmetry assumption (SPSS v.12). Mauchly's test is an examination for sphericity that assesses the circularity of a variance-covariance matrix (the sphericity assumption is that the standard error of the difference between pairs of means is constant across all pairs of means) (Von Ende, 2001).

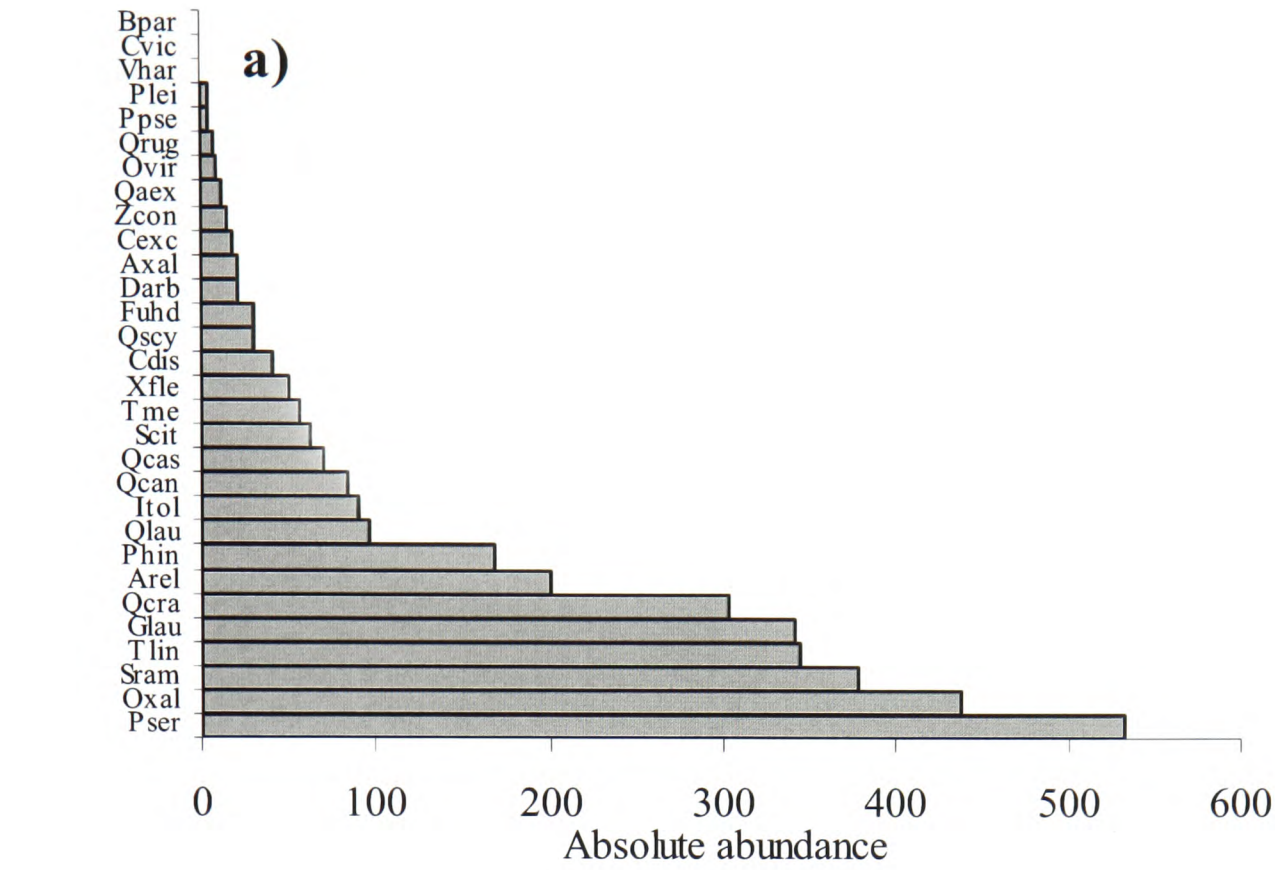
* Also described as the treatment (*see* VON ENDE, C. N. 2001).

5.4 Results

5.4.1 The floristic richness in seedlings

A total of 3,434 seedlings (≤ 1.30 m tall) were found regenerating in 85 of the 86 psps re-measured in 2002. These embodied 30 species from 23 different genera and 20 families. The mean absolute density was 40.4 seedlings per plot. Of the nine *Quercus* species represented in the overhead canopy (*see* Table 3.4, Chapter 3), two species: *Q. gentry* and *Q. obtusata* were not recorded as seedlings. The most important species in terms of absolute seedling density and rank abundance values were *Prunus serotina, Oreopanax xalapensis* and *Styrax ramirezzi*, whilst the least important were *Viburnum hartwegii, Buddleia parviflora* and *Clethra vicentina* (Figure 5.2). The highest number of species occurring in any plot was 7; however there were a number of plots with just two species of seedlings co-occurring. No plot had only one species. This floristic pattern was consistent in all the 85 psps in which regeneration was recorded during the inventory carried out in 2002, even in those plots with monospecific canopies. For example, plots 11 and 32 (2.841 km apart from each other) were both entirely dominated by *Quercus crassipes* in the upper canopy. Particularly, in plot 11 four different species of seedlings: *Arbutus xalapensis, Cornus excelsa, Prunus serotina,* and *Ternstroemia lineata* were found regenerating; while in plot 32, seedlings of *Q. crassipes, Prunus serotina* and *Arbutus xalapensis* were recorded.

Considering seedling position with respect to the overhead canopy (beneath, at the edge or gaps; *see* Chapter 2 for their definition), ANOVA results showed that the pattern of recruitment, regardless of the species, was not significantly different ($F = 0.875$ $p = 0.417$) among the three positions. Thus, 75% ($n = 2596$) of the total number of individuals were encountered beneath the canopy, 22% ($n = 738$) at the edge of the canopy and 3 % ($n = 100$) were in canopy gaps. The non-statistical differences among the three seedling positions with respect to the overhead canopy may be explained by the fact that their average occurrences were about the same (position 1 = 5.7; position 2 = 6.0 and; position 3 = 4.1). These results represented the standardised percentage of occurrence by canopy position with respect to the total sampled area (604 sub-sampling units of 1 m^2).



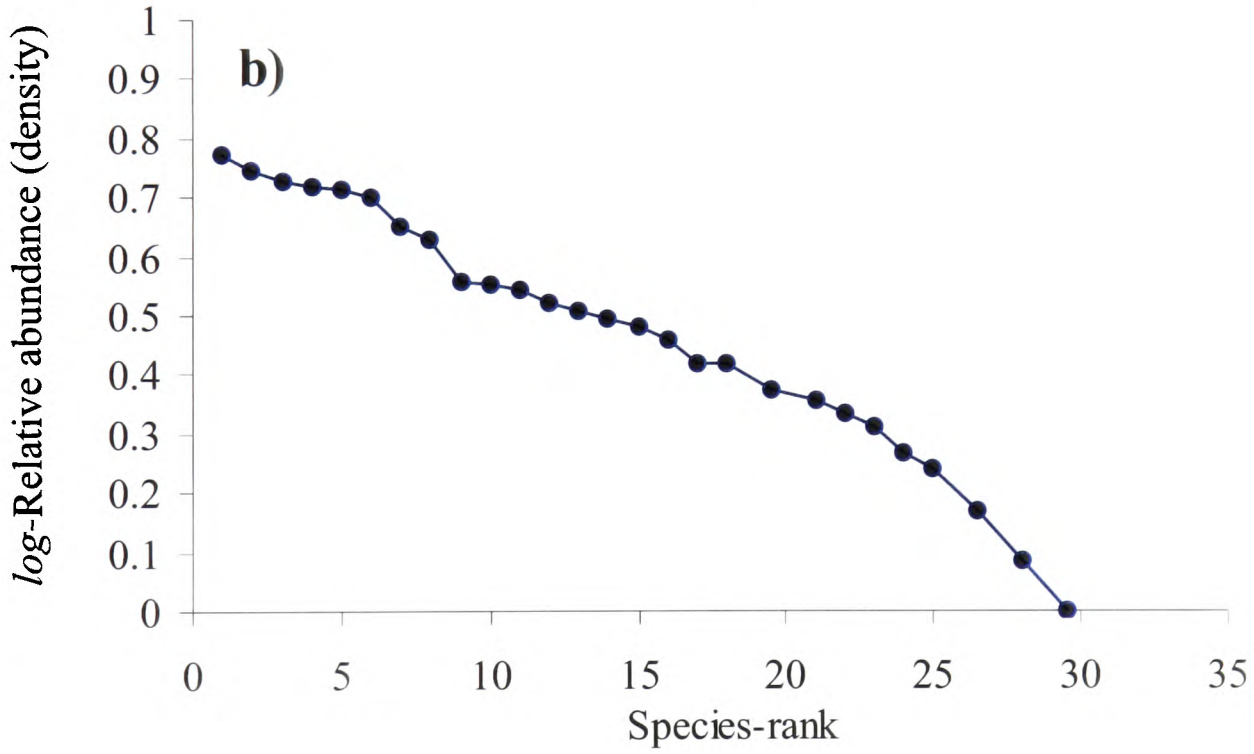
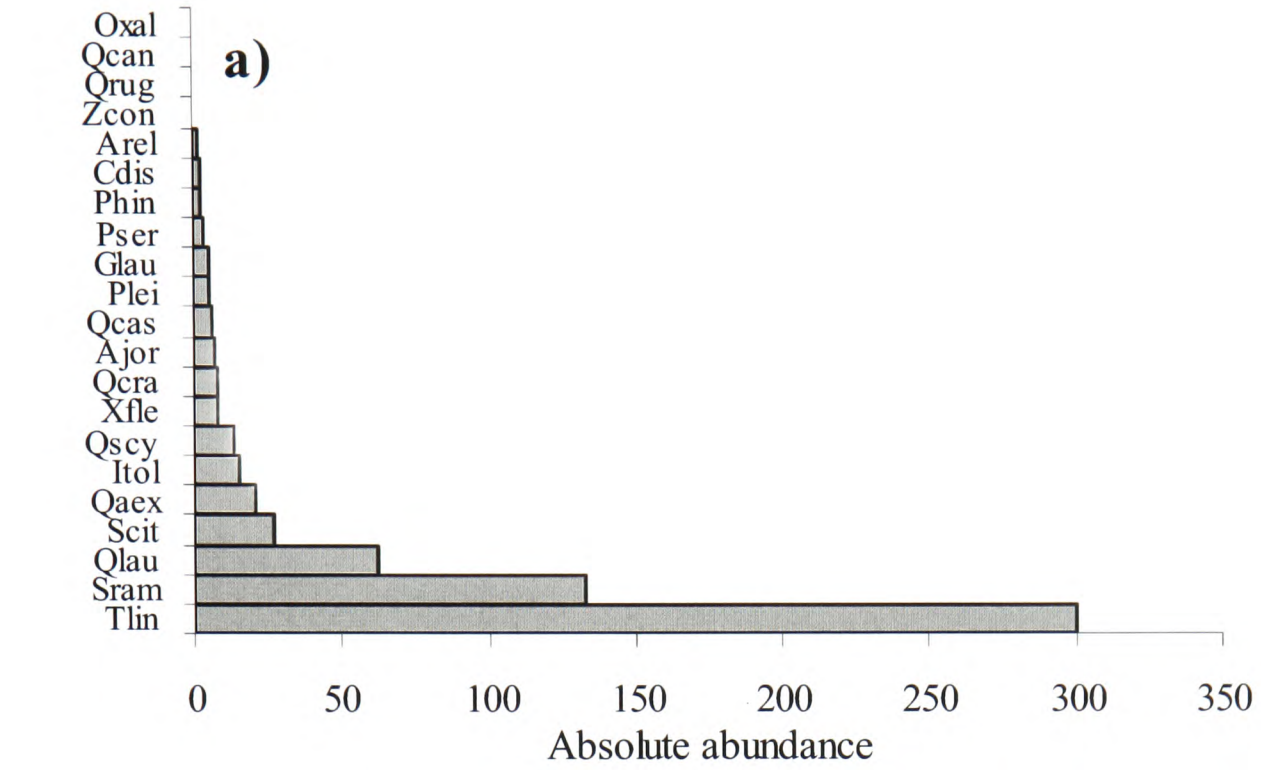


Figure 5.2. Variation in absolute abundance (a) and species rank abundance (b) for the total number of seedlings (n = 3,434) encountered in 85 psps (604 sub-samplings of 1 m^2) in 2002. The y-axis in (b) represents the *log*-relative abundance of the species, while the *x-axis* ranks each species in order from the most (*Prunus serotina* -Pser-) to the least (*Clethra vicentina* -Cvic-) abundant (*after* Magurran, 2004).

5.4.2 The floristic richness in saplings

Saplings were found in only 54 of the 86 psps remeasured in 2002. From this, a total of 627 individuals (< 5 cm dbh but ≥ 1.30 tall) were counted. Comparatively, the number of saplings corresponds to only 17.8% of the total number of seedlings inventoried. Floristically, saplings were represented by 21 species from 20 different genera and 14 families. The same *Quercus* species absent in the seedling stage (*Q. gentry* and *Q. obtusata*) were missing as saplings. The most important species in terms of absolute density and rank abundance values were *Ternstroemia lineata*, *Styrax argenteus* and *Quercus laurina*. In contrast, *Quercus candicans, Quercus rugosa* and *Zinowewia coccinea* were the least important (Figure 5.3).

Plots 64, 66 and 105 were the most species-rich with a maximum of six species of saplings each. However, in most of the plots there were simultaneously no more than three species of saplings. These low values in species richness were commonly accompanied by low density (*see* histograms of species abundance in Appendix 5.2**a-c**). This is a rather contrasting result to the pattern observed in the seedling community, where typically more than two or three species were always regenerating.



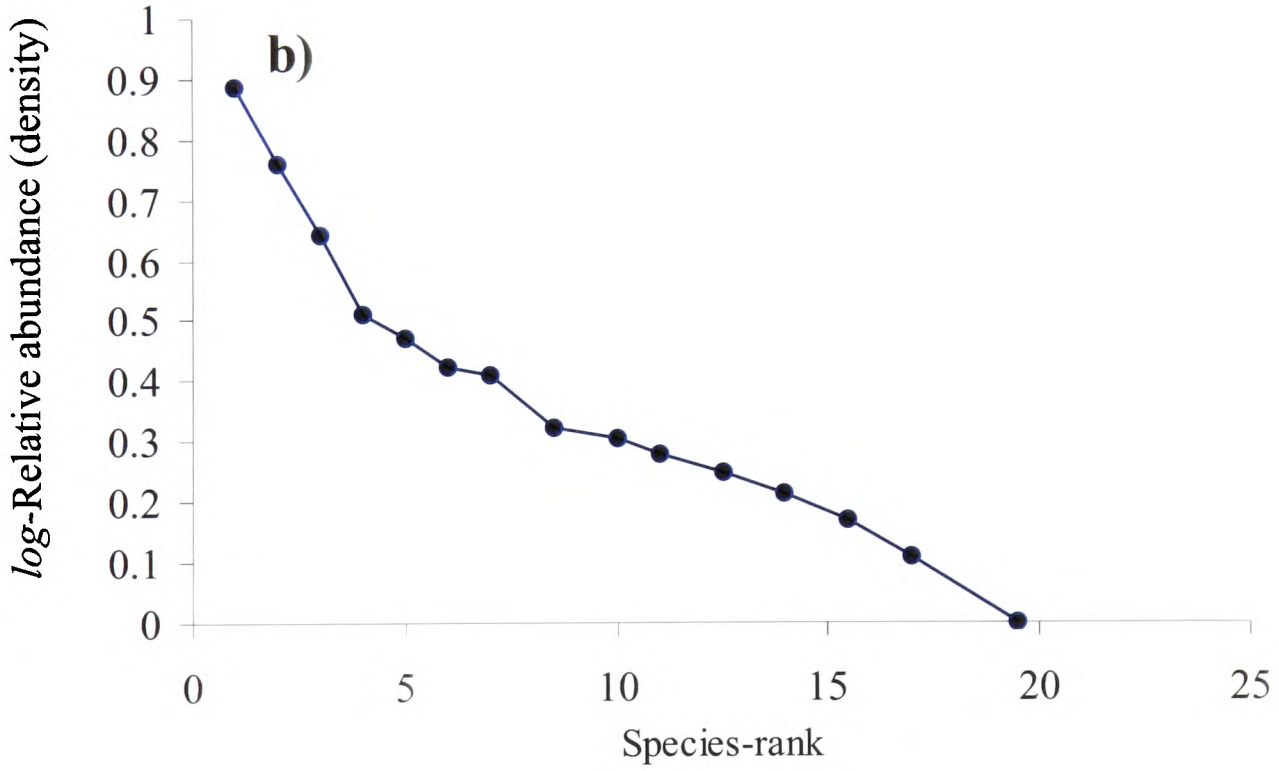


Figure 5.3. Variation in absolute abundance (a) and species rank abundance (b) for the total number of saplings (n = 627) encountered in 54 psps sub-samplings of 50 m^2 each in 2002. The y-axis in (b) represents the relative abundance of the species, while the x-*axis* ranks each species in order from the most (*Ternstroemia lineata* -Tlin-) to the least abundant (*Oreopanax xalapensis* -Oxal-).

For sapling position with respect to the overhead canopy, ANOVA results showed that the pattern of recruitment, regardless of the species, was statistically significant among the three positions ($F = 6.633$ $p = 0.002$). Thus, 76% ($n = 478$) of the total number of individuals were encountered beneath the canopy, 19% ($n = 121$) at the edge of the canopy and 5 % ($n = 28$) were in canopy gaps. The statistical differences among the three sapling positions can be explained by the fact that their average occurrences contrasted more than those in seedlings (position 1 = 9.4; position 2 = 4.5 and; position 3 = 2.1). An examination of the data from previous inventories indicates similar patterns of occurrence with respect to the canopy cover. For instance, data collected in 1998 showed that 88.9% of the individuals occurred beneath the canopy, 9.5% at the canopy edge and 1.5% in gaps.

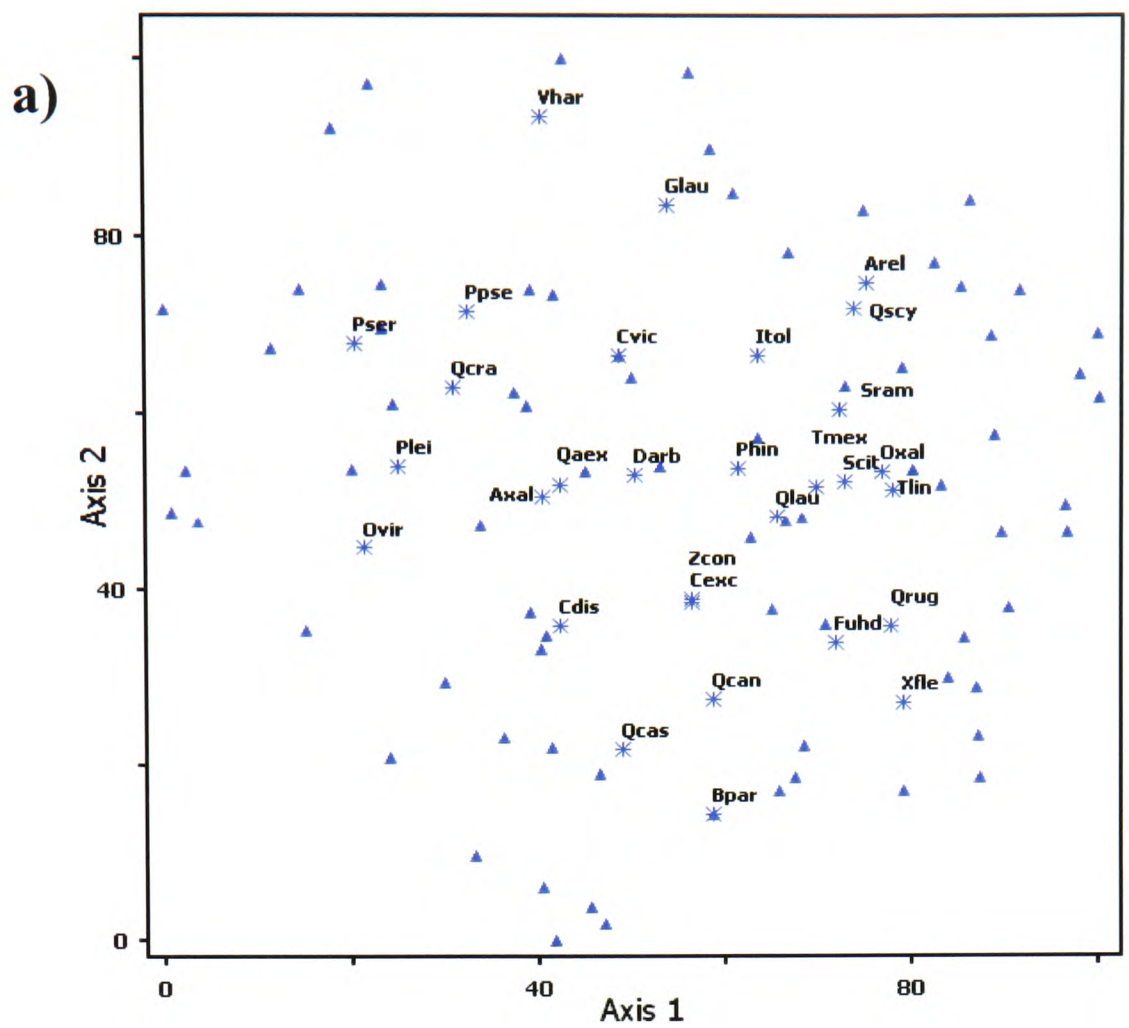
5.4.3 The spatial patterns of floristic variation of juveniles

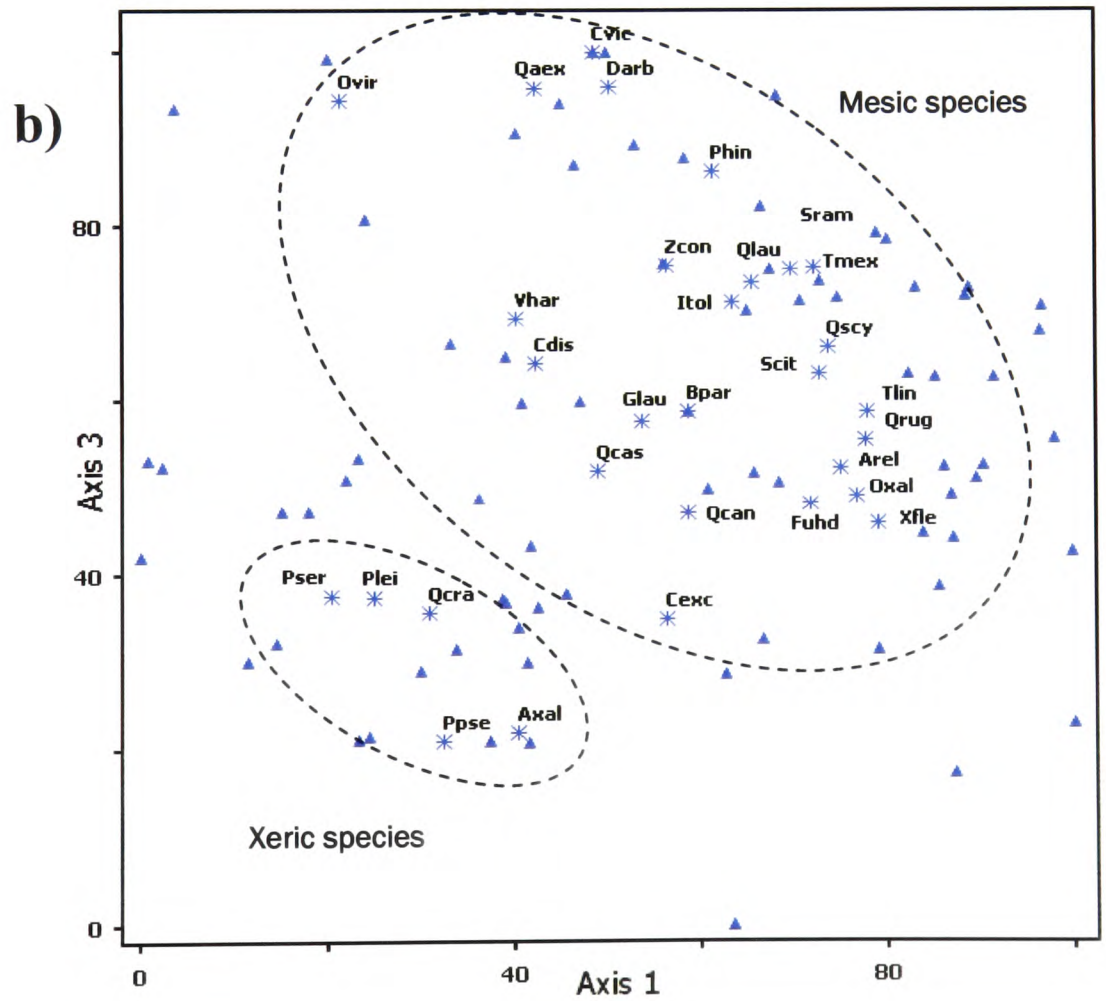
Seedlings

Figures 5.4a-b show the NMDS ordination results run on seedling absolute density. Three dimensions (axes) as determined by the Monte Carlo randomisation test (p>0.005; *STRESS* 18.5) were sufficient to explain most of the floristic heterogeneity previously described, which altogether explained 71.8 % of the total variation. In these two figures, it was clearly evident that the overall floristic pattern of distribution was relatively balanced over the ordination space. The first visual inspection, mainly on axes 1 and 2 (Figure 5.4a) on the NMDS ordination, which accounted for 40.8% of the variability in the data, did not reveal any obvious pattern of assemblages among the psps based on their species composition. Nonetheless, a careful examination may suggest that those species labelled as a xeric group (*Q. crassipes, Prunus serotina, Pinus leiophylla, P. pseudostrobus* - *see* Chapter 3) tended to gather in close proximity at the middle left-side of the NMDS diagram (Figure 5.4a).

Furthermore, if taking into consideration the NMDS projections on axes 1 and 3 (Figure 5.4b), which explained 24% and 31% of the variation respectively; a clearer floristic pattern emerged in both axes. Although not as visibly demarcated as in the sapling community (further discussed in this chapter), the floristic arrangement was more similar to the one depicted by the adult community (Figure 3.3; Chapter 3). The most

obvious floristic trend in the seedling community was again shown by the species of the xeric group (*Quercus crassipes, Prunus serotina, Pinus leiophylla* and *Pinus pseudostrobus*), which seem to be spatially associated whilst those taxa of mesic areas were more heterogeneously distributed over the NMDS ordination space.





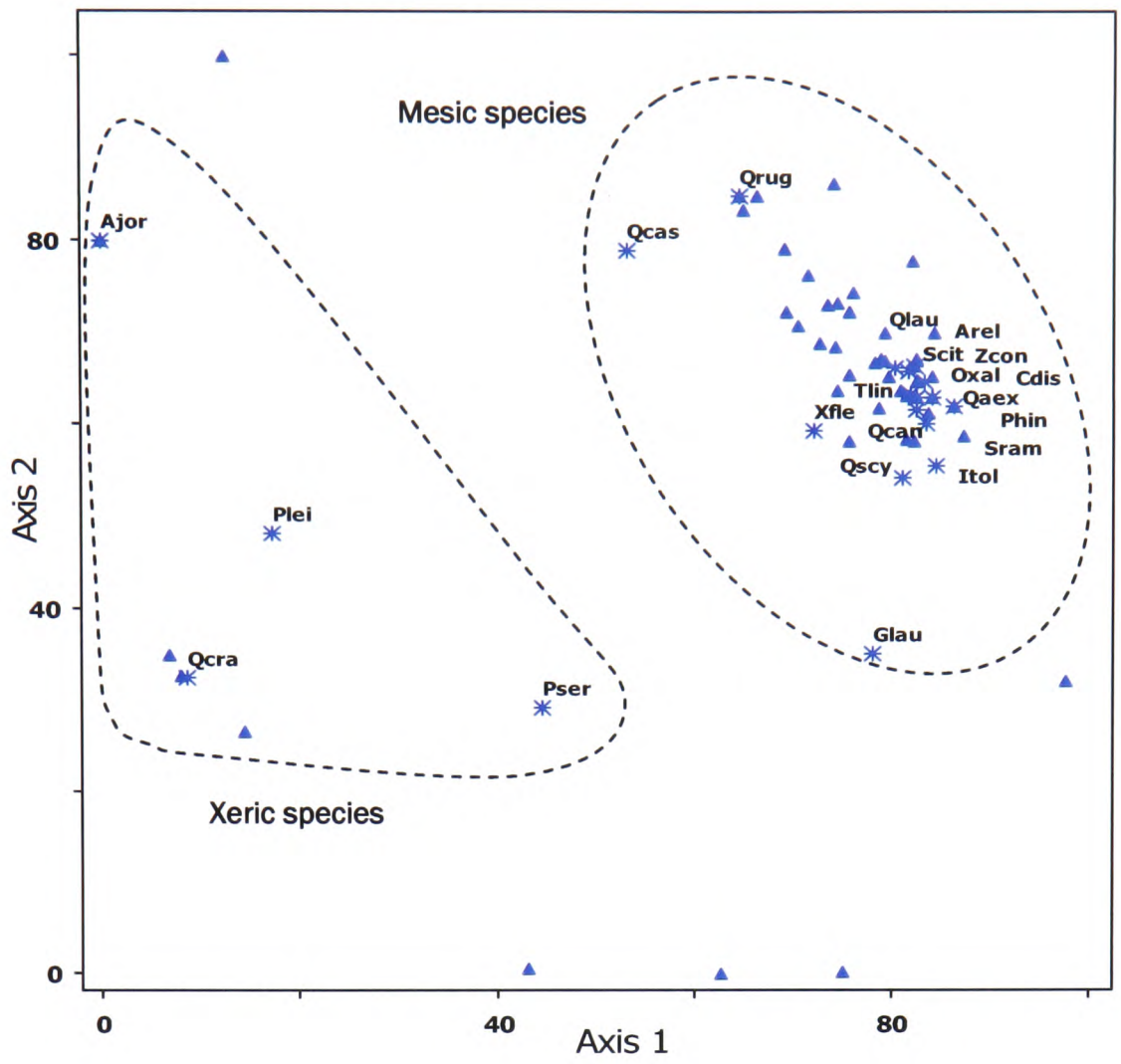
Figures 5.4a and **5.4b.** First three axes of non-metric multidimensional scaling for seedlings (85 sub-plots x 30 species) (*STRESS* 18.5; p=0.02) based on Sørensen dissimilarity index. Solid triangles represent psps. Asterisks show species centroids relative position. (*For species names see* Chapter 3; Table 3.3).

Results from the multi-response permutation procedures (MRPP; Berry et al., 1983; Zimmerman et al., 1985) indicated that there are significant floristic differences between the Mesic-Xeric (M_E-X_E), Mesic-Transition (M_E-T_R) and Xeric-Transition (X_E-T_R) zones (all p = <0.0001). Floristic differences between groups were consistent, based on presence-absence seedling data with the Euclidean distance as a measure, but also when using abundance data with the Sørensen dissimilarity index as a measure of ecological distance. Both testify to the occurrence of different vegetation zones in the study area.

Saplings

Figure 5.5 shows the NMDS results for saplings. The first two dimensions were sufficient to explain the variability of the sapling community as determined by the Monte Carlo randomisation test (p>0.002; *STRESS* 17.3), which explained 67.3 % of the total variation. The NMDS projection for saplings, as with the adult community (Chapter 3), extracted two main vegetational zones, one clearly dominated by species characteristic of the wettest (mesic) habitats of the study area such as *Quercus laurina, Q. scytophylla, Ilex tolucana, Oreopanax xalapensis,* etc. (Figure 5.5) and another of xeric habitats.

Discrete vegetational assemblages occurred in saplings as in seedlings and adult trees. However, an interesting but at the same time unexpected result that emerged in the sapling community was that species which appear associated (*e.g. Quercus crassipes, Prunus serotina, Alnus jorullensis* and eventually, *Pinus leiophylla*) over the NMDS ordination diagram, were positioned relatively far apart from each other along axis 2. These results suggested a greater dissimilarity exits in species composition between plots in the xeric group than in the mesic group. Furthermore, no transition floristic zone was observed in saplings. This was an inverse pattern to the one manifest by seedlings (Figure 5.4a-b) and by adult trees (Figure 3.2).



Figures 5.5. First two axes of non-metric multidimensional scaling for saplings (54 sub-plots x 21 species) (*STRESS* 17.3; p=0.02) based on Sørensen dissimilarity index. Solid triangles represent psps. Asterisks show the relative position of species centroids. Species names are abbreviated as described in the previous figure.

These results could partially be explained by the fact that most of the sapling sub-psps were monospecific as well as of low tree density. This was a common pattern observed mainly in those sites classified as xeric. In contrast, the ones established in the mesic areas always had two or three species and were relatively denser. Because of this, NMDS classified the xeric ones as more dissimilar sites, separating the plots within the ordination space.

MRPP comparison based on presence-absence data with Euclidean distance as a measure revealed significant floristic differences (p = 0.0002) between the Mesic and Xeric (M_E-X_E) floristic zones in saplings. As in seedlings, this result applied when using abundance data with the Sørensen dissimilarity index as a measure of ecological distance. These results demonstrate the occurrence of different vegetational zones in the

study area. However, in the sapling community floristic differences were more pronounced when using presence-absence ($p = 0.0002$) than when using abundance data ($p = 0.0004$).

5.4.4 The role of micro-environmental heterogeneity on floristic patterns

Seedlings

The CCA showed the degree to which the observed floristic heterogeneity is related to the environmental heterogeneity. CCA ordinations conducted on seedlings revealed that seven main environmental gradients are responsible for the patterns of species distribution in the *Quercus*-dominated forests of Cerro Grande (Figure 5.6). The most significant explanatory variables (according to the forward selection procedure, $\alpha = 0.05$) for the first axis ($\lambda_1 = 0.2966$) were canopy height (CAHE) and canopy openness (CAOP); whilst in the second axis ($\lambda_2 = 0.1446$) were litter and non-grazed (Gra0) and light grazing areas (Gra1) (Table 5.3). Graphically in both axes, considering the length and direction of the vectors, several other micro-environmental variables resulted nearly parallel in importance as well (Figure 5.6) (*e.g.* aspect, crown length -CRLH). This suggests likely close correlations, although this may be obscured by the higher weight of the former variables.

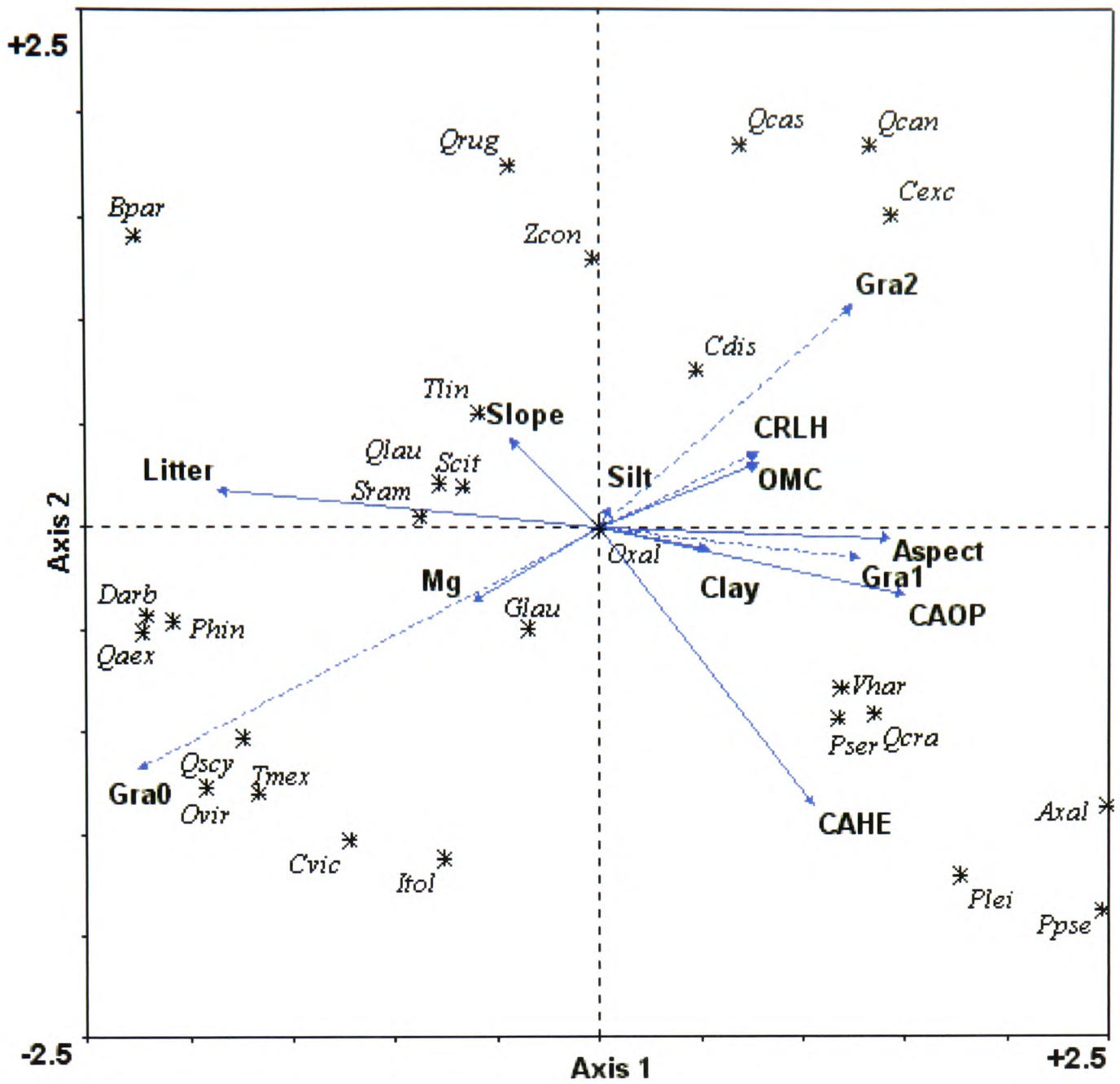


Figure 5.6. Canonical correspondence analysis biplot showing the relationship between 30 species of seedlings and 13 environmental variables (after the PCA and Broken-stick method for variable selection). The scales marked on both axes are in standard deviation units. The biplot captures 44.5 percent of the total variation. Solid and dashed arrows indicate the centroids of both interval and nominal variables respectively. The length and direction of the arrows indicate the strength and sign of the correlations. Perpendicular arrows suggest lack of correlation while those pointing in opposite directions indicate negatively correlated variables. Species names are abbreviated as follows: **Arel** = *Abies religiosa var. religiosa;* **Axal** = *Arbutus xalapensis;* **Bpar** = *Buddleia parviflora;* **Cdis** = *Comarostaphylis discolor subsp. discolor;* **Cexc** = *Cornus excelsa;* **Cvic** = *Clethra vicentina;* **Darb** = *Dendropanax arboreus;* **Fuhd** = *Fraxinus uhdei;* **Glau** = *Garrya laurifolia;* **Itol** = *Ilex tolucana;* **Ovir** = *Ostrya virginiana;* **Oxal** = *Oreopanax xalapensis;* **Phin** = *Persea hintonii;* **Plei** = *Pinus leiophylla;* **Ppse** = *Pinus pseudostrobu;* **Pser** = *Prunus serotina;* **Qaex** = *Quercus aff. excelsa;* **Qcan** = *Quercus candicans;* **Qcas** = *Quercus castanea;* **Qcra** = *Quercus crassipes;* **Qlau** = *Quercus laurina;* **Qrug** = *Quercus rugosa;* **Qscy** = *Quercus scytophylla;* **Scit** = *Symplocos citrea;* **Sram** = *Styrax ramirezii;***Tlin** = *Ternstroemia lineata subsp. lineata;* **Tmex** = *Tilia mexicana;* **Vhar** = *Viburnum hartwegii;* **Xfle** = *Xilosma flexuosum;* **Zcon** = *Zinowewia concinna.* A key to the other variables is given in Table 5.3, on the next page.

Table 5.3. Canonical correspondence analysis statistics for seedling absolute density data. Correlation coefficients (cc) of environmental variables and *t*-values (*t*) are presented for axes 1 and 2; critical value* ($df \geq 18$; $\alpha = 0.05$) =2.1.

		Axis 1		Axis 2	
EIGENVALUES		**0.2966**		**0.1446**	
Variable	**Code**	**cc**	***t***	**cc**	***t***
Litter		-0.1395	-1.9161	0.1529	**2.1174**
Clay		0.0598	0.8368	-0.0268	-0.3786
Silt		0.0918	1.4584	0.0125	0.2003
Aspect	**ASP**	0.0835	1.1996	-0.0797	-1.1551
Canopy height	**CAHE**	0.1578	**2.3187**	-0.1273	-1.8852
Canopy openness	**CAOP**	0.1449	**2.3153**	-0.0691	-1.1134
Crown length	**CRLH**	-0.0448	-0.6419	-0.0121	-0.1747
No grazing	**Gra0**	-0.1682	-1.2458	-0.4915	**-3.6699**
Light grazing	**Gra1**	0.1744	1.6619	-0.2464	**-2.3728**
Moderate grazing	**Gra2**	0.1764	1.6375	-0.1052	-0.9843
Magnesium	**Mg**	0.0265	0.4151	0.0339	0.5296
Organic matter content	**OMC**	-0.0208	-0.3239	0.0732	1.1493
Slope	**SLO**	-0.1033	-1.5767	0.0904	1.3909

* Critical value for a t-test at 5% significance is ca. 2.1, if n-q-1 > 18; n = number of samples, q = number of environmental variables.

A careful examination of the length and direction of the overall vectors, as well as the species' centroid position over the CCA biplot, revealed two major aspects. First, all those species of xeric habitats such as *Pinus pseudostrobus* (*Ppse*), *P. leiophylla* (*Plei*), *Quercus crassipes* (*Qcra*), *Prunus serotina* (*Pser*) and *Arbutus xalapensis* (*Axal*) (The latter is not particularly a typical species of xeric habitats in CG, although it may be observed in this environments -*personal observation*) are distributed at the lower right side of the CCA diagram, reinforcing the evidence of a floristically distinct group. The distribution of the species over the CCA biplot is congruent with those results obtained in NMDS in this chapter when just floristic data was involved in the analysis. The remaining species are randomly allocated over the three other portions of the CCA biplot, although some species are closely correlated to grazing (Figure 5.6). Secondly, a wide-range of environmental characteristics may be equally important in explaining seedling species distribution in the *Quercus* forests of Cerro Grande.

According to the CCA results, the occurrence of species labelled as xeric may be explained by variables such as sun-aspect (ASP), canopy openness (CAOP), canopy height (CAHE) and low levels of grazing (Gra1). Species such as *Fraxinus uhdei*

(*Fuhd*), *Xilosma flexuosum* (*Xfle*), *Quercus castanea* (*Qcas*), *Q. candicans* (*Qcan*) and *Cornus excelsa* (*Cexc*), which were placed towards the top right of the CCA ordination diagram, are linked to the effect of moderate grazing (Gra2), organic matter content (OMC) and crown length (CRLH) (Figure 5.6). Those taxa of the mesic group such as *Clethra vicentina* (*Cvic*), *Ostrya virginiana* (*Ovir*), *Quercus scytophylla* (*Qscy*), *Persea hintonii* (*Phin*), among others positioned towards the middle left side of the CCA biplot, appear to be strongly explained by non-grazed areas (Gra0), litter, slope and magnesium (Mg). An observation that may be worth pointing out is that not all the micro-environmental information achieved the expected explanatory significance. For example, contrary to expectations slope terrain, an important environmental controlling factor for seedlings in many forested ecosystems (Sternberg & Shoshany, 2001; Wang et al., 2002; Baker et al., 2003 and Hirayama & Sakimoto, 2003) proved to be an unimportant environmental filter for seedling species distribution in the study area.

Saplings

Figure 5.7 shows the corresponding sapling species-environment CCA biplot. In this figure it is clearly evident that the length and direction of the vectors are more evenly distributed over the ordination diagram. These results may imply that in the sapling community, environmental heterogeneity has a relatively balanced importance in explaining their spatial distribution. The first axis ($\lambda_1 = 0.2479$), which captured the biggest amount of variation, was strongly associated with litter depth and canopy openness (CAOP); while the second axis ($\lambda_1 = 0.1867$) was linked to a wider range of environmental variables (Table 5.4). In this table it is clearly evident that slope is the most important gradient differentiating floristic patterns, with aspect, canopy height (CAHE), crown length (CRLH) and indications of moderate grazing (Gra2) covarying almost with the same level of importance. Except for silt, clay and organic matter content (OMC), it is evident that almost all the environmental gradients co-vary by approximately the same amount, either negatively or positively (Figure 5.7).

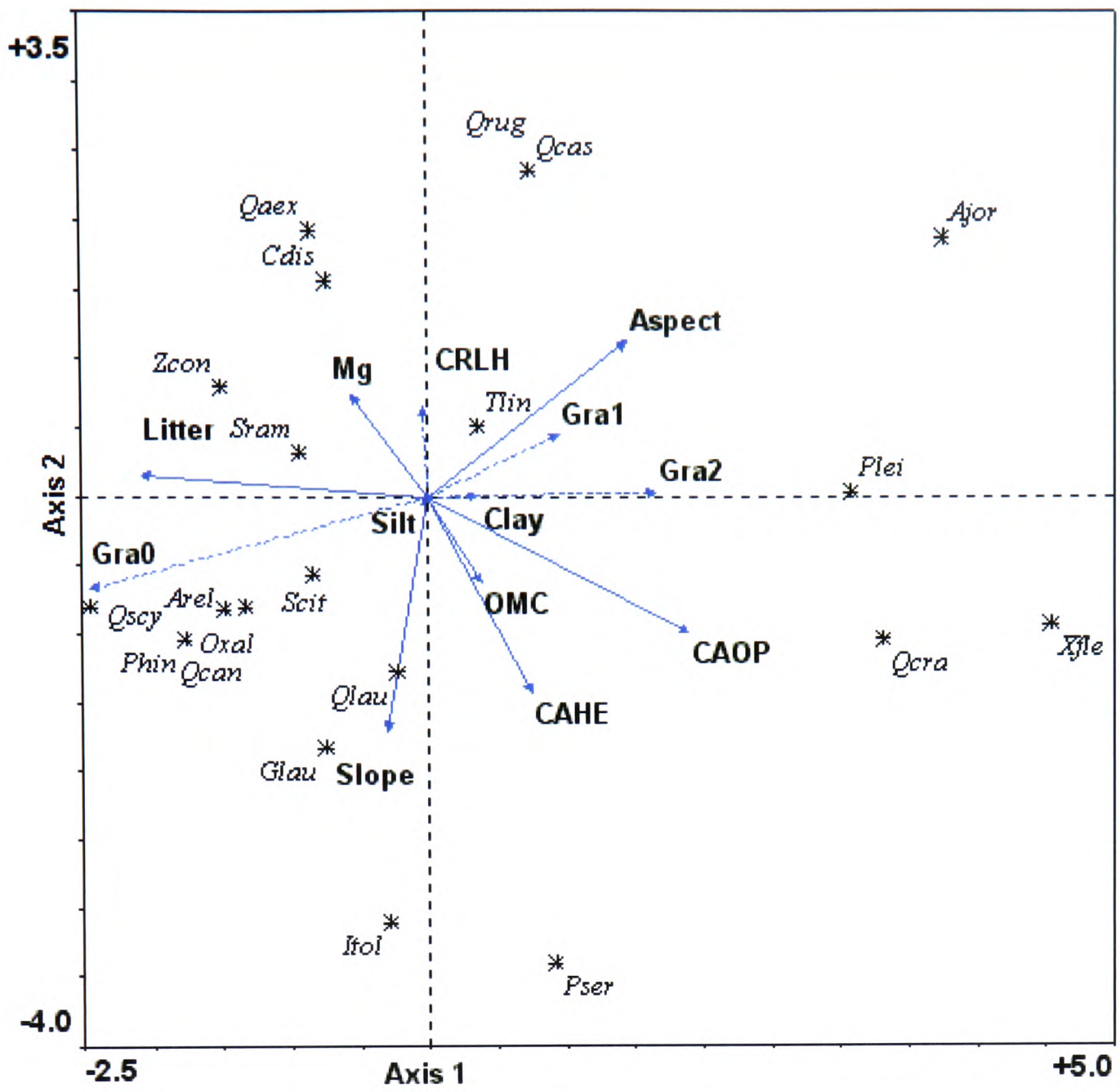


Figure 5.7. Canonical correspondence biplot showing the relationship between 21 species of saplings on 13 environmental variables (after the PCA variable selection). The scales marked are in standard deviations units. The biplot captured 39.3 percent of the total variation. Dashed and solid arrows indicate the centroids of both interval and nominal variables respectively. Arrows pointing in the same direction indicate positively correlated environmental variables. The length and direction of the arrows indicate the strength and sign of the correlations. Perpendicular arrows to each other suggest lack of correlation; while those pointing in opposite directions indicate negatively correlated variables. Interpretation of species name abbreviations are given in Figure 5.6.

CCA results coincided well with the sapling configuration obtained by the NMDS ordination taking into account just floristic information. All species of xeric conditions (*Prunus serotina, Quercus crassipes, Pinus leiophylla*, etc.) are separated from the other species across axis 1 at the right side of the CCA biplot. An interesting pattern observed in this biplot is that all species of this group are distant from any vector, which may be an indication that this group of species is unrelated to any of the environmental

variables (Figure 5.7). The remaining species, with exception of *Quercus rugosa*, were distributed along axis 2 suggesting a clear distinct floristic gradient.

Table 5.4. Canonical correspondence analysis statistics for sapling absolute density data. Correlation coefficients (cc) of environmental variables and *t*-values (*t*) are presented for axes 1 and 2; critical value* (df ≥ 18; α = 0.05) =2.1.

		Axis 1		Axis 2	
EIGENVALUES		**0.2479**		**0.1867**	
Variable	**Code**	**cc**	***t***	**cc**	***t***
Litter		-0.3088	**-2.52613**	0.0411	0.5514
Clay		0.1715	1.1864	-0.0445	-0.5064
Silt		0.2266	1.8767	-0.1506	-2.0444
Aspect	**ASP**	0.2127	1.7334	0.1732	**2.3139**
Canopy height	**CAHE**	-0.0818	-0.6609	-0.2174	**-2.8807**
Canopy openness	**CAOP**	0.3174	**2.6837**	-0.0673	-0.9321
Crown length	**CRLH**	-0.1816	-1.5932	0.1473	**2.1191**
No grazing	**Gra0**	0.0579	0.2474	-0.2739	-1.9177
Light grazing	**Gra1**	0.1142	0.6973	-0.1355	-1.3557
Moderate grazing	**Gra2**	0.1586	0.8792	-0.2407	**-2.1879**
Magnesium	**Mg**	-0.0537	-0.5235	0.0934	1.4933
Organic matter content	**OMC**	0.0372	0.3325	-0.0932	-1.3547
Slope	**SLO**	-0.1046	-1.0595	-0.2778	**-4.6147**

* Critical value for a t-test at 5% significance is ca. 2.1, if n-q-1 > 18; n = number of samples, q = number of environmental variables.

5.4.5 Is the floristic variation spatially autocorrelated with the environment?

The simple and partial Mantel tests for seedlings and saplings respectively indicated that there is a significant positive correlation (Pearson's r; $p<0.005$) between ecological distances (floristic similarity) and geographic distances (spatial linear psps' separation), both before and after controlling for the effect of environmental distances. However, in both cases (simple and partial test) there was no evidence for a significant correlation between environmental distances and geographic distances. The overall Mantel results were concordant in both seedlings and saplings, although the correlations of the partial tests were slightly more pronounced in seedlings (r=0.2651; p=0.0002) than in saplings (r=0.2049; p=0.0006) (Tables 5.5a-b).

Table 5.5 Results from the simple (above the diagonal) and the partial (below the diagonal) Mantel tests for **a)** seedlings and **b)** saplings showing the correlation(*r*) between floristic variation (Sørensen percentage dissimilarity), environmental heterogeneity (13 variables) and geographical distances (0.0010-9.5 km for seedlings and 0.0010-8.5 km for saplings) to test the null hypothesis that there is no association between each pair of distance data matrices.

a)

Simple / **Partial**	Seedling abundance	Environment	Geographical distance
Seedling abundance		**r** = -0.0595 ***p*** = 0.0852	**r** = 0.2531 ***p*** = 0.0002
Environment	**r** = 0.0618 ***p*** = 0.0657		**r** = 0.0302 ***p*** = 0.1182
Geographical distance	**r** = 0.2651 ***p*** = 0.0002	**r** = 0.0456 ***p*** = 0.0415	

b)

Simple / **Partial**	Sapling abundance	Environment	Geographical distance
Sapling abundance		**r** = -0.0068 ***p*** = 0.4946	**r** = 0.2047 ***p*** = 0.0004
Environment	**r** =-0.1202 ***p*** = 0.4704		**r** = 0.0240 ***p*** = 0.2737
Geographical distance	**r** = 0.2049 ***p*** = 0.0006	**r** = 0.0259 ***p*** = 0.2577	

The fact that the Mantel tests involving geographic distance did not produce significant correlations with the environmental distance, in both seedlings and saplings, may suggest that all the psps established in Cerro Grande relatively are environmentally similar as a result, the difference in species composition amongst plots may not be primarily due to their environmental variation, but to other factors such as seed dispersal a result that may appear contradictory to the stated in previous Chapters. However, the lack of a positive association between the species composition and the geographic separation of the psps may be in fact to the effect of the environmental heterogeneity of Cerro Grande. Thus, two psps may be totally different in both species composition and environmental characteristics even within a same cluster of psps, while a complete similarity may occur in both species composition and environmental characteristics between two distant psps.

5.4.6 Temporal fluctuations in pattern of recruitment

Appendices 5.1a-c for seedlings and 5.2a-c for saplings show the temporal patterns of density variation for the three periods analysed (4, 8 and 11 yrs) corresponding to Qc, Mm and It groups respectively. Visual inspection of these histograms clearly shows that there are obvious temporal fluctuations in recruitment in all species through time. Independently of the period of observation, the histograms also showed that there seems to be a predictable pattern of recruitment among the species. For instance, in the Qc group (Appendix 5.1-**a**), not all species nor psps had a consistent pattern of seedling species abundance across the sampled range. A clear example of this is evident with *Oreopanax xalapensis* and *Pinus serotina* seedlings; both species were relatively well represented in the 1991 inventory (dashed bar), three years later (during the 1994 inventory) these two species had lower abundances (open bars) in the same psps. In 2002, the abundances of these species were dramatically different than to two previous censuses. An inverse trend of recruitment was observed to occur with *Quercus castanea* and *Styrax ramirezii*; both species had greater abundance in the first two censuses than the last census. Conversely, at shorter time intervals, particularly for the 4 (It) year group (Appendix 5.1-**c**) there seems to be a reasonable balance in this process between the two sample periods, meaning that the patterns of abundance of these species did not change over time. This was particularly evident with a number of species, such as *Ternstroemia lineata, Persea hintonii* and even with *Styrax ramirezii.*

As described above, there have been conspicuous fluctuations in the seedling and sapling communities across the psps through this investigation. As a result repeated-measures analysis (RMA -ANOVA) showed that time (the within-subject treatment) and species (between-subject factor) both had a significant (p<0.005) effect on the temporal density variation across sample periods (Table 5.6a-b). Nonetheless, time effect was not always significant. This particularly arose in the 8 year (Mm) group (F = 2.47; P<0.116) in seedlings and; in the 8 (Mm) and 11 (Qc) year groups (F = 0.07; P<0.778 and F = 2.62; P<0.781 respectively) in saplings. These last results indicate that, although there were significant floristic differences among species across the plots, the overall trends in density (total number of individuals of all species) in one period of observation was not significantly different from that in the last period. Additionally, RMA showed that the time x species interaction was significant (p < 0.001) across

periods for both seedlings and saplings (Table 5.6a-b), indicating that there was at least one period when the density of one of the species in the psps was different. The significant results in all interactions prevented interpreting the effect of time and species alone (Gurevitch & Chester, 1986; Von Ende, 2001).

Table 5.6. Summary of the Repeated-measures analysis ANOVA for log-transformed *log*(x+1) absolute density data (total number of individuals per plot) for the effect of time on species density of: a) seedlings and b) saplings for 11 (Qc), 8 (Mm) and 4 (It) yrs with three and two repeated time periods respectively. *df* = degrees of freedom; MS = mean square; F-value of statistics. The Greenhouse-Geisser (G-G) and the Huynh-Feldt (H-F) corrections are also presented. All tests were conducted separately.

a)	Seedlings					
Sources of variation	***df***	**MS**	**F Ratio**	**G-G**	**H-F**	***p****
11 years (Qc Group)						
Time	2	148.80	27.62	<0.001	<0.001	<0.001
Species	19	326.00	14.00	<0.001	<0.001	<0.001
Time x species	38	22.95	4.26	<0.001	<0.001	<0.001
Error (time)	1120	5.38				
8 years (Mm Group)						
Time	1	75.60	2.47	ns	ns	ns
Species	24	128.40	3.03	<0.001	<0.001	<0.001
Time x species	24	49.83	1.63	0.004	0.004	0.004
Error (time)	450	30.53				
4 years (It Group)						
Time	1	262.92	12.76	<0.001	<0.001	<0.001
Species	27	270.64	5.60	<0.001	<0.001	<0.001
Time x species	27	44.65	2.16	<0.001	<0.001	<0.001
Error (time)	1036	20.60				

b)	Saplings					
Sources of variation	***df***	**MS**	**F Ratio**	**G-G**	**H-F**	***p****
11 years (Qc Group)						
Time	2	0.84	2.62	ns	ns	ns
Species	12	8.00	3.34	<0.001	<0.001	<0.001
Time x species	24	0.76	2.37	<0.001	<0.001	<0.001
Error (time)	572	0.32				
8 years (Mm Group)						
Time	1	0.09	0.07	ns	ns	ns
Species	11	40.45	7.45	<0.001	<0.001	<0.001
Time x species	11	3.21	2.72	<0.003	<0.003	<0.003
Error (time)	180	1.18				
4 years (It Group)						
Time	1	18.34	16.39	<0.001	<0.001	<0.001
Species	18	131.04	19.37	<0.001	<0.001	<0.001
Time x species	18	5.75	5.14	<0.001	<0.001	<0.001
Error (time)	570	1.11				

* *p*-values for within effect treatment effect of repeated measures were adjusted with the Greenhouse-Geisser and Huynh-Feldt epsilon corrections (SPSS, 2003).

5.5 Discussion

5.5.1 The floristic variation in seedlings and saplings

The results described in this chapter go some way towards explaining the high floristic richness in the juvenile communities of mixed-oak forests of Cerro Grande. Twenty-seven broadleaved species, including at least seven species of *Quercus*, were found to be coexisting to various degrees. This floristic richness has not been reported elsewhere in the scientific literature for similar high-altitude *Quercus* sub-tropical mountain forests.

The results showed, as expected, that there were many more absolute number of seedlings than saplings. On grounds of demographic investigations carried out elsewhere, major variations are assumed to take place within the seedling community in which a lack of seedling persistence may occur after seed germination, leading to failure of recruitment into the sapling stage. For example, Whitmore (1996) pointed out that in the recruitment phase, the passage from seedling to sapling gives the biggest 'demographic squeeze' to populations in tropical rain forests. The results found in this thesis regarding the marked contrast between the number of seedlings and saplings are in agreement also with several ecological investigations carried out in temperate (Cuevas, 2002; Harcombe et al., 2002) as well as in subtropical and tropical forests (Burslem et al., 2000; Nebel et al., 2001), that report contrasting demographic differences between population of seedlings and samplings within a same locality, events linked to periodic seedling mortality unable to reach a bigger demographic stage.

Although there is a wide range of factors identified as drivers of seedling mortality, the most commonly cited in the scientific literature are mostly to those previously described in this chapter such as: *i*) browsing and herbivory, *ii*) seedling desiccation and, *iii*) competitive effects. In the case of browsing and herbivory on oaks (Callaway, 1992a) found experimentally that acorns and seedlings of *Quercus douglasii* and *Q. lobata* experience high levels of mortality due to predation and herbivory. According to Callaway (1992a) events of herbivory on oaks mainly occur at early stages of seedling development. The author also observed that these events might be dependent on habitat

type; for example, he pointed out that in open forest conditions (gaps) about 40 % of acorns/seedlings were eaten or removed by birds or small mammals. In closed conditions the proportions drastically increase, severely impacting the structure of the juvenile community. In non-*Quercus* species Augspurger & Kitajima (1992), report that seedlings of the tropical tree *Tachigalia versicolor* Standl. and Wms. (Leguminosae), die within two months of germination mainly due to small mammal depredation, and about 88-94% mortality occurs after one year. Seedling mortality due to desiccation is highlighted by Battaglia et al. (2000) and Meentemeyer et al. (2001). They have demonstrated that solar radiation is generally more intense over higher-altitude micro-physiographical catenas than lower-altitude sites. They are usually more exposed to sun, which in turn heats soil surfaces, increasing water losses from seeds and seedlings and soil evaporation. These investigations also report that seedlings of a number of species do not establish readily in open areas, mainly as a consequence of seedlings developing a chlorotic appearance attributed to photoinhibition that ultimately results in death.

Nagamatsu et al. (2002) also observed that seedling emergence and survival in *Quercus serrata* and *Q. crispula* is often inhibited by water deficiency and litter accumulation; both factors are possibly related to soil fertility. In this thesis it was discovered that litter depth was one of the most important explanatory variables for both seedlings and saplings (Figures 5.6 and 5.7 and; Tables 5.3 and 5.4). In the case of competitive interactions as a potential source of seedling mortality, Brown et al. (1999) noted that seedlings growing in the understory of dipterocarp forests of Sabah, Borneo would always experience competition with adult trees and shrubs for scarce resources. Shortly after gregarious fruiting events while seedling densities remain high, they will also compete with each other. On the other hand, it has been experimentally established (Humphrey & Swaine, 1997a) that seedlings of *Quercus petraea* (Matt.) Leibl. and *Q. robur* L. are inhibited by herbaceous competition such as *Pteridium aquilinum* L. in Scottish oak forests. This is a common herbaceous species in Cerro Grande, mainly in the most disturbed locations.

Assuming that the numerical disparity between seedlings and saplings reported in this chapter is due to seedling mortality, all the processes described above may well explain the likely causes of seedling mortality in Cerro Grande. Therefore competitive interactions and environmental constraints, mainly micro-topographic variations, light

conditions, and soil fertility may all act as environmental filters for species' survival. In addition, because most of the psps are not particularly overcrowded, nor the ground flora extremely dense, competitive interactions with the surrounding vegetation are unlikely to occur. The results thus intuitively point towards environmental constraints as the main drivers of numerical discrepancies between seedlings and saplings.

5.5.2 Is the floristic variation of juveniles spatially structured?

Species composition is said to be spatially structured if patterns of species' distributions are repeatedly confined to particular spatio-temporal gradients and portray discrete floristic associations (Tuomisto et al., 2003b). It has long been acknowledged (MacArthur & Levins, 1967; Chesson & Warner, 1981; Dale & MacIsaac, 1989; Roberts & Gilliam, 1995; Clark et al., 1998; Ritchie & Olff, 1999) that spatial scale is of prime importance not only to quantify species diversity but also for discerning whether floristic patterns exist across the environment. In seedlings, at the measured spatial scale of 0.0010 to 9.5 km in this investigation, the distribution of both species centroids (asterisks) and psps (triangles) along axes 1 and 2 (Figure 5.4a) in the NMDS ordinations suggests that there is no well-defined floristic gradient. Rather, there is a gradual shift in species composition across the study area. However, when projecting axes 1 and 3 (Figure 5.4b) a certain degree of spatial floristic delimitation emerged. This was true at least for some species, mainly for those labelled as xeric species. Hence, the hypothesis that seedling species composition is not spatially determined in the *Quercus* communities of Cerro Grande could be partially accepted if considering only the NMDS projections on axes 1 and 2. The spatial arrangement portrayed by the species over the NMDS diagram can be partially explained by the fact that most of the psps share a number of species of seedlings so that NMDS classified them as floristically equivalent, providing evidence for a lack of a clear floristic gradient.

In saplings, the results showed (Figure 5.5) that the spatial distribution by the species over the NMDS diagram visibly contrasted with the ones previously described for seedlings. An interesting observation that emerged from the analysis of the sapling floristic data was that, despite the lack of any dominant species among saplings, the overall species distribution across the study area nearly resembled the floristic patterns described for the adult community (*see* Figure 3.2; Chapter 3).

The sapling distribution pattern depicted by the NMDS ordination diagram was assumed to be a consequence of a number of combined factors. Firstly, there was the lower floristic similarity between pairs of plots. For instance, in almost all the psps there was only one species of sapling. This seemed to create a lower similarity in the number of species between psps, and as a result, NMDS classified them as distinct entities. But perhaps the most important factors causing more floristic differentiation in the saplings than in seedlings could be because saplings display greater habitat specialisation than seedlings. This may imply that even when seeds reach distant sites from their original habitat and eventually germinate, many die at early developmental stages as a consequence of unsuitable environmental conditions for their permanence.

Ecological studies affirm that seed supply to empty sites is one of the most important processes for explaining spatio-temporal patterns of recruitment and the consequent floristic distribution (Dalling et al., 1998; Condit et al., 2000; Barot & Gignoux, 2004). In oak forests, for example, Gómez (2003) reports that the average distance of acorn dispersal is estimated at over 250 m, with some dispersal occurring up to 1 km from the source oak trees. He affirms that this is a key process determining the spatial distribution of seeds and the subsequent recruitment probabilities of individuals. Opposing ideas have seen seed dispersal processes as less important than environmental heterogeneity as a way to explain species recruitment and thus floristic patterns across the landscape (Chesson & Warner, 1981; Mohler, 1990; Pulliam, 2000). The results in this thesis point more to environmental determinism (as will be further discussed) than seed dispersal limitation. Although the above might appear conflicting with the observations made in plots 11 and 32, in which seedlings of species different than the ones present in the canopy were found. However, these were trends observed in just two plots of the 86 sampled and even more those species were not found as saplings.

5.5.3 The role of environmental heterogeneity

Co-occurring tree species differ in their abilities to exploit resources resulting in differences in species rank order of abundance (Latham, 1992). Manabe et al. (2000) claim that micro-environmental requirements vary among developmental stages of conspecific individuals. In the vegetation of Cerro Grande, according to the species rank abundances for seedlings and saplings (Figures 5.2 and 5.3) and the CCA ordinations

(Figures 5.6 and 5.7) conducted on the same suite of environmental variables, data were consistent with Latham's and Manabe's results. Whilst it was found that *Prunus serotina* as seedlings showed the highest values in both absolute and rank abundance (Figure 5.2), as a sapling this species had one of the lowest values (Figure 5.3). These are indications that environmental heterogeneity in the psps of Cerro Grande has different impacts on the vegetation depending on the developmental stage. Specifically, in this thesis it was found that for seedlings, the observed patterns of floristic distribution might be explained mainly by the size of the canopy gaps than any other environmental filter. For saplings, a relatively wider range of micro-physiographical constrains may equally explain the observed floristic pattern of distribution. Battaglia et al. (2000) and Meentemeyer et al. (2001) have arrived at similar conclusions as the ones given in this thesis. Both investigations claimed that micro-physiographic variability acts as a strong habitat control that has an independent interacting effect on patterns of regeneration influencing seedling recruitment, and that the nature of these effects can vary among demographic stages. In other words, seedlings appear over a variety of environmental conditions, but survival and recruitment to sapling stage radically alters the vegetation-environment patterns.

5.5.4 Patterns of spatial floristic variation across the environment

The results of the Mantel test revealed that similarity in species compositions across the plots correlates poorly with similarity in environmental conditions. On the other hand, the Mantel test results showed that in both seedlings and saplings, there is a decrease in floristic similarity as the geographic separation between each pair of psps increases. This was true even when decoupling the potential effect of the environmental differences between psps from both the geographic and floristic effects. Thus, the results of the Mantel test indicated that there is an effect of isolation by distance as a potential source of floristic differentiation between two environmentally similar psps.

However, because the study area is physiographically heterogeneous, the above results merit a more careful examination. In order to discover whether there is a true linear relationship between the geographic distance and the compositional similarity between each pair of psps, both parameters were contrasted. If the Mantel test results hold, then it would be expected that a monotonic linear relationship would decrease as psps

become more geographically distant (Tuomisto et al., 2003b), as an effect of dispersal limitation processes. Thus, in Figure 5.8a-b the relationship between the Sørensen (Bray-Curtis) similarity index and the geographic distances between each pair of psps in seedlings and saplings respectively are shown. The results of this exercise showed that in fact there is a rather stochastic spatial floristic trends across the study area, somewhat contradicting the results of the Mantel test.

Some abiotic site factors that influence species distribution in forest ecosystems are known for their high variation at very fine scales (Bruelheide & Udelhoven, 2005). Pyke et al. (2001); Tuomisto et al. (2003b) and Gilbert & Lechowicz (2004) in a rather similar approach to the one developed in this thesis arrived at similar results. Their investigations showed that there was no a linear decay in species similarity as sampling points become further apart. Gilbert and Lechowicz, in particular, using *Carex* vegetation data collected in forest ecosystems of Montreal, Canada, found that along a geographical gradient of ca. 3.5 km environmental determinism offered a stronger explanatory power than the effect of seed dispersal ability, discounting any possibility of a neutral explanation for their observed floristic patterns.

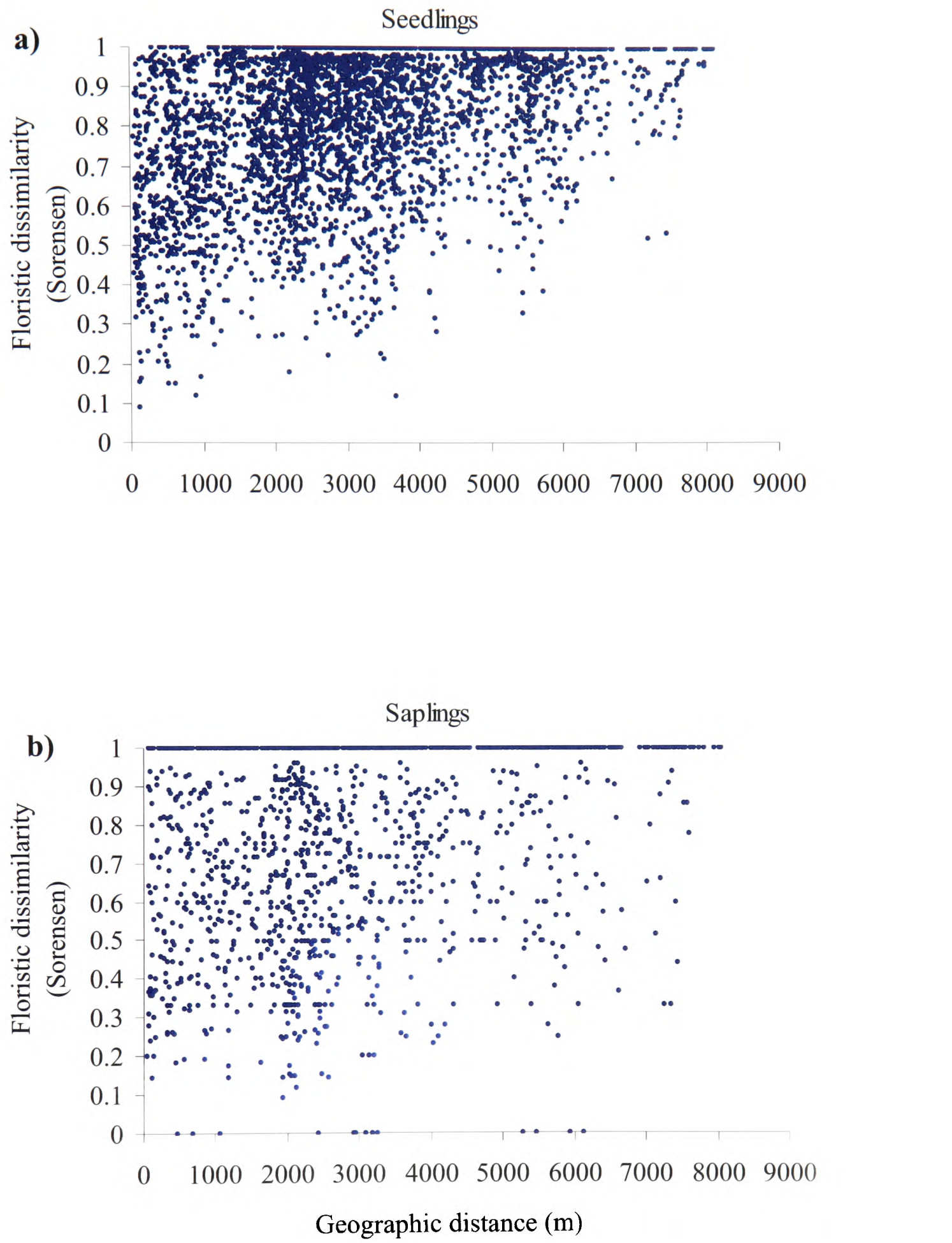


Figure 5.8. Scatter plots showing the bivariate relationship between psps of similar species composition as measured by the Sorensen (Bray-Curtis) similarity index and the geographic distance of close and distant psps for **a)** seedlings (n = 85 psps) and **b)** saplings (n = 54 psp).

5.5.5 Patterns of temporal variation

For a number of poorly represented species (mainly in the sapling category) it was difficult to ascertain whether they underwent changes over time. All species that had good representativeness in the data showed rather interesting dynamics, as shown in the Appendices 5.1a-c and 5.2a-c. Contrasting seedlings with their counterpart saplings a number of differences between them became apparent:

i. Not all species had individuals in both vegetational categories. For example, *Cornus excelsa* occurred as seedlings in several plots, but not as saplings; the reverse arose with *Fraxinus uhdei.*

ii. Even when several species were relatively well represented both as seedlings and saplings, such as *Quercus crassipes*, *Ternstroemia lineata* and eventually *Ilex tolucana*, there were large numerical differences between the absolute numbers of seedlings and the absolute numbers of saplings.

iii. The irregular frequency distribution in most of the histograms in these appendices suggested that fluctuating patterns of recruitment within and among species is likely to occur both in time and space (Appendix 5.1a-c).

iv. This indicates that there are localised boosted patterns of recruitment (*e.g.* *Quercus candicans* (plot 21), *Q. crassipes* (plot 14) in 2002 (solid black bar); *Ternstroemia lineata* (plot 52), *Garrya laurifolia* (plot 48) in 1994 (open bar) and; *Oreopanax xalapensis* and *Garrya laurifolia* in 2002 (solid black bar).

v. Several species had a constant density across periods of observation in both seedlings and saplings. These were mostly species with fleshy seeds such as *Prunus serotina*, a species that does not exhibit masting behaviour (LoGiudice & Ostfeld, 2002).

Additionally, the histograms of the most abundant species clearly show that, even when several species were always represented by a good number of individuals (mainly seedlings) in the plots, none of them retained a constant level of abundance over time, a result also confirmed by the RMA results (Table 5.6).

In Chapter 1 it was acknowledged that the upper canopy of some psps in Cerro Grande is composed of 3-5 oak species. An interpretation of the results described above is that spatio-temporal fluctuations in patterns of recruitment in seedlings and saplings might allow closely related species to coexist as adults. Thus, similar species may occupy comparable niches at different times within a psp. The basic premise that is put forward here to support this hypothesis is that a *storage effect*, the occurrence of overlapping generations of seedlings and fluctuating recruitment rates, (Warner & Chesson, 1985; Chesson & Huntly, 1989), could be a mechanism by which sympatric oak and allied species minimise competitive interactions, allowing their coexistence.

The storage effect emerges from the recognition that the maintenance of a population is a function of both dissimilar patterns of recruitment and the storage of seedling or sapling survivorship over generations (Hairston et al., 1996; Higgins et al., 2000a). Theoretical studies on coexistence (Warner & Chesson, 1985; Enright & Lamont, 1992; Schupp, 1995; McGuire et al., 2001) have demonstrated that variations in recruitment rates can allow the coexistence of strongly competitive organisms. It implies that spatio-temporal segregation might reduce the use of similar resources by different organisms, thereby facilitating the coexistence of congeneric and conspecific individuals.

As it was discussed in the introduction and in this chapter, it is well established in the ecological literature that *Quercus* exhibit masting events (Schmidt, 2003), a phenomenon by which there is spatio-temporal variation in acorn production which is highly synchronised among all individuals (Liebhold et al., 2004). Masting mechanisms might, in part, explain the observed fluctuating patterns of recruitment in the psps of Cerro Grande. Thereby, soon after masting and gregarious seed germination, *Quercus* and its sympatric species may undergo competitive interactions. This, predation on acorn processes and a lack of suitable environmental conditions could be one the main factors of seedling mortality, and thus a way to explain the observed fluctuations over time.

Seeds of oak trees are dispersed via zoochory, or seed-hoarding behaviour. Acorns that fall from a tree are transported and cached by a varied number of animals such as deer, mice, squirrels, or jays. For example, it has been reported (Iida, 2004) that a high percentage of fallen acorns are eaten or transported by mice before next germination

season in temperate forests. In the study area, it has been observed that mammals and birds quickly predate a high proportion of acorns that drop on bare soil (*personal observation*).

The relative importance of seed dispersed in the study area might be partially explained by several studies carried out in order to evaluate the biological diversity of birds and mammals. In this line of evidence, Romero Mariscal (1998) in an investigation carried out in order to discover the most common visitor birds associate to three vegetation types (*Quercus* forest, mountain mesophytic forest and *Pinus-Quercus* forests) in Cerro Grande, found 74 species of birds common to these vegetation types, of which 60 were recorded as frequent visitors of *Quercus* forests. Of the 60-birds species dweller of *Quercus* forests, 10 per cent were reported to be granivorous (seed-consumers) and 7 per cent were frugivorous. Thus, species such as *Penelope purpuranscens, Melanerpes formicivorous, Campefilus guatemalensis, Columba faciata, Turdus migratorius* and *T. assimilis* were the most representative species. It is likely that this group of birds might be important acorn consumer-transporters of acorns away from the producer tree as a result explain the patterns of seedling establishment observed in this research.

However, in Cerro Grande there are another acorn predator/consumers that inhabit these ecosystems such as wild pigs, deer, mice, squirrels, etc, (Moreno Gómez et al., 1992) that may predate or transport (internally or externally) acorns in absence of birds as well. These animals are usually important acorn predators in different woody ecosystems. These observations agree with high rates of acorn predation by small mammals, especially rodents have been observed to be important acorn consumers in oak forests in northern Spain (Leiva & Fernández-Alés, 2003). In addition, according to McShea & Schwede (1993), deer consume up 70% of acorn crops in deciduous forests. Understanding the role of different seed dispersers in determining patterns of seedling establishment is critical to predicting forest regeneration and community floristic composition in landscapes on which there is a high number of potential dispersers such as those of SMBR.

There are evidences of masting cycles amongst the *Quercus* species of Cerro Grande (Olvera Vargas et al., 1998). During a mast year, a number of individuals of a particular species (*e.g. Quercus crassipes* or *Q. castanea*) produce a vast amount of seeds in

synchrony. This is, within a population of *Quercus* it was observed that only a number of individuals produced seeds while other individuals of the same species did not show evidences of seeds production during the same time period of observation. This was a process that was found to be mainly correlated to micro-environmental conditions and to geographic location of the species (Olvera Vargas et al., 1998). Several studies have indicated that masting cyclic events occur because different oak species require different numbers of years for their acorns to mature (Koenig et al., 1994) or because it is a strategy of the several species to escape from predation (Bossema, 1979) both events have not been validated for the study area. The variable patterns of abundance observed to occur in seedlings (appendix 5.1a-c) over the sampling periods seems to match or could be explained by such cyclical masting events. Nevertheless, it foreseen that silvicultural practices must, therefore, be timed carefully in Cerro Grande in order to take advantage of processes but mainly of the apparent masting cyclical events and thus to facilitate regeneration processes after harvesting.

Similarly, fauna preservation is one of the main objectives appointed for the core zones of the Reserve (It is also true even for the buffer zone). It is therefore important to take into account cyclic masting events in order secure enough food for wildlife populations. In particular, for those species of birds (*e.g. Penelope purpuranscens, Melanerpes formicivorous* etc.) or mammals (*e.g. Odocoileus virginianus, Tayassu tajacu,* etc.) that consume seeds for feeding. If forestry practices are not carefully timed (programmed) there might be the risk of harvesting tree species in masting years and consequently to compromise both a satisfactory seedling establishment and an adequate supply of seeds for fauna feeding.

For saplings, the graphical representation in Appendices 5.2a-c suggests that temporal pattern of abundances was relatively more homogeneous. However, it should not be interpreted that saplings tend to be less dynamic than seedlings. The results showed that, except in a few occasions, within a plot the same species was not recorded in two consecutive inventories, suggesting a rapid species turnover (Appendix 5.2**a-c**).

Tree seedling and sapling performance (defined in terms of growth and survival) along these complex micro-environmental gradients is relatively unexplored. Observations and the results of this thesis suggest that there is a broader distribution of seedlings than

saplings. This pattern might be explained by two interrelated conditions. Firstly, the broader distribution of seedlings could be due to the fact that there is a high chance that several agents disperse seeds. As it was discussed in this chapter, there are a number of potential mammals and birds that consume or transport seeds around the study area. In this case, seeds once disseminated, might be able to germinate and to survive on the deposited sites as long as the cotyledon has enough nutrients to nourish the seedling. When this occurred seedlings were recorded assuming they were already established. However, the limited distribution of saplings might be a consequence of seedling mortality once cotyledon's run out of nutrients and thus hampering a significant number of individuals to reach the sapling stage.

A number of investigations argue that seed size may affect plant survival in stressful environments. These studies have documented that initial seedling growth is positively correlated with seed size (Kennedy et al., 2004). Larger seeds may enhance speed of germination and overall growth (Osunkoya et al., 1994; Reich et al., 1994). Seedlings grown from large seeds have also been shown to have higher rates of establishment than those grown from small seeds (Kennedy et al., 2004). However, many studies have shown weak or no correlation between seed size and growth rate (St. Clair & Adams, 1991) and thus it is unclear if seed size influences are widespread or rare (Long & Jones, 1996).

Collectively, the overall assemblage in seedlings and saplings is relatively similar between periods of remeasurement, according to the RMA results. The significant results of RMA can be explained by the fact that, even when there are evident floristic changes within and between psps, the different populations seem to maintain a constant community assembly dynamic.

Understanding how the seedlings and samplings become established after seed dispersal and germination is important for understanding successional processes in managed forest landscapes. Studies testing whether sampling are not established because of the lack of nutrients after the ones contained in their cotyledon are used by the plant or because they are not in a suitable habitat for their establishment are thus urgently needed for the study area.

5.6 Conclusions

The analysis of spatial patterns of floristic co-occurrence in juveniles has provided evidence to argue that the seedling community is, more heterogeneous than the sapling community in the *Quercus*-dominated of Cerro Grande. In addition, probably due to of wider geographical distribution across the study area, the seedling community is not depicting as obvious a spatial floristic gradient as occurred in saplings and as in adult trees (Chapter 3).

The restricted distribution range of the most abundant species, such as *Quercus crassipes, Q. castanea* and *Ternstroemia lineata*, support the view that species are spatially structured so that the predictions of Ho_1 (Seedling and sapling species are not randomly distributed across the study area) was supported.

The observed floristic patterns over specific environmental characteristics lead to the conclusion that the micro-environmental heterogeneity of Cerro Grande sets limits for species colonisation at all potentially vacant sites. Even when seeds eventually reach distant areas and, at some point germinate, it seems unlikely that distantly dispersed seeds will become established if they are not in their correct habitat. However, this observation would require further experimental research. Here, Ho2 was also supported.

A clear relationship between acorn weight and seedling performance were found by Long & Jones (1996); apparently there is a tendency for larger seeded oaks to produce seedlings with large mean leaf and rapid growth rate. Oak seedlings it appears that receive the majority of energy obtained from the acorn in the first growing season facilitating their establishment (Long & Jones, 1996). However, the results reported in this thesis do not agree with these observations. For example, comparatively *Quercus crassipes* has one of the smallest seed sizes of all *Quercus* species present in Cerro Grande; in contrast *Q. candicans* has one of the biggest. The results presented in appendices 5.1a-c and 5.2a-c shows that *Q. crassipes* tend to be more able to be established than *Q. candicans*. Additional factors such as canopy cover and type, micro-environmental conditions, etc are probably playing important roles that deserve further investigation.

Since the passage from seedling to sapling is perhaps one of the most critical phases for the maintenance of the *Quercus* communities in Cerro Grande (as indicated by the difference in absolute numbers of saplings in relation to seedlings), care should be taken to ensure a process of self-replacement in these communities. This observation is of outstanding importance particularly in all those areas under commercial silvicultural operations in Cerro Grande.

The motivation of using the Mantel test and Canonical Correspondence Analysis (CCA) was because the Mantel test gives an overall measure of spatial patterns, whilst CCA discriminates only those environmental variables that significantly explain the variance of species distribution. From both approaches it is concluded that only a reduced number of environmental variables, in particular canopy openness and canopy height for seedlings and, canopy openness and litter for saplings are the most important variables explaining the dynamics of the juvenile *Quercus* communities in Cerro Grande.

Convincing graphical and statistical evidence of temporal patterns of species abundances in both seedlings and saplings were found so that the prediction of Ho_3 was not supported.

CHAPTER 6 - General discussion and conclusions

6.1 Introduction

This final chapter includes three main sections. The first section summarises the overall findings of this research thesis. To accomplish this, the results and conclusions reached in Chapters 3, 4 and 5 are briefly outlined following additional comments. The second section discusses the implications of the overall results for the definition of alternatives of management for mixed oak forests for both sawtimber production and for maintenance of biodiversity. In the third section avenues for further lines of research are given.

6.1.1 Patterns of floristic variation and coexistence

Ordination-based results (NMDS) run on the adult *Quercus*-dominated community data in Chapter 3 showed that there are at least two main contrasting floristic zones, including a transitional floristic area representing the overall vegetation of Cerro Grande, at the Sierra de Manantlan. The main floristic zones seem to correspond to a xeric-mesic moisture gradient. According to the NMDS ordination results, *Quercus* and non-*Quercus* species of xeric habitats (*e.g. Quercus crassipes, Prunus serotina, Alnus jorullensis*) were consistently segregated from those species found across mesic habitats (*e.g. Q. candicans, Ilex tolucana, Symplocos citrea,* etc.).

In addition, experience over 15 years in the study area and supported with the NMDS results suggests that within the mesic zone, which is floristically and environmentally more heterogeneous than the xeric zone, there are localised micro-vegetational patterns of assemblage resembling discrete micro-floristic patterns. The results reported in Chapter 3 also showed that in the study area several species have a fairly restricted geographic distribution such as *Tilia mexicana, Ostrya virginiana* and *Abies religiosa.* The first two species are mostly confined to the wettest and the most complex micro-physiographical spots of Cerro Grande, whilst *Abies religiosa*, although geographically restricted, it seems that this species do not require of a complex physiography but of good moisture conditions and significantly reduced solar radiation; environmental

features observable only in small ravines and/or inter-mountain valleys of Cerro Grande. Environmentally restricted floristic patterns of distribution within the mesic zone may hold even for the most ubiquitous sub-canopy and canopy-dominant species such as *Ternstroemia lineata* and several *Quercus* species including *Q. candicans*, which are not entirely spread across the entire mesic floristic zone. These results suggest that there are micro-geographical areas of relatively uniform vegetation that make them different from adjacent ones in terms of species composition and stand structure. Such floristic conditions create floristic patchiness of complex vegetational patterns with overlapping transitional floristic zones that usually contain elements of the two main floristic zones but spatially co-occurring in various degrees of mixtures and extension.

Palmer (1988) claims that the observation of ecological processes has fractal properties whereby vegetation is a prime example of a fractal because it has detail at all spatial scales of interest. This signifies that there are delimited vegetation patterns at all spatial scales making it difficult to assign a true scale of observation for defining the size of a community. If the entire vegetation of Cerro Grande is put into context to explain Palmer's view, it could readily be concluded in this thesis that a uniform floristic assemblage with no clear spatial floristic patterns does exist across the study area, supporting a compositional drift view (*sensu* Hubbell, 2001). At smaller spatial scales, however, for example considering 500 m^2 plots, the evenness of the vegetation varies, as it was described above and hence supporting a niche-based view. The combined results of NMDS and CCA in Chapter 3 suggest that patterns of floristic variation emerge with changes environmental conditions across the landscape. To illustrate this, Figure 6.1 hypothetically exemplifies the role of environmental heterogeneity on species richness and its spatial distribution in the *Quercus*-dominated forests of Cerro Grande. In Table 6.1, are given the average floristic and environmental values for the mesic, xeric and transition zone.

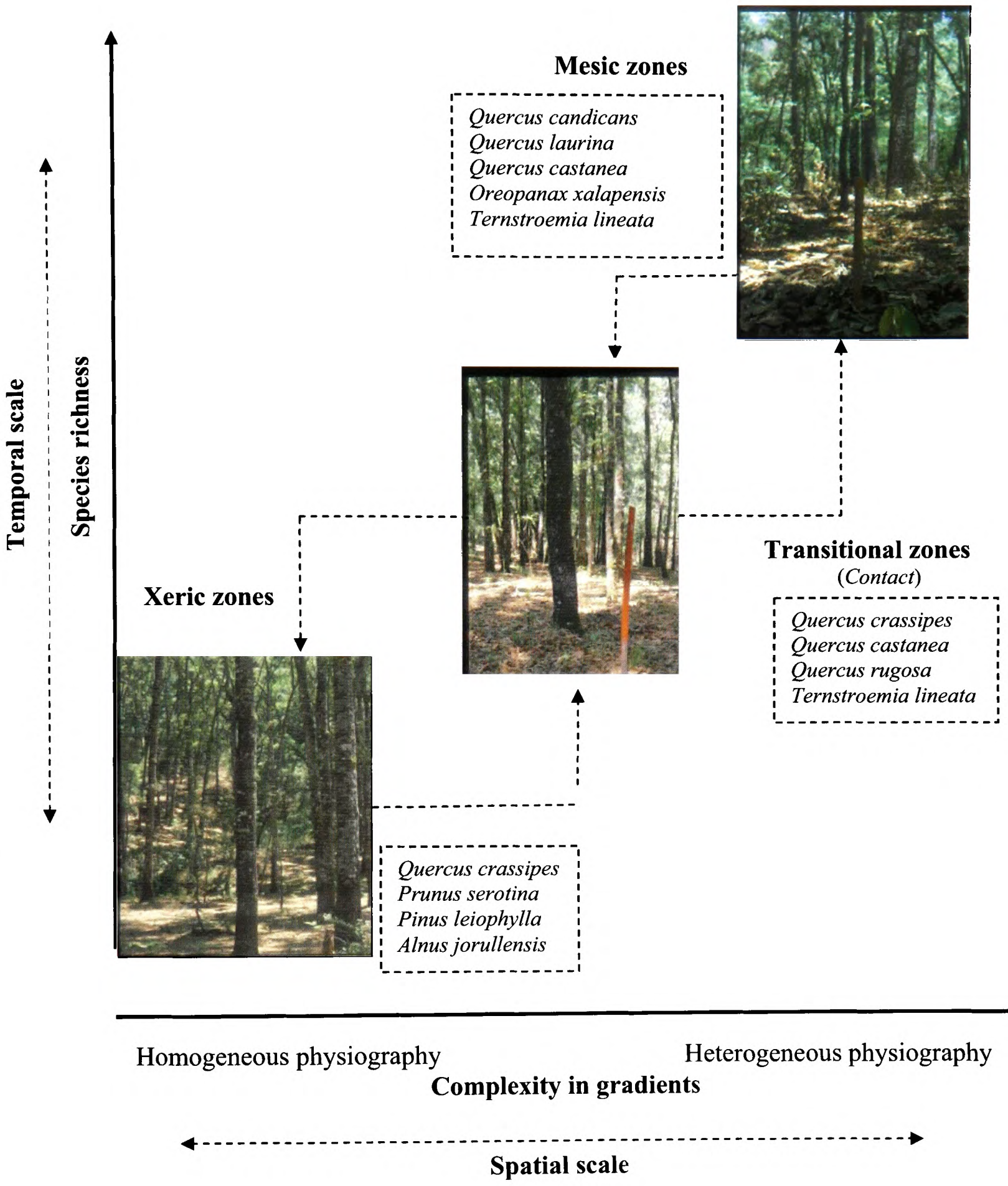


Figure 6.1 Complexity in gradients along spatio-temporal scales creates the observed species associations in sub-tropical mountainous *Quercus* forests at Cerro Grande, Sierra de Manantlan. Black dashed arrows indicate forward or backward movement between species assemblages.

Table 6.1 Floristic and environmental characteristics of the xeric, mesic and the transition zones. Figures were calculated as an averaged for all psps in each floristic zone. For nominal variables figures represent the most frequent condition (mode).

Variable	Floristic zone		
	Mesic	**Xeric**	**Transition**
Floristic			
Height (m)	12.7±0.61	14.4±0.26	14.9±0.49
Diameter (cm)	18.6±1.37	22.1±2.31	22.5±2.67
Basal Area (m^2)	2.0±0.18	2.0±0.18	1.8.0±0.31
Environmental (*interval*)			
Elevation (m a.s.l.)	2235±21.5	2300±12.81	2164±42.5
Aspect	0.9±0.18	1.3±0.25	1.26±0.40
Slope (%)	32.8±3.55	29.7±6.92	32.5±3.95
Litter (cm)	5.8±0.71	4.4±0.65	4.9±0.80
Canopy openness (%)	10.2±1.55	15.7±5.13	13±4.92
Canopy height (m)	12.6±0.59	14.4±0.28	14.8±0.49
Environmental (*nominal*)			
Maturity	4	3	3
Canopy layers	3	1	2
Catena	1-3	2	2-3
Grazing	3	2	3
Topography	2	1	2

Finally, it is concluded that micro-environmental heterogeneity appear to control where and which species constitute a forest community. These finding are in agreement with MacArthur & MacArthur's (1961) habitat heterogeneity hypothesis, which maintains that an increase in the number of habitats leads to an increase in species diversity across the landscape due to an expansion in the number of partitionable niches.

The main conclusions derived from Chapter 3 are:

- Two main floristic gradients were recognised to be representing the mixed-oak forests in Cerro Grande. In addition, a transitional floristic zone located between the two main floristic gradients also emerged during the analysis. As a result, it was concluded in Chapter 3 that rather than a compositional drift *Quercus* and their allied non-*Quercus* species constitute discrete communities in the environment such as it was hypothesised.
- CCA showed that there are particular environmental variables that best correlate with the observed patterns of floristic variation. These observations leaded to

reject the hypothesis that environmental heterogeneity does not promote community differentiation in the *Quercus* dominated forests of the study area (**Ho_2**).

- Considering the two previous observations the niche paradigm is the best model for explaining the observed patterns of floristic variation in Cerro Grande. Therefore, the prediction that the niche paradigm rather the neutral paradigm explains species coexistence made in **Ho_3** is also accepted.

6.1.2 The dynamics of successional processes

Forest succession is understood as a gradual and orderly process of ecosystem development brought about by changes in community composition and structure (Watt, 1947). Forest succession has also been described as a predictable series of changes in vegetation that occur over a specific period and the time required for the vegetation of recovering after a major disturbance has occurred. Or just the rate of floristic changes that take place over time (Prach, 1993). When the dynamics succession was first codified by several plant ecologists (*e.g.* Odum, 1969; Connell & Slatyer, 1977) they mainly focused on three key features:

i. A discrete starting point of development,
ii. A clear directional trajectory of development and,
iii. An unambiguous end mainly as an effect of species interactions.

Because of the ecological similarity of the vegetation of Cerro Grande (mostly *Quercus* canopy-dominated stands), it was predicted that a reasonably unidirectional (constant pattern of dominance) and uniform (constant rate of change) successional trend over time would occur. However, one of the most outstanding results found in Chapter 4 was that, almost all the plots experienced a rather stochastic successional trajectory and had a somewhat dissimilar rate of change over time. According to the results, the most evident cause of such successional dynamics seems to be the effect of both species and individual turnover, which in turn generate alternated patterns of species dominance.

The results reported in Chapter 4 are in agreement with those results reported by Shmida & Ellner (1984) that claimed that forest succession is a conventional process

characterised by spatial or temporal shifts in patterns of species dominance. Such spatial and temporal successional changes, according to this author, is characterised by an alternating pattern of dominance by the several species that integrate a community. In this process, there are a number of species that exert dominance over the rest of the species in the community. After a period of dominance by the dominant species starts an ongoing decline of control by the dominant species. When this occurs, suppressed species gradually become dominants in the community.

Thus, stochastic patterns observed (Figures 4.1a-f) closely correspond to a process called "*stem exclusion stage*" which was described in Chapter 4 (section 4.1.1). According to Oliver and Larson (1996; pp 148-152) after several years of stand dynamics new individuals do not appear and some of the existing ones die. The surviving ones grow larger and express differences in height and diameter; first one species and then another may appear to dominate the stand. The authors claim that, in a stand before the available growing space is reoccupied, plants are expanding in open growth condition; after the available growing space is reoccupied, new individuals do not become establish successfully. Those plants with competitive advantage in size or growth pattern are able to expand into growing space occupied by other plants and reduce their growth rate or kill them. This process is called 'stem exclusion' because new stems are prevented from successfully invading and because some existing stems die and thus are excluded from the stand. The authors also argue that in some cases, early dominance is a strong indication of which species will maintain the dominance in the stand. In other cases, a species can become dominant even if it begins at a relatively low canopy position. The dynamic occurred in stands dominated by *Quercus crassipes* and by *Quercus candicans* and *Oreopanax xalapensis* respectively could counterpart the previous cases described by Oliver and Larson. In the study area, there are a number stands on which, at early stages of their development; these are dominated by fast-growing species such as *Ternstroemia lineata, Prunus serotina,* etc. Under their canopy it is common to observe individuals of *Q. crassipes*. However, *T. lineata* and *P. serotina* are species that, in mature stands, never reach the upper canopy consequently *Q. crassipes* tend to dominate the stand as it approach to maturity. In contrast, almost invariably *Q. candicans* but particularly *O. xalapensis* are two species that always behaves as dominant individuals in the study area. *O. xalapensis* always shows to be a

good sprinter both in diameter and height growth a characteristic that allows to this species to dominate always the stand.

In addition, this thesis compelling evidence suggested that more rapid successional changes are triggered and eventually accelerated by anthropogenic factors. For instance, there were indications that logging operations can speed up and, eventually, alter the route of an ongoing successional progression such as it was evident to take place in plot 17 (in the Qc group, Figure 4.1a). Though this deduction was derived from observations made in just a single plot, it deserves further experimental research in order to confirm its validity.

Interesting evidences emerged from results of the community and population structural dynamics analyses. At community level, the results of the Gini coefficient (*G*) and the coefficient of skewness (*Sk*) suggested that no substantial structural changes have occurred since the first group of plots was established, providing clues that the mixed oak forests in the study area are, at least floristically, relatively stable resembling a compositional equilibrium state (*sensu* Pickett, 1980). At population level, the overall variation in diameter size distributions, as expressed by the coefficient of skewness (Sk), was very variable suggesting that tree proportions within the population was different in every period of measurement suggesting a more dynamic process.

The observation that there is little overall structural change at community level would be an indication that the dynamics of the species constituting the three groups of plots (It, Mm and Qc group) are very similar amongst them and although, at population level, the structural changes are more evident, it appears that there is a compensatory mechanism that maintains the community in structural equilibrium with no substantial changes occurred over time.

Based on the overall findings of Chapter 4, it is argued that the future canopy species composition in the *Quercus* forest in Cerro Grande, will most probably be a function of three closely linked elements: *i*) species composition and their individual turnover, *ii*) the spatial scale at which the latter take place (*e.g.* at plot level, group level or across landscape level) and; *iii*) the local environmental surroundings. These factors may act in combination producing different successional trends in which some species are

favoured at one time whilst others are not resulting in alternate patterns of dominance over time.

The main conclusions derived from Chapter 4 are:

- Alternate patterns of forest succession in either abundance or dominance, are occurring in the vegetation of Cerro Grande such that the prediction of unidirectional and constant successional trends over time ($\mathbf{Ho_1}$) is not confirmed.
- Forest succession occurs at different rates of change amongst groups of plots (*e.g.* It, Mm and Qc groups) and within groups, the data suggest that successional dynamics might differ according to species composition and individual turnover.
- The stochastic directions observed on the DCA ordination diagrams and the alternate patterns of dominance also suggest that the *Quercus* forests in Cerro Grande resemble a non-equilibrium successional condition.

6.1.3 Regeneration dynamics and the role of spatio-temporal filters

The results described in Chapter 5 reveal that the floristic structure of the juvenile communities (seedlings and saplings) varies spatially and temporally across the study area (*see* Appendix 5.1 for seedlings and in Appendix 5.2 for saplings). Particularly, convincing evidences observed on this group of figures suggest that, patterns of regeneration for most of the species are both temporally and spatially structured. This signifies that a number of species may abundant in a plot during a particular year but, the same species may notoriously diminish its abundance or even be absent in a subsequent year of observation. The overall dynamics of the juvenile communities was assumed to be an effect of several combined causes such as site conditions, dispersal capability and anthropogenic impacts particularly grazing and logging on the juvenile vegetation. However, the last two causes (seed dispersal and the effect of grazing) were not directly evaluated in this thesis therefore deserve further research in order to confirm this assumption.

In general terms, one of the most remarkable results reported in Chapter 5 is the contrasting spatial variation between seedlings and saplings in terms of species

abundance and species composition as it is evident in Figures 5.8a and 5.8b. These figures suggest that within the seedling community (Figure 5.8a) there is a close floristic resemblance between pairs of plots so that the spatial separation between each pair of plots seems to have little effect on species composition variation. This implies that plots, which are geographically far apart from each other, may have similar species composition. As it was pointed out in Chapter 3, Neutral theory (Hubbell, 2001) predicts a consistent decrease in community similarity with distance, an expectation no observed in the seedling results presented in Chapter 5 (Figure 5.8a). In saplings (Figure 5.8b), in contrast, the floristic likeness between each pair of plots tended to decrease as plots became further apart. This contrasting floristic pattern observed in saplings hold even for plots that are in close geographic proximity.

The Mantel test in turns indicated a lack of correlation between the floristic and environmental distance for both seedlings and saplings, but a strong correlation between the floristic and the geographic distances (Table 5.5). The importance of geographic separation of the plots in explaining floristic patterns of distribution suggest that dispersal limitation may play a strong role. There are several ways of explaining why the Mantel test did not reveal a significant correlation between floristic variation and the environment variation, as it would be expected. One of these could be an effect of the micro-environmental patchiness (heterogeneity) of the study area. Even plots within the same nested-group (*see* Chapter 2) may not share any species in common; whereas distant plots may have very similar compositions (*see* also Figure 3.4). Interpreting this results, at smaller scales (*e.g.* within a 500 m^2 plot) dispersal limitation and niche differentiation might not be necessarily mutually exclusive views for explaining the floristic pattern of assemblages in the study area but complementary. However, at larger geographical scales (100 – 150 m. from plot to plot or from a nested group of plots to another) from a seed dispersal point of view it would be difficult to explain the observed floristic patterns. Considering the general evidence in Chapter 5 it is concluded that environmental determinism rather than dispersal capability could be the most responsible for floristic patterns of distribution in the *Quercus* communities of Cerro Grande.

The most significant findings in Chapter 5 can be summarised as follows:

- Species composition in seedlings and saplings is spatially structured, though this was more evident in saplings than in seedlings. So the prediction of a non-random floristic distribution in seedlings and saplings (**Ho_1**) is supported.
- There are a number of specific environmental variables that best explain the patterns of floristic distribution in the juvenile communities, being different for seedlings and saplings. These observations lead to rejection of the hypothesis (**Ho_2**) that environmental heterogeneity does not promote discrete floristic assemblages in both seedlings and saplings.
- Because of the relative floristic similarity across the study area it was hypothesised that the absolute density of the different species will not vary significantly over time. The results showed, however, that there are fluctuations so that the prediction of a stable species abundance of the different species of seedlings and saplings over time (**Ho_3**) is not supported.

6.2 Implications for forest management

Contemporary scientific and technical publications emphasise that sustainable forest management is a major challenge facing modern silviculture (Emborg, 1998). It calls for balancing diverse ecological, economic and social values over space and time (Sheppard & Meitner, 2005). Current forest management objectives in Cerro Grande are basically focussed on the production of high-quality timber (mainly oak timber) and in significantly minor proportion, to produce charcoal or gathering non-timber forest products (mainly to collect flowers from *Ternstroemia lineata* to produce tee). These activities are being carried out in stands located in the buffer zone and currently guided (as indicated in Chapter 2) by the indications included in the forest management plan for this area. On the other hand, conservation of biodiversity and tourism visitation are two of the main that have been developed in the core zone in the study area. In this area, basic infrastructure has been built to offer to visitors to stay in place overnight. The management, administration and supervision of these activities relay on a group of people designated by the "asamblea ejidal" (this is council integrated by members of the Ejido) of the ejidos El Terrero and Toxin respectively. Thus, to establish realistic goals

of forest management for Cerro Grande before outlining the potential scenarios aiming at both to produce high-quality timber for commercial purposes and to promote biological conservation as well as alternatives for tourism visitation; a checklist of the most important ecological, silvicultural and conservation issues derived from the results of this thesis are given:

1. Following the results reported in chapter 3, there are three main distinct floristic zones across Cerro Grande. One floristic zone was classified as xeric type, which is mainly canopy monospecific (*Quercus crassipes*). A second major floristic zone was classified as mesic type, which is canopy dominated by several *Quercus* and *non-Quercus* species. This is richer in species composition than the former. The third floristic zone was classified as a transitional zone due to it showed physiognomic and environmental characteristics from both of the two previously described floristic zones.
2. Most of the stands in the xeric zone are of regular diameter structures however, in the sub-canopy it is common to find non-*Quercus* species such as *Alnus jorullensis, Prunus serotina* and, in localised geographic areas, *Quercus crassipes* may be codominating the stand with pine species such as *Pinus leiophylla* and *P. pseudostrobus*. In contrast the mesic zone, if compared to the xeric zone, has opposite floristic and structural characteristics. In the sub-canopy of this floristic zone may be coexisting by several broadleaved species such as *Arbutus xalapensis, Ilex tolucana, Symplocos citrea, Ternstroemia lineata,* etc. This vegetation type corresponds to the mountain mesophytic (cloud mountain) forests, a threatened type of vegetation in México.
3. The biggest proportion of the mesic zone runs across the core zone whilst the xeric zone mainly locates across the buffer zone of the Reserve. The mesic zone has the major micro-environmental and floristic heterogeneity in the study area. Furthermore, as a result of past logging activities, cattle grazing, forest fires and agriculture clearance, there are a number of localities highly disturbed within both zones on which woody vegetation does not exist.
4. Although it was not directly analysed in this thesis, the mixed species composition of most of the stands where psps were established suggests that

within the same stand there may be species with different ranges of tolerance to shade. This condition seems to occur particularly in the mesic zone.

5. There are several species in the study area (*e.g. Alnus jorullensis, Garrya laurifolia, Viburnum hartwegii, Lippia umbellate* and *Xilosma flexuosum*) that have neither timber commercial value nor a domestic use and no evidence exists as to whether they are important to fauna conservation (*e.g.* nesting trees, foraging, roosting, etc.).
6. In addition, the above listed species are not particularly abundant in the study area (*see* Figure 3.1; Chapter 3) however; in most of the stands, which are currently subject to timber loggings, they are left standing. It is assumed that if these species do not receive a silvicultural treatment (*e.g.* pre-thinnings) they may eventually become competitive individuals in the stand at least for growing space.
7. Most of the *Quercus* species have a relatively slow diameter growth (Table 6.2) but at the same time they co-occur with a number of fast-growing, commercially valuable tree species such as *Ternstroemia lineata, Prunus serotina, Ilex tolucana* or *Pinus leiophylla* and *P. pseudostrobus*.
8. The floristic dissimilarity and variable abundances over time shown in Appendix 5.1 for seedlings and Appendix 5.2 for saplings, suggest that there is a fine-scale temporal and spatial variation in patterns of distribution and establishment. Although it was not directly examined since it was beyond the scope of the objectives of this thesis (as discussed in Chapter 5), the floristic heterogeneity occurred in both time and space may be an effect of masting events, the impact of grazing or human-induced disturbances.
9. Regeneration of *Quercus* and associated species (or at least seed germination) appear not to be a problem in Cerro Grande, but considering the results in Chapter 5 and the graphical results shown in Appendix 5.2, what eventually might be a challenge is to achieve a successful transition from seedling into sapling individuals. Evidences reported in this thesis suggest that sapling recruitment is one of the most critical steps in securing long-term sustainable management in the study area.

Table 6.2 Silvicultural characteristics of tree species (n=38) by floristic zone, present in oak and mixed-oak forest in Cerro Grande Sierra de Manantlán, Western México. **Focus of management: S** = sawtimber; **HC** = habitat conservation. **MDI** = Mean diameter increment **CRCL** = Crown social position: 1= dominant; 2 = codominant; 3 = intermediate; 4 = overtopped. **Stem/trunk shape: St** = straight; **C** = clean; **Cr** = Crooked; **R** = round; **A** = angular; **U** = unforked; **M** = multiple stems. **CA** = crown architecture: **Sy** = symmetrical, **Ay** = asymmetrical; **Branches:** Ab = abundant; Rb = regular; Fb = few. **Vigour**: **1** good; **2** regular **3** bad.

Species	Floristic zone	Potential Focus of management	Silvicultural characteristics				
			MDI	CRCL	Stem/trunk	CA/Branches	Vigour
Abies religiosa (H.B.K.) **Schlecht. & Cham** *var. religiosa* **Loock et Martínez ex Martínez**	Mesic	S	1.4	1	S/U/R	Sy/Fb	1
Acacia farnesiana **(L.) Willd**	Mesic	HC	1.09	4	Cr/M/A	Ay/Rb	3
Buddleja parviflora ***H.B.K.***	Mesic	HC	-	4	Cr/M/A	Ay/Ab	3
Carpinus tropicalis **(Donn. Sm.) Lundell**	Mesic	HC	-	2	St/C/U/R	Ay/Ab	1
Clethra vicentina **Standl.**	Mesic	HC	0.88	2	St/C/U/R	Ay/Rb	1
Comarostaphylis discolor subsp. *discolor* **Digss**	Mesic	HC	0.39	4	Cr/M/A	Sy/Rb	3
Cornus excelsa **H.B.K.**	Mesic	HC	0.63	4	Cr/M/A	A/Rb	3
Dendropanax arboreus **(L.) Deene & Planch.**	Mesic	S	1.13	1	St/C/U/R	Sy/Fb	1
Fraxinus uhdei **(Wenzig) Lingelsh.**	Mesic	S	0.94	2	St/U/R	Sy/Rb	1
Garrya laurifolia **Hartweg ex Benth.**	Mesic	HC	0.06	4	Cr/M/A	A/Rb	3
Ilex tolucana **Hemsl.**	Mesic	HC	1.52	3	St/U/R	S/yRb	2
Lippia umbellata **Cav.**	Mesic	HC	-	-	-	-	-
Oreopanax xalapensis **(H.B.K.) Deebe & Planch.**	Mesic	HC	1.87	1	St/U/A	Sy/Fb	1
Ostrya virginiana **(Mill.) K. Koch**	Mesic	HC	0.98	2	St/U/A	Sy/Ab	1
Persea hintonii **Allen**	Mesic	HC	1.09	2	St/U/A	Sy/Rb	2
Quercus aff. *excelsa* **Liebm.**	Mesic	S	0.67	1	St/U/R	Sy/Rb	2
Quercus candicans **Née**	Mesic	S	0.53	1	St/U/R	Sy/Rb	1
Quercus gentryi **C.H. Muller**	Mesic	S	0.34	1	St/U/R	Sy/Rb	2
Quercus laurina **Humb. & Bonpl.**	Mesic	S	0.66	1	St/U/R	Sy/Rb	1
Quercus scytophylla **Liebm.**	Mesic	S	0.35	1	St/U/R	Sy/Rb	1
Styrax ramirezii **Greenm.**	Mesic	HC	0.94	4	St/M/A	Ay/Rb	3
Stmplocos citrea **Lex.**	Mesic	HC	1.17	3	St/M/A	Sy/Rb	2
Tilia mexicana **Schlecht.**	Mesic	HC	0.87	2	St/U/A	Sy/Ab	2
Zinowewia concinna **Lundell.**	Mesic	HC	1.33	2	St/U/R	Sy/Fb	2
Alnus jorullensis subsp. ***Lutea*** **Furlow**	Xeric	HC	1.11	4	St/U/A	Ay/Ab	3
Pinus douglasiana **Martínez**	Xeric	S	1.88	2	St/U/R	Sy/Rb	1
Pinus leiophylla **Schlecht. & Cham.**	Xeric	S	1.69	2	St/U/R	Sy/Rb	1
Pinus pseudostrobus **Lindl.**	Xeric	S	2.07	2	St/U/R	Sy/Rb	1
Prunus serotina **Ehrh.** subsp. *capuli* **(Cav.) McVaugh**	Xeric	S	2.98	3	St/U/R	Sy/Ab	1
Quercus crassipes **Humb. & Bonpl.**	Xeric	S	0.30	1	St/C/U/R	Sy/Fb	1
Xilosma flexuosum **(H. B. K.) Hemsl.**	Xeric	HC	-	-	-	-	-
Acacia farnesiana **(L.) Willd**	Transition	HC	-	-	-	-	-
Crataegus pubescens **(H.B.K.) Steud.**	Transition	HC	-	-	-	-	-
Quercus castanea **Née**	Mesic-Transition	S	0.41	1	St/M/R	Sy/Rb	2
Quercus obtusata **Humb. & Bonpl.**	Mesic-Transition	S	0.51	1	St/U/R	Sy/Rb	2
Quercus rugosa **Née**	Mesic-Transition	S	0.39	1	St/M/A	Sy/Rb	1
Ternstroemia lineata **DC.** subsp. *lineata*	Mesic-Transition	S	2.0	3	St/C/U/R	Sy/Ab	1
Viburnum hartwegii **Benth.**	Xeric-Transition	HC	-	-	-	-	-

Average estimations based on data collected since plot establishment in each floristic zone for adult trees (≥ 5 cm dbh).

Establishing the goals of forest management

Based on the overall results reported in previous Chapters each of the main floristic zones described in this thesis should have different objectives of management. This is because, besides being located in different geographic and administrative zones of the Reserve (the core and the buffer zones, described in Chapter 2), they also have contrasting structural, floristic and environmental characteristics. For example, even

though the mesic floristic zone is richer in species and has potentially significant more commercially valuable timber species, according to federal regulations the focus of management should be upon conserving biodiversity and/or tourism (SEMARNAP, 2000). These goals can only be achieved through protection and maintenance of natural habitats, fauna and flora. In respect to the dry zone, which essentially corresponds to the buffer zone of the Reserve, even when the silvicultural characteristics of species present in it are not as commercially attractive as in the mesic zone, the main objective of management should be the production of high-quality timber.

Management alternatives for the mesic zone for the conservation of biodiversity

Guidelines for management for timber production require that at least some areas within management units are protected from intervention because of their fragility and ecological importance (*e.g.* steep slopes, buffer zones) or because they serve as refuges for pollinators and vertebrate seed dispersers (Guariguata & Pinard, 1998). The state regulations for Biosphere Reserves in México prohibit any sort of ecosystem manipulation in their core zones. The protection of fragile ecosystems and provision of shelter for vulnerable species of plants and animals is paramount (SEMARNAP, 2000). According to the *Strategic Plan of Management* for the Sierra de Manantlán Biosphere Reserve, the conservation of flora and fauna must be the primary use of the core zones (Jardel Pelaez, 1992). One of the most convincing arguments given to regard the mesic zone of Cerro Grande as an important forest fragment was because it encompasses a significant amount of Mountain Cloud Mesophytic Forest, a threatened type of vegetation in México (Vázquez-García, 1994). As a result, the production of high-quality timber should not be an objective of any management policy for this area. The only alternative uses are biodiversity conservation and tourism and recreation.

Thus, biodiversity conservation and restoration of currently disturbed areas within the mesic zone is one of the most important foci of management. It is an objective that can be accomplished only through the strict protection of the most fragile areas, while at the same time restoring disturbed areas in the expectation of an eventual expansion of the vegetation type. This strategy would eventually reverse the long-term decline in the

quality and extent of mountain mesophytic forest in Cerro Grande. Nonetheless, this view discourages any use of the forest which generates incomes for the owners.

In this thesis, it is anticipated that tourism might be an important alternative use for the mesic zone. As describe in Chapter 2, across the study area there are innumerable natural caves formed by the collapse of the limestone these constitute a distinctive landscape. Local physiography is exceptionally irregular, characterised by a series of disconnected sandy ridges that could be a great attraction for tourists. Whilst promoting tourism however, it would be important to provide and maintain a range of visitor opportunities but at the same time to ensure that environmental values such as fragile micro-geographic areas containing species of restricted distribution, specific habitats for fauna, etc. are not adversely affected. Personal observations during the fieldwork indicate that some species such as *Tilia mexicana, Ostrya virginiana,* and *Persea hintonii* have restricted ranges in the study area. In addition (in the case of *T. mexicana* and *P. hintonii*) regeneration is inadequate to replace the existing population of adult trees (*see* Appendix 5.1a-c and 5.2a-c). It would therefore be very important to keep people away from these zones.

Several areas of the mesic zone would benefit from some low intensity silvicultural treatments such as pre-commercial thinning or thinning directed towards releasing suppressed trees in dense stands in order to improve scenic values since many stands are unattractive with very high densities and large accumulations of debris on the forest floor which makes access difficult and reduces visual attractiveness.

Management alternatives for the xeric zone: timber production

Because the dry floristic zone corresponds to the buffer area of the Reserve, it makes sense to assume that this area should be designated for the production of high-quality sawtimber for commercial purposes. Nevertheless, it is important to consider that, as previously stated; the xeric zone is mainly dominated by *Q. crassipes* which is one of the slowest growth trees in Cerro Grande (Table 6.2). This characteristic is one of the major obstacles for encouraging timber production in the dry zone. However, *Q. crassipes*, as previously described, is commonly associated with a number of commercially important and faster-growing trees such as *Prunus serotina* and

eventually, *Pinus leiophylla* and *P. pseudostrobus*. Therefore a forest management strategy integrating the growth of all species would represent a promising alternative.

Some species in the xeric zone, due to their form or timber characteristics are not of commercial interest. For example, *Alnus jorullensis* has weak wood for lumber and firewood/charcoal production so that it should not be incorporated into the objectives of management for commercial purposes. The value of *A. jorullensis* might however be, for fauna conservation including cavity nesting and perching. However there is no evidence so far that this species is being used by any specific fauna.

Apart from producing seed prolifically, *Q. crassipes* and *P. serotina* have exceptional coppicing abilities. *Q. crassipes* in particular can resprout from roots and stumps. Personal experience suggests that in the study area, when a tree of *Q. crassipes* is felled, almost it almost always re-sprouts prolifically from around the stump. The new individuals originating from coppice invariably grow faster and more vigorously than those originating from seed. These characteristics contribute significantly to the establishment of new stands after harvesting.

The structural and silvicultural traits exhibited by the dominant species of the dry zone make this area appealing for the implementation of more than one cutting method under an even-aged system, the replacement of a new stand after harvesting is easy and relatively safe since regeneration can originate from seeds or coppice. However, since data reported in this thesis does not provide sufficient evidence to determine to what extent coppice should contribute to a seed-based regeneration strategy, it is anticipated that a low intensity, even-aged, cutting method should be considered for the management of this zone. In this context, a shelterwood system would potentially be successful. The ecological and technical foundations for suggesting the implementation of this silvicultural system (Olvera Vargas & Figueroa-Rangel, 1998) are:

- Shelterwood cuttings can be applied at the initial phases of management activity due to the species and the stand structures in the dry zone. At this stage, only overtopping and all badly shaped or crooked trees should be removed. Also only mature oak trees should be considered for removal, although other commercially attractive "secondary" tree species (*e.g. Prunus serotina*) might be included for

removal as well. This would allow a gradual improvement of the current stand, including a refining by the elimination of undesirable species. This can be brought about by the application of partial cuttings of low intensity; essentially the first cuttings (the seeding felling") could be directed towards the most undesirable individuals in the stand including those species referred to in bullet-point 5. *Alnus jorullensis* in particular, could be partially or entirely removed from some stands without representing a serious ecological loss. If removed it would improve the structure and the dynamics of the stand by reducing competition and at the same time releasing growing space and nutrients.

- Since the xeric zone is dominated by *Q. crassipes*, a moderately shade tolerant species (Rzedowski, 1978; Vázquez-García et al., 1995), high stand stocking densities do not necessarily need to be maintained. It would be more desirable to keep just the number of individuals necessary to achieve an adequate canopy cover and thus to promote diameter growth, particularly if growing with *Prunus serotina*. This would have a double effect, control of competition and to prevention of excessive branching so that high-quality timber can be produced.
- The current stand density and structural characteristics suggest that there is no need to apply early thinnings in most of the stands because densities are mostly low. Also because their moderate shade tolerance *Quercus crassipes* is able to grow beneath closed canopies, though the management of a shelterwood system involves the several thinnings (Smith, 1986). What might be eventually be needed is the promotion or maintenance of adequate stand densities during the juvenile phases in order to provide continuous shading in the stand and hence to prevent excessive branching. If the stand density is too low, fast growing species such as *Prunus serotina* would thrive.
- Previous research (Olvera Vargas, 1995; Olvera Vargas & Figueroa-Rangel, 1998) has shown that a diameter at breast-height of 50-60 cm for commercial purposes can only be achieved over rather long rotations of 100-110 years. This does not represent a sustainable alternative for management given the social and economic conditions in the study area. Therefore, it is extremely important to generate alternatives which provide partial incomes. Here, target species for obtaining revenues in the shorter term could be fast-growing trees such as *Prunus serotina, Pinus leiophylla* and *P. pseudostrobus*.

- It would therefore be important to maintain a mixture of species in order to provide an opportunity to apply intermediate cuttings before the final harvest of oak is reached.

Finally, the definition of a "commercially profitable diameter" would be one of the major constraints across Cerro Grande, independent of the vegetation type and silvicultural method employed. In Chapter 4 it was pointed out that the mean diameter at breast height (dbh), at both community and population levels, rarely exceeds 35 cm and, because of the slow diameter growth, production periods to reach this size would be extremely long. This is an important constraint for the management of *Quercus* as the primary species.

6.3 Proposals for further research

Based on the work presented in this thesis, three major lines of research are envisaged that, apart from providing additional insights into the ecological functioning of forests would also provide a deeper understand of the mechanisms that contribute to encouraging the integration of species-rich communities and coexistence; these are:

- Observational research.
- Experimental research.
- Silvicultural and ecological modelling.

6.3.1 Observational research

It is well acknowledged that long-term data collected on permanent sample plots is fundamentally important to a full understanding of the ecological dynamics of forest ecosystems. Most of the ecological investigations that are based on data collected in permanent plots are of relatively short duration, usually less than five years. Direct measurements of ecological processes over longer time periods (*e.g.* greater than 15-20 years) are very rare and even nonexistent for many forest ecosystems (Foster & Tilman, 2000). At the time the fieldwork for this thesis was finished the earliest established plots were approaching the range considered by Foster and Tilman as "exceptionally" rare (ca

15 years). In this line of evidence perhaps, the empirical results obtained about the demographic processes such as structural changes, successional trends, the dynamics of recruitment, mortality rates, etc. are amongst the most valuable contributions presented in this thesis since it represents novel information that has not been reported in the scientific literature for this type of forest ecosystem. Additionally, it provides important baseline knowledge for initiating further observational and experimental research. For example, a constraint of the psps network established in Cerro Grande is that it covers a relatively narrow floristic, altitudinal and spatial gradient. Therefore, an important/appealing further line of observational research would be to expand the range of establishment in order to capture wider spatial, floristic and environmental variability; this would represent an important step to scale up the patterns and processes observed in the existing plots.

Furthermore, in Chapter 3 it was reported that both Neartic and Neotropic elements merge at Cerro Grande, a circumstance that represents a unique species-rich forest ecosystem mainly dominated by *Quercus* species. Narrative documents and informal talks with local peasants suggest that the natural vegetation of Cerro Grande was *Pinus*-dominated and that there have been marked vegetational changes over the last 60 years. However, so far, no investigations have been conducted with the aim of determining the relative contributions of ancient biota on the present-day floristic richness and its ecological dynamics. In this context, palaeoecological and biogeographical investigations would provide valuable retrospective information and eventually contribute greatly to deciphering these enquire. Alternatively, palaeocological investigations would also help to provide a better perspective and understanding of the successional patterns observed in Chapter 4. In addition to this, the vegetation of Cerro Grande clearly differs from that of the surroundings (*see* Chapter 2); this represents an excellent example to test whether the area acts as a dispersal barrier between the floras of adjacent geographical sites.

In addition, in spite of the fact that the seedlings and saplings' sampling subplots were consistently positioned in the same spot within the 500 m^2 plot, in none of these vegetational categories were the individuals mapped or tagged. This was considered to be one of the major handicaps to track confidently the fate of the juvenile vegetation, mainly seedlings. An important line of observational research would therefore consist in

bridging the lack of information between seedlings and saplings to identify more dynamic processes in each of the two vegetational stages. The censuses were carried out every 3 or 4 years, a time-span that seems adequate for the adult vegetation, but not for seedlings and saplings as this period limits the characterisation of critical events such as establishment and recruitment.

6.3.2 Experimental investigations

Observational research can be important to document occurrences of species and structures within a stand through time. It can also provide insight into diverse processes from slope stability and its relation to species composition to carbon storage (Kremsater & Bunnell, 1998). However, it is difficult though not impossible to establish direct causes just by observations made in chronosequence research. Most of the results and conclusions stated in the preceding chapters are based on observation made on the psps. Experimental research should therefore be orientated towards solving multiple perspectives not covered in this thesis. Firstly, experimental research should be conducted to verify the results generated by the preceding observational investigations.

As a starting point, experimental research could be initiated by investigating the effect of those environmental parameters that revealed to be as important to vegetation based on CCA results for seedlings and saplings. For instance, litter was one of the important explanatory variables for seedlings (Chapter 4). This may be an indication that acorns/seeds may be sensitive to litter depth. From fieldwork observations it was found that a depth of 8 cm or more practically prevents acorns/seeds (or their roots after germination) reaching the mineral soil. It appears that litter may also act as an important humidity shelter for young seedlings and thus prevent desiccation. These observations suggest that, in order to have acceptable regeneration, litter should be removed or at least reduced to levels that allow seedling establishment after germination but at the same time, ensuring an adequate litter depth to minimise the risk of seedling desiccation. Thus, experimental research on litter removal to different depth levels would provide not only basic but also important baseline information.

In both juvenile and adult trees it was predicted that environmental heterogeneity greatly contributes to the species richness in the area as well as to the observed patterns

of floristic distribution. It was also hypothesised that the present-day pattern of floristic distribution is an effect of previous patterns of seedling establishment in which niche differentiation may play an important role. The results in Chapters 3 and 5 partially confirmed these predictions. To prove whether these observational predictions are true a series of experiments could be performed. For instance, to consider the effect of topography, aspect, catena position, etc, as factors (treatments) in a experimental design with acorns of different species to determine whether there is a positive relationship between some site characteristics and particular species. The results of this experimental approach would confirm or reject the findings in this thesis mainly the ones related to the CCA ordinations.

In this thesis it was sought to establish to what extent niche differentiation or neutral processes explain species richness and coexistence. Another area of potential research derived from the previous objective, would be to determine why some species are able to reach distant sites from their original release place. Studies on seed dispersal mechanisms, potential dispersers or seedlings transplanted into different areas would greatly support the observations made on the juvenile communities and, at the same time, could be used to evaluate whether species distributions are indeed environmentally determined or the environment imposes filters for species distributions and thus confidently sustain whether the niche differentiation hypothesis is testable in *Quercus* forests.

Additional research on physiology, competitive interactions and regeneration under various effects would provide a more thorough understanding of many of the yet unanswered questions in community ecology. These and other basic lines of research are worth of exploring before convincing statements can be formulated about the factors that mediate species richness and coexistence in the *Quercus*-dominated forests of Cerro Grande.

6.3.3 Silvicultural and ecological modelling

Finally, it is suggested that an integrative approach combining long-term observation with manipulative experimental research could be undertaken and to use the results of both approaches to develop simulation models. Particularly, silvicultural and ecological

modelling of basic and complex processes would be useful to identify various scenarios of management. For instance, defining the effect of silvicultural interventions on species composition and stand yield; or for visualising ecological processes such as the effect of competitive interactions, the role of seed dispersal and its impact on patterns of establishment and recruitment. The latter would be extremely important in discovering the contribution of juvenile stages in re-building the floristic structure of the adult communities after commercial logging.

Similarly, silvicultural and ecological modelling at different levels is needed. Both approaches would substantially help in many areas, not only in the design of sustainable silvicultural interventions but for predicting the fate of these ecosystems either under commercial logging or for conservation management. However, it is anticipated that the species composition and the degree of species mixtures in most of the stands make the development of growth models a difficult but not impossible task.

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APPENDIX

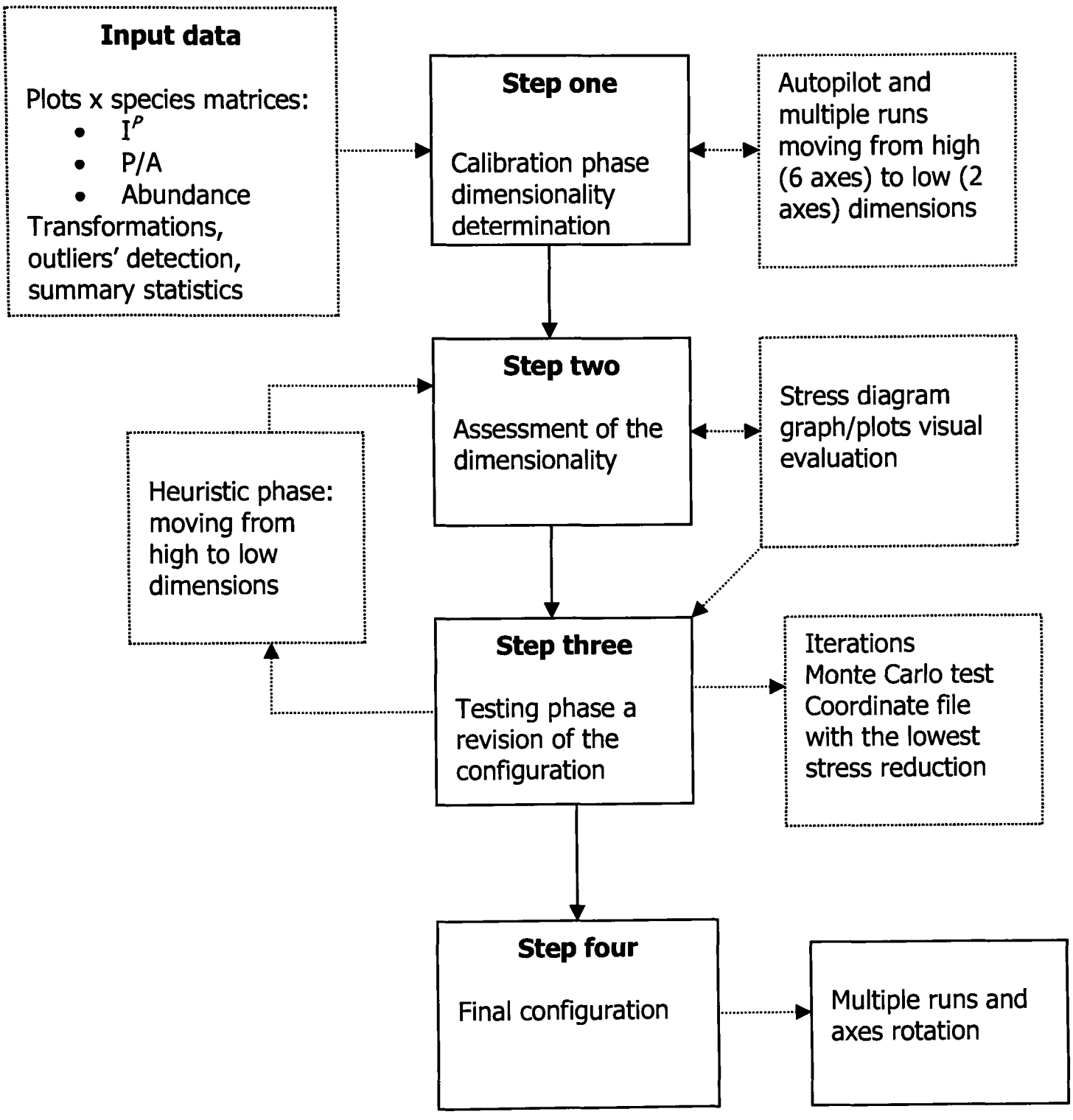
APPENDIX 2.1. Checklist of shrubs and herbaceous species found in the understory of oak dominated forests presented by family.

Family	Species
ADIANTACEAE	*Adiantum andicola* **Liebm.**
ANACARDIACEAE	*Rhus schmidelioides* **Schlecht.**
ARACEAE	*Araceae sp.*
ASCLEPIADACEAE	*Cynanchum sp.*
ASPLENIACEAE	*Asplenium cuspidatum* **Lam.** *Asplenium monanthes* **L.** *Dryopteris aff cinnamomea* **(Cav.) C.Chr.** *Vel aff.* *Dryopteris cinnamomea* **(Cav.) C. Chr.** *Vel aff.*
BORAGINACEAE	*Macromeria longiflora* **(Sessé & Moc.) D. Don**
CAMPANULACEAE	*Lobelia laxifolia* **H.B.K.** *Lobelia longicaulis* **Brandegee**
CAPRIFOLIACEAE	*Symphoricarpos microphyllus* **H.B.K.**
CARYOPHYLLACEAE	*Arenaria lanuginosa* **(Michaux) Rohrb.** *Caryophyllaceae*
CELASTRACEAE	*Celastrus pringlei* **Rose**
COMMELINACEAE	*Tradescantia commelinoides* **Schult.**
COMPOSITAE	*Archibaccharis schiedeana* **(Benth.) J.D. Jackson** *Erigeron velutipes* **Hook. & Arn.** *Eupatorium arsenei* **B.L.Rob.** *Piqueria triflora* **Hemsl.** *Senecio angustifolius* **H.B.K.** *Gnaphalium sp.* *Senecio sp.* *Stevia sp.*
CYPERACEAE	*Cyperus hermaphroditus* **(Jacq.) Standl.**
DENNSTAEDTIACEAE	*Pteridium arachnoideum* **(Kaulf.) Maxon**
EUPHORBIACEAE	*Acalypha langiana* **Muell. Arg.** *var. vigens* **McVaugh** *Euphorbia graminea* **Jacq. S. l.**
GENTIANACEAE	*Gentiana aff spathacea* **H.B.K.**
	Geranium seemanii **Peyr.**
GRAMINEAE	*Festuca breviglumis* **Swallen** *Piptochaetium virecens* **(H.B.K.) Parodi**
LABIATAE	*Salvia longispicata* **M.Martens & Galeotti** *Salvia vazquezii* **Iltis & Ramamoorthy** *ined.* *Scutellaria caerulea* **Sessé & Moc. ex Benth.** *Stachys aff coccinea* **Ort.** *Stachys aff pacifica* **B. Turner** *Salvia sp.*
LEGUMINOSAE	*Cologania broussonetii* **(Balbis) DC.** *Crotalaria aff mollicula* **H.B.K.** *Crotalaria mollicula* **H.B.K.** *Lupinus exaltatus* **Zucc.**

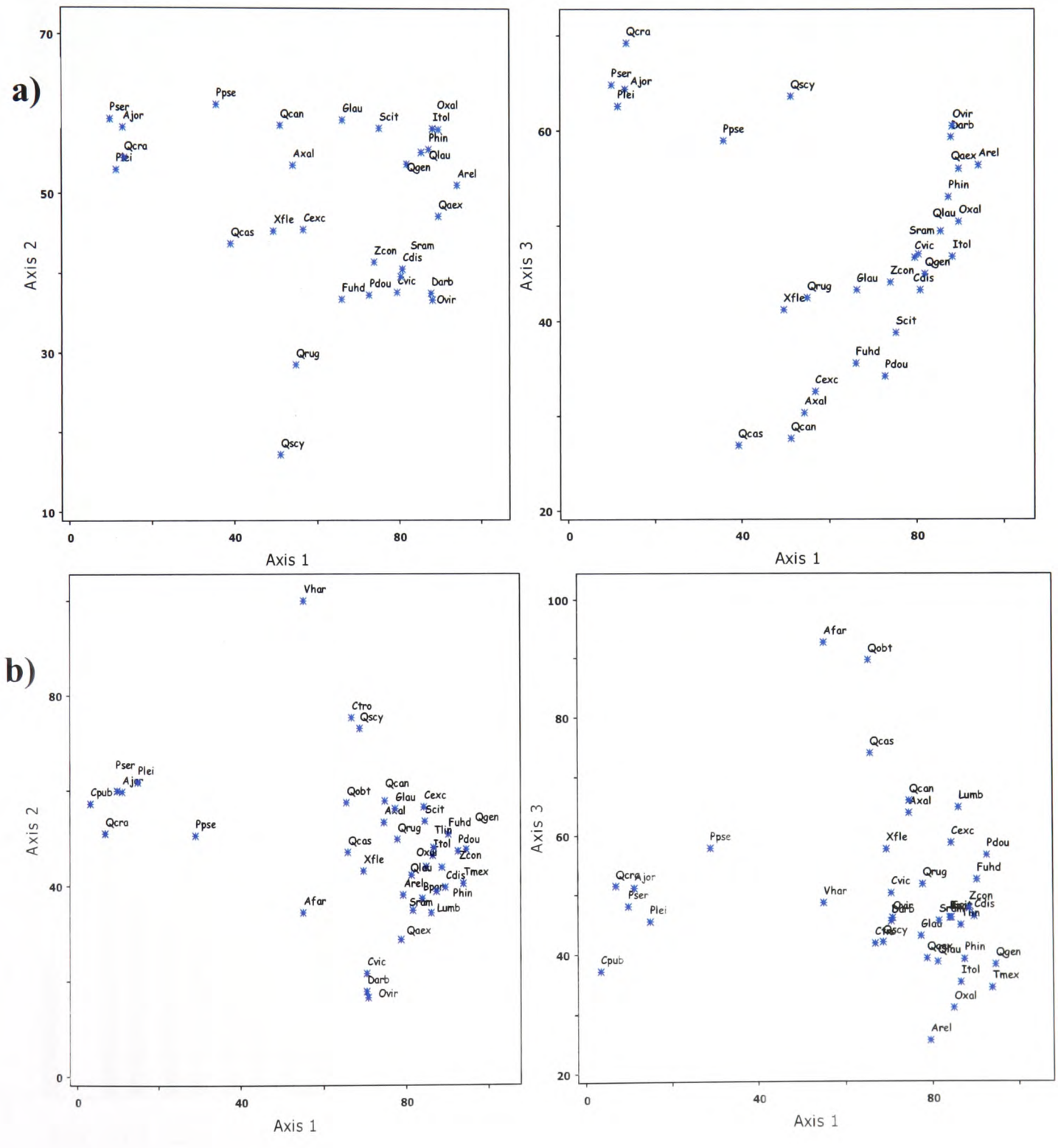
Appendix 2.1 (*Continued*).

	Crotalaria sp.
LILIACEAE	*Bomarea hirtella* **(H.B.K.)** *Herb.*
LYTHRACEAE	*Cuphea watsoniana* **Koehne**
ONAGRACEAE	*Fuchsia thymifolia* **H.B.K.**
OPHIOGLOSSACEAE	*Botrychium virginianum* **(L.) Sw.**
OXALIDACEAE	*Oxalis corniculata* **L.**
	Oxalis sp.
PASSIFLORACEAE	*Passiflora pavonis* **Mart.**
PIPERACEAE	*Peperomia sp*
POLYGALACEAE	*Polygala myrtilloides* **Willd.**
RANUNCULACEAE	*Delphinium subscandens* **Ewan**
	Ranunculus petiolaris **H.B.K.**
ROSACEAE	*Alchemilla pringlei* **Fedde**
	Fragaria mexicana **Schlecht.**
RUBIACEAE	*Didymaea alsinoides* **(Cham. & Schlecht.) Standl.**
SAXIFRAGACEAE	*Philadelphus mexicanus* **Schlecht.**
	Ribes pringlei **Rose**
SCROPHULARIACEAE	*Penstemon roseus* **(Sweet) G. Don**
SMILACACEAE	*Smilax moranensis* **M. Martens & Galeotti**
SOLANACEAE	*Cestrum thyrsoideum* **H.B.K.**
	Solanum sp.
TILIACEAE	*Triumfetta semitriloba* **Jacq.**
UMBELLIFERAE	*Daucus montanus* **Humb. & Bonpl. ex Spreng**
	Hydrocotyle mexicana **Cham. & Schlecht**
VIOLACEAE	*Viola grahamii* **Benth.**
VITACEAE	*Vitis tiliifolia* **Planch.**

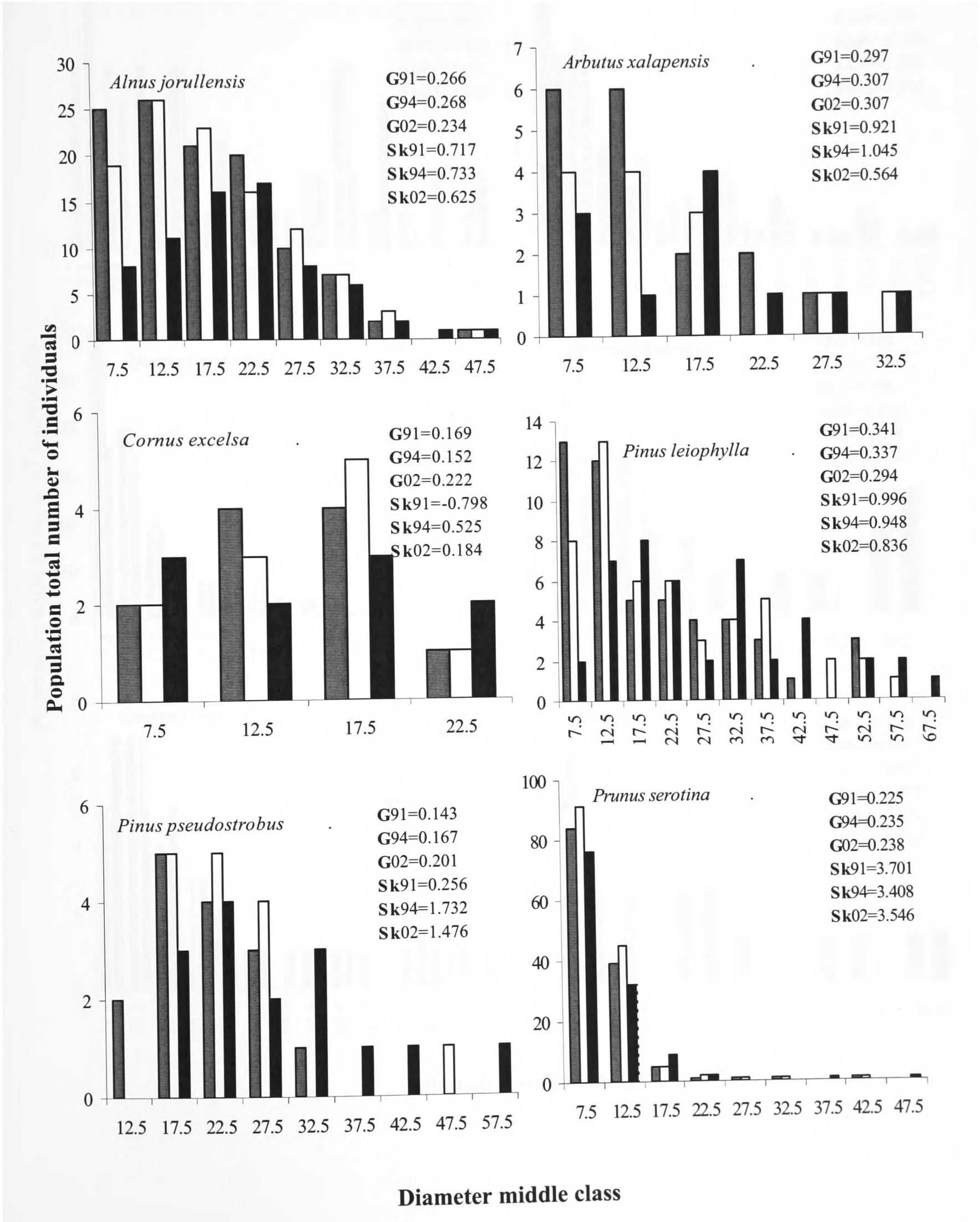
APPENDIX 3.1. Technical workflow procedures followed when performing NMDS in PC-ORD v.4. Dashed double ended arrows indicate a looping interactive process. Solid and dashed single pointed arrows indicate directional processes.



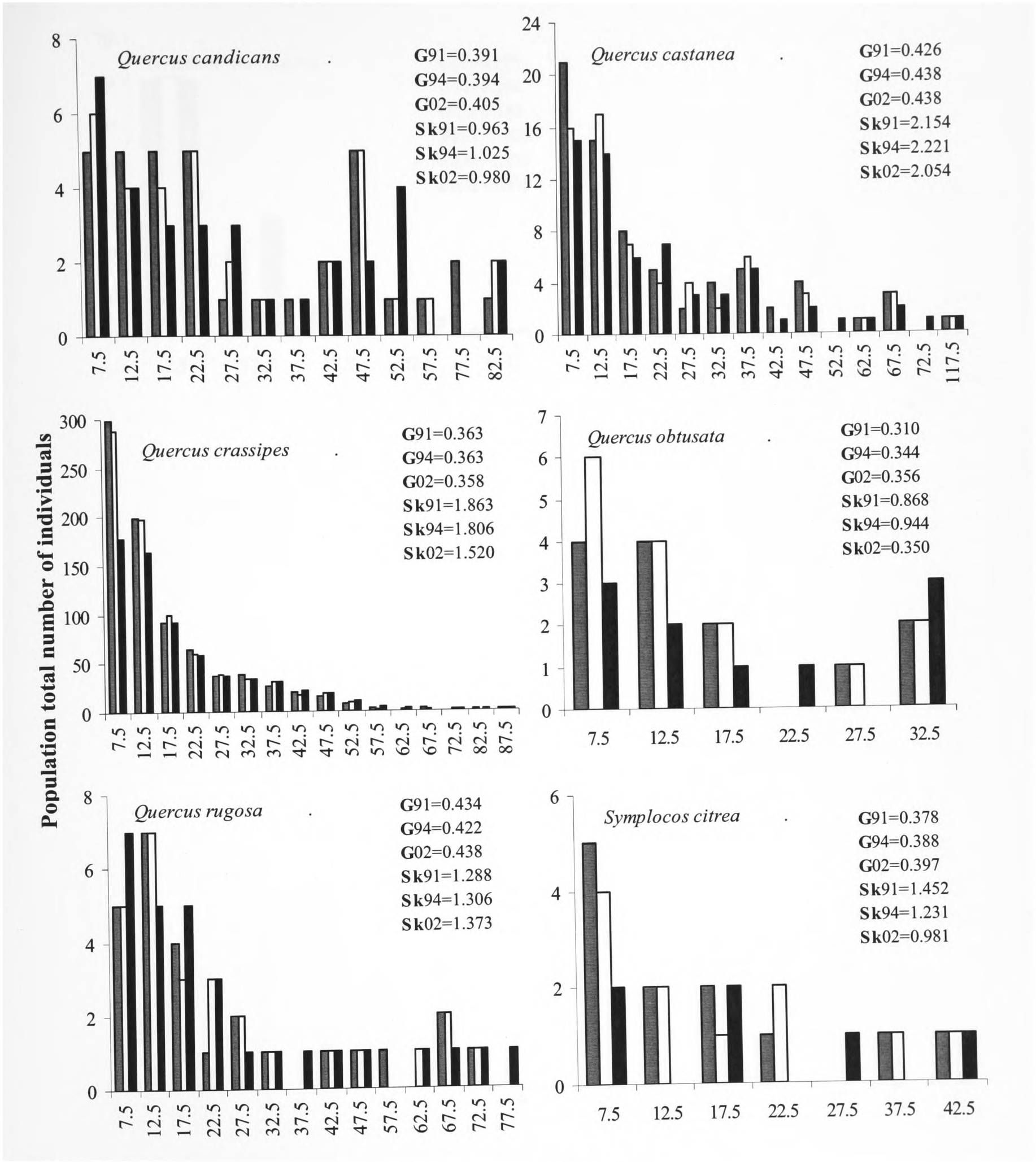
APPENDIX 3.2. NMDS ordinations for **a)** P/A and **b)** BA data sets (86 psps x 38 species) (*STRESS* 15.9 and 15.2; $p = 0.019$ respectively) showing groups of plots and species that share similarities (Sørensen index). Asterisks indicate relative position of species on the axes. Geographical range distance between psps 0.0010-9.5 km. Species name are abbreviated as follows: **Arem** = *Abies religiosa var. emarginata;* **Arel** = *Abies religiosa var. religiosa;* **Afar** = *Acacia farnesiana;* **Ajor** = *Alnus jorullensis subsp. lutea;* **Axal** = *Arbutus xalapensis;* **Bpar** = *Buddleja parviflora;* **Ctro** = *Carpinus tropicalis;* **Cvic** = *Clethra vicentina;* **Cdis** = *Comarostaphylis discolor subsp. discolor;* **Cexc** = *Cornus excelsa;* **Cpup** = *Crataegus pubescens;* **Darb** = *Dendropanax arboreus;* **Eama** = *Eupatorium aff. mairetianum;* **Fuhd** = *Fraxinus uhdei;* **Glau** = *Garrya laurifolia;* **Itol** = *Ilex tolucana;* **Lumb** = *Lippia umbellata;* **Mcil** = *Monnina ciliolate;* **Oxal** = *Oreopanax xalapensis;* **Ovir** = *Ostrya virginiana;* **Plot** = *Perrottetia longistylis;* **Phin** = *Persea hintonii;* **Pgue** = *Picramnia guerrerrensis;* **Pdou** = *Pinus douglasiana;* **Plei** = *Pinus leiophylla;* **Ppse** = *Pinus pseudostrobu;* **Pser** = *Prunus serotina;* **Qaex** = *Quercus aff. excelsa;* **Qcan** = *Quercus candicans;* **Qcas** = *Quercus castanea;* **Qcra** = *Quercus crassipes;* **Qgen** = *Quercus gentryi;* **Qlau** = *Quercus laurina;* **Qobt** =*Quercus obtusata;* **Qrug** = *Quercus rugosa;* **Qscy** = *Quercus scytophylla;* **Sram** = *Styrax ramirezii;* **Scit** = *Symplocos citrea;* **Tlin** = *Ternstroemia lineata subsp. lineata;* **Tmex** = *Tilia mexicana;* **Vhar** = *Viburnum hartwegii;* **Xfle** = *Xilosma flexuosum;* **Zcon** = *Zinowewia concinna*



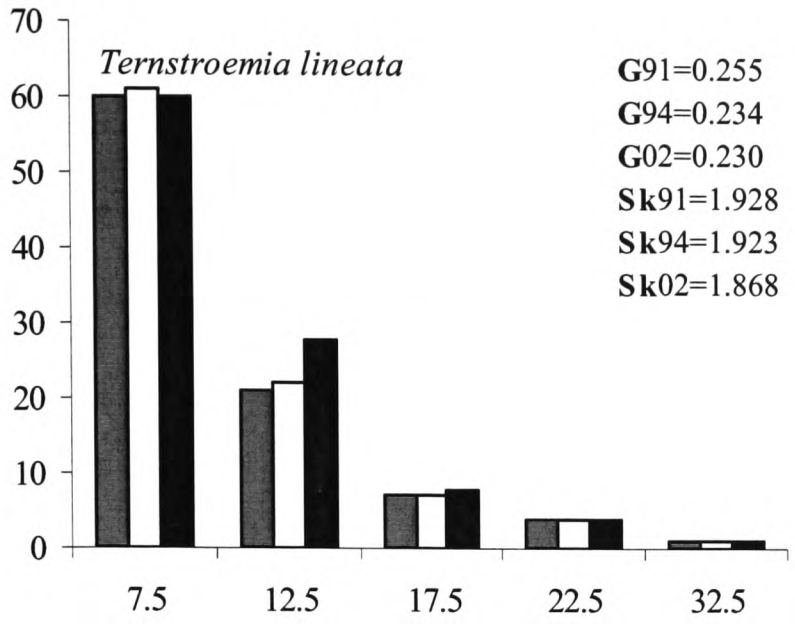
Appendix 4.1a. Patterns of diameter frequency distributions for the **Qc** group presented, by species, in classes of 5 cm represented by the mid point of the diameter class. **G** = Gini coefficient. **Sk** = Coefficient of skewness. Species are given in alphabetical order. ▤ = 1991; □ = 1994; ■ = 2002.



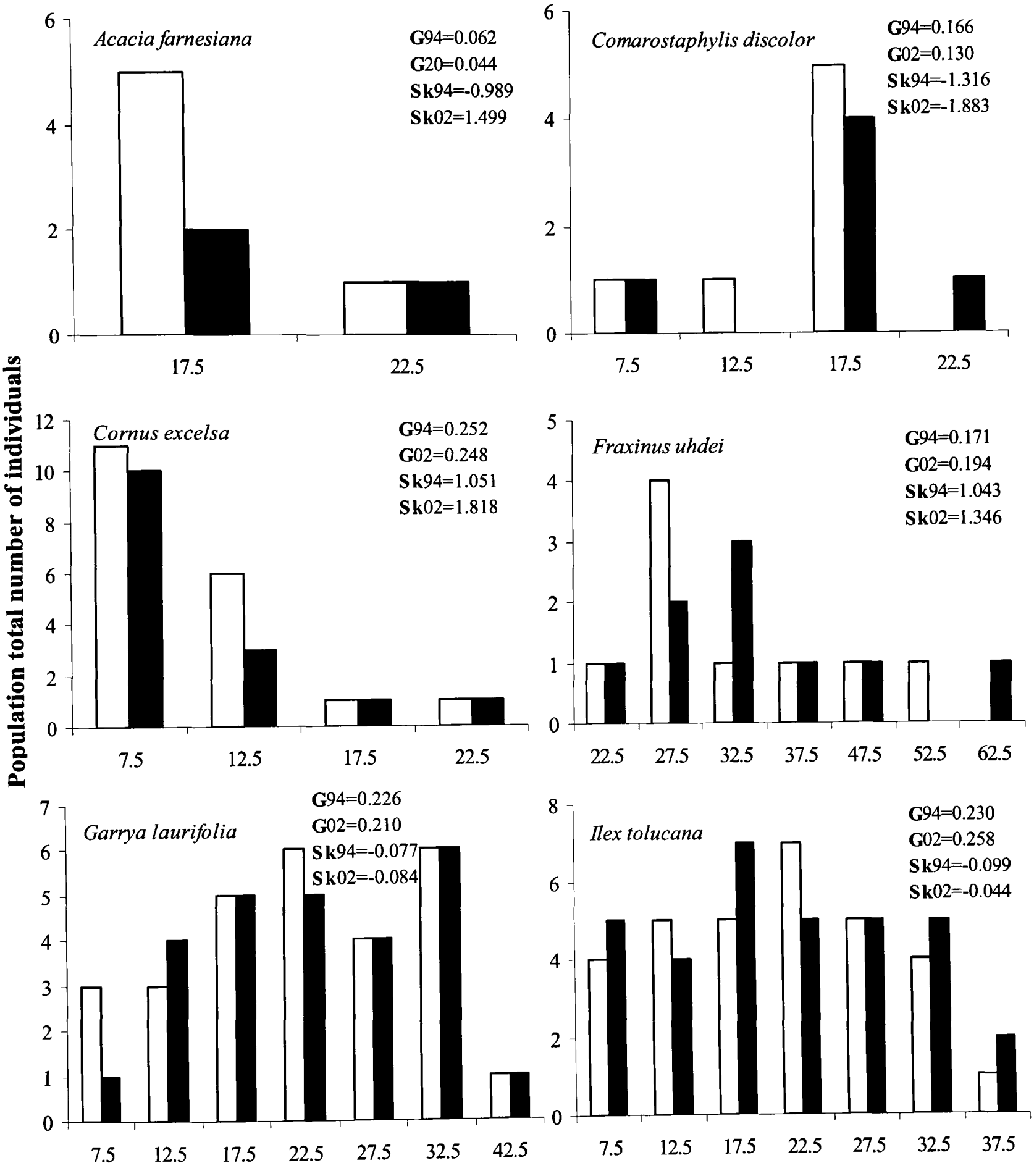
Appendix 4.1a (*Continued*)



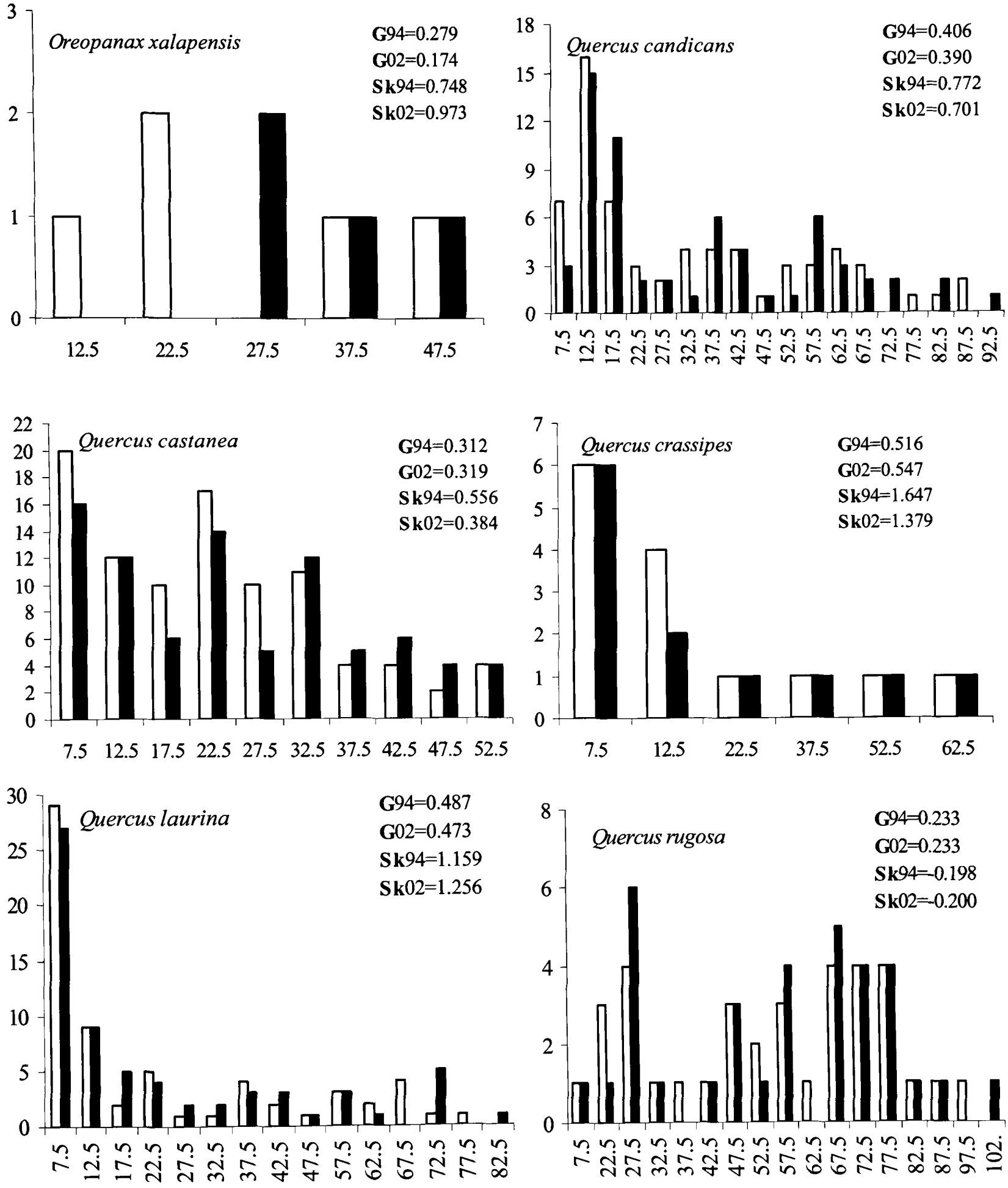
Appendix 4.1a (*Continued*)



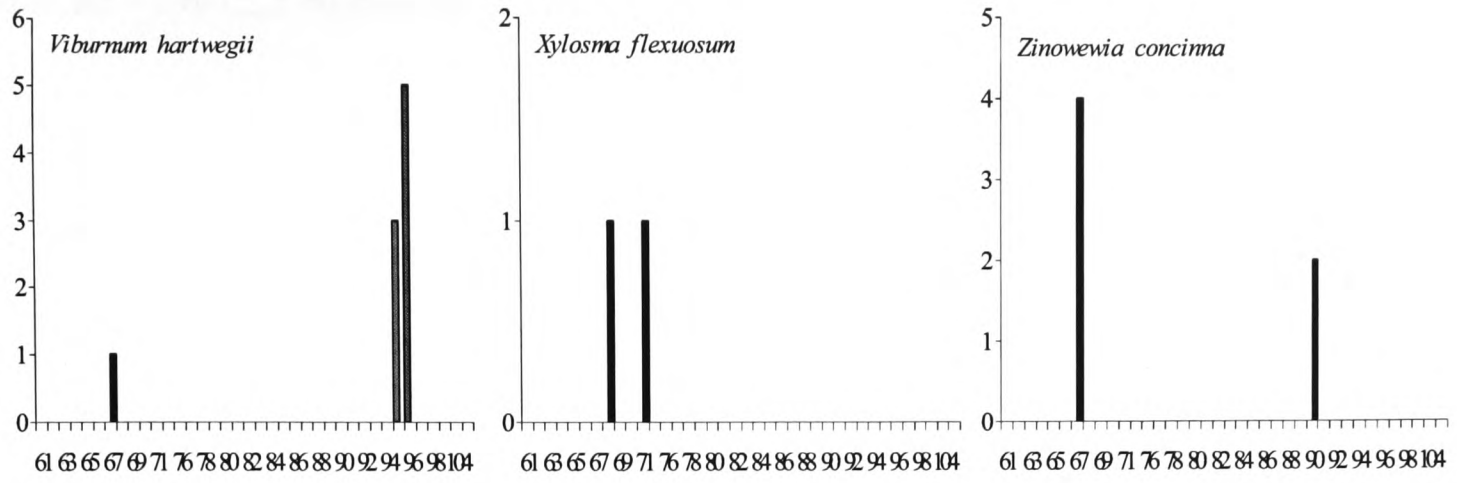
Appendix 4.1b. Patterns of diameter frequency distribution during succession for the **Mm** group given, by species, in classes of 5 cm represented by the mid point of the diameter class. **G** = Gini coefficient. **Sk** = Coefficient of skewness. Species are presented in alphabetical order. □ =1994; ■ = 2002.



Appendix 4.1b (*Continued*)

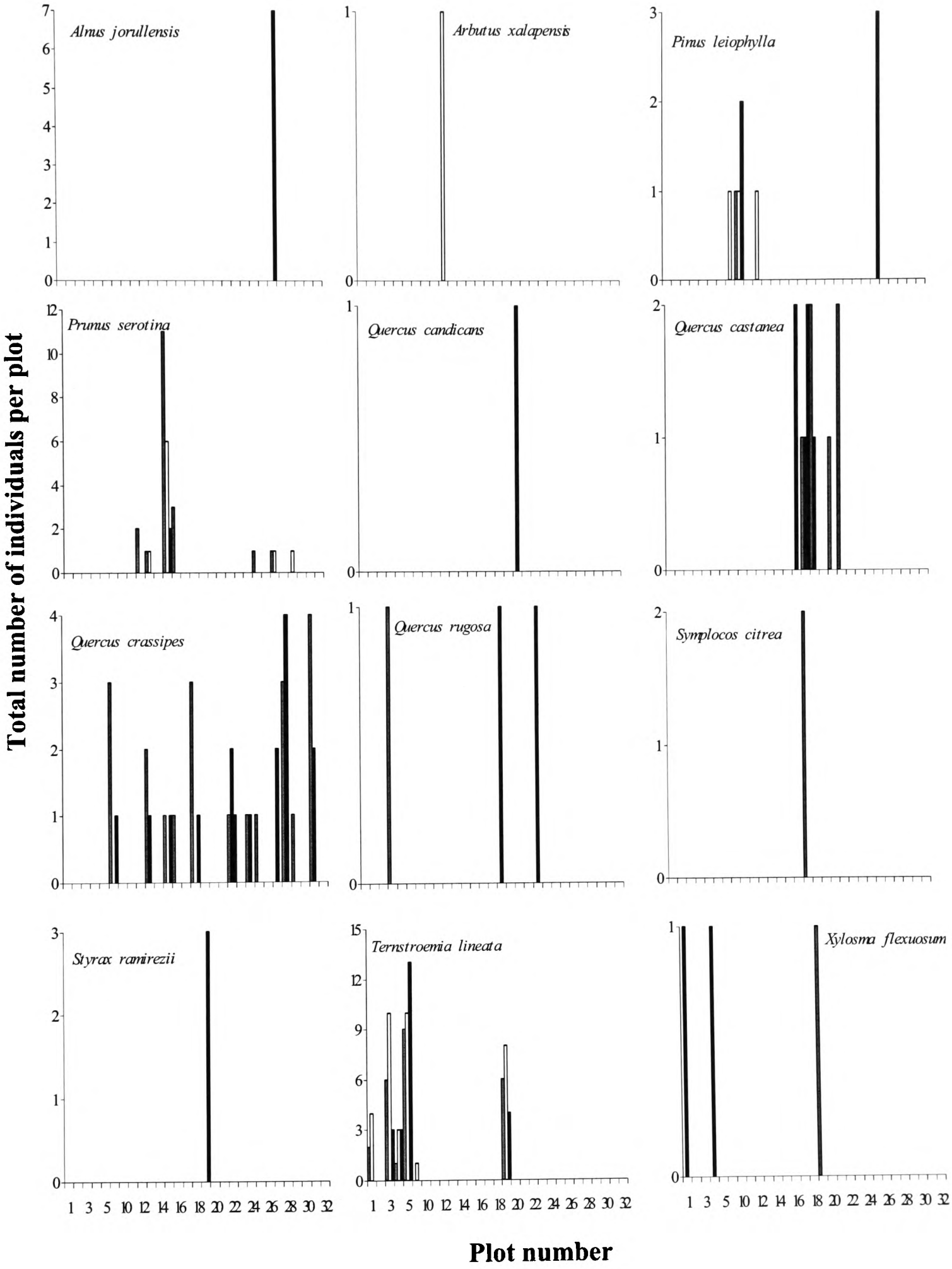


Continued **5.1c**

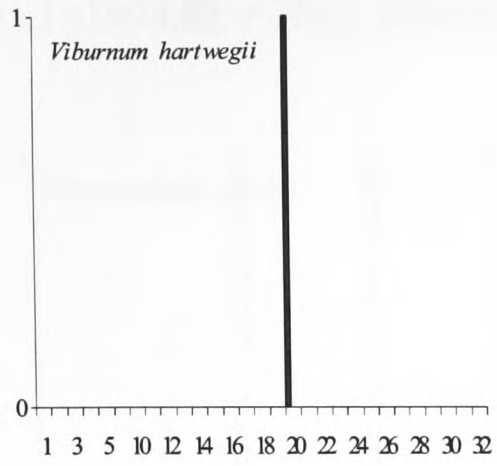


Plot number

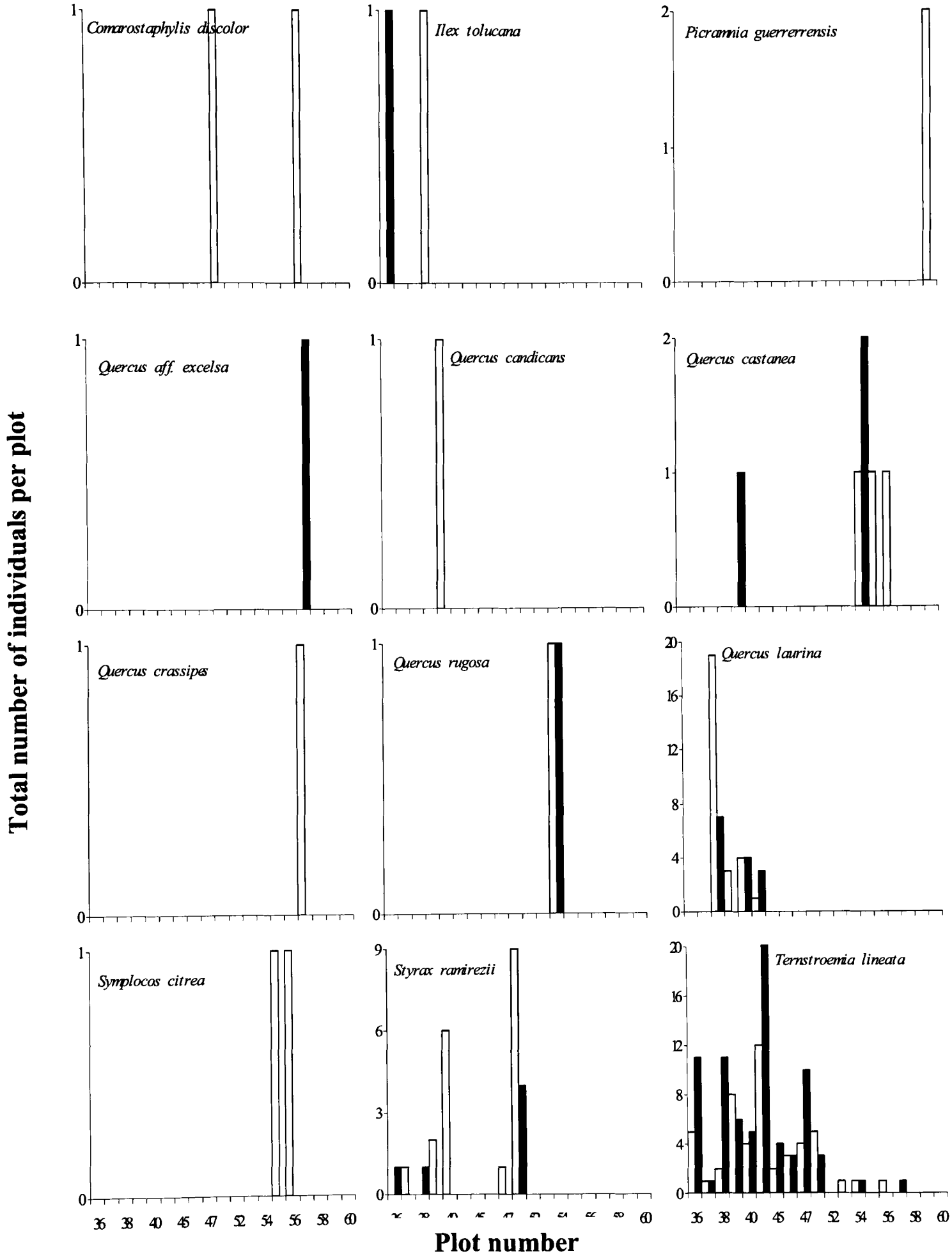
Appendix 5.2a. Sapling changes over time (different bar pattern) in absolute density for the **Qc** group by species, per plot, per year. Each bar represents the species' absolute value. ▤ =1991; □ =1994; ■ = 2002. Note different scales on the '*y*' axes.



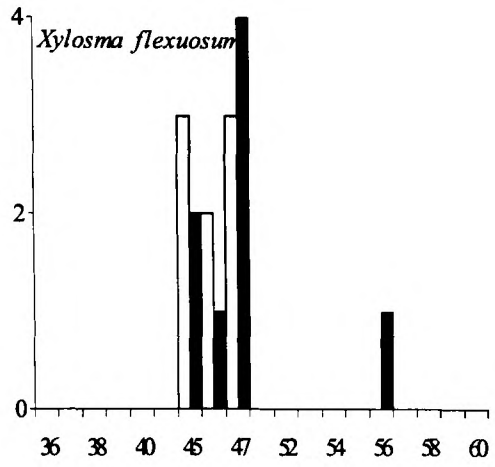
Continued **5.2a**



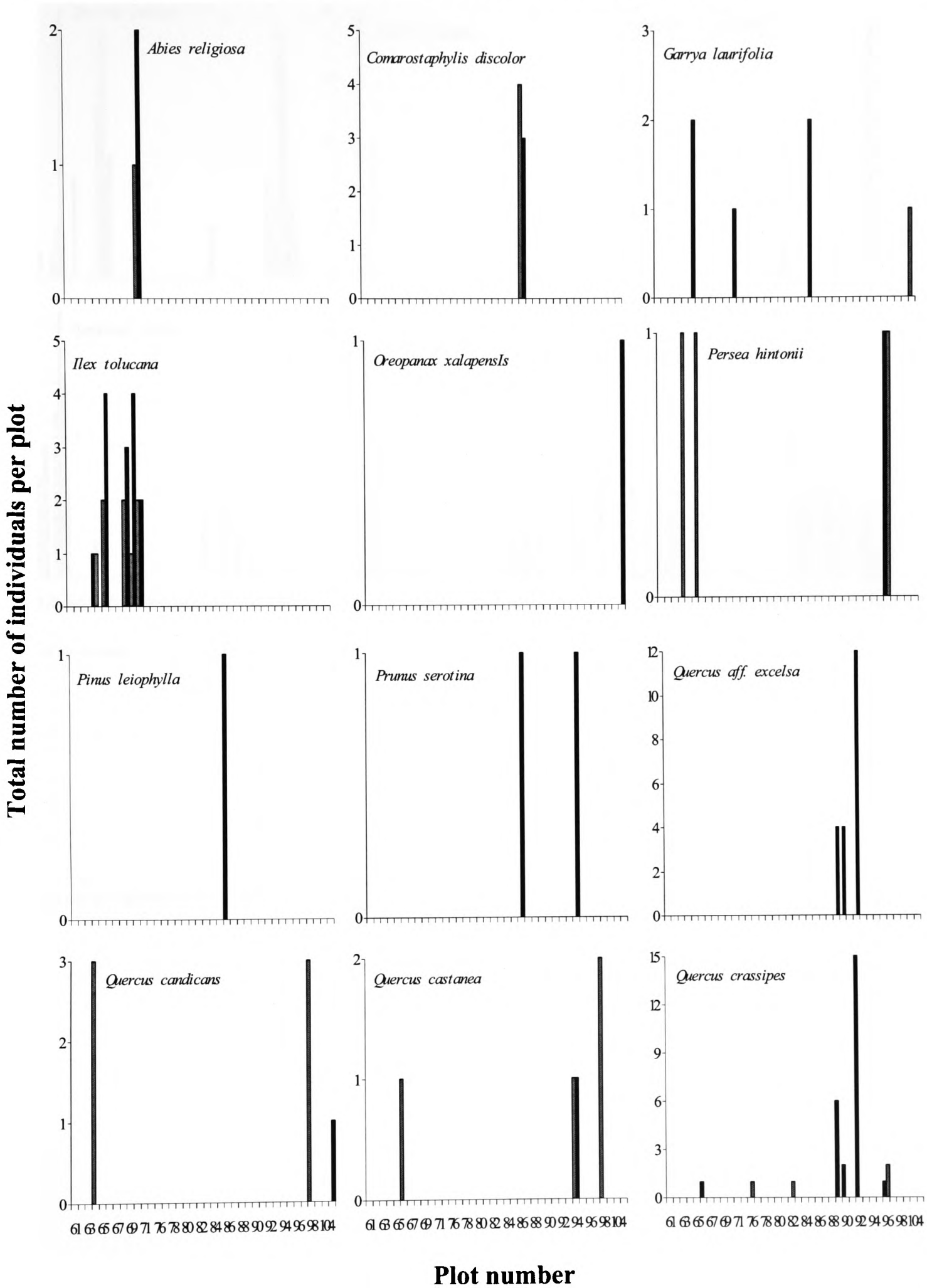
Appendix 5.2b. Sapling changes over time (different bar pattern) in absolute density for the Mm group by species, per plot, per year. Each bar represents the species' absolute value.□ =1994;■ = 2002. Note different scale values in the '*y*' axes.



Continued 5.2b



Appendix 5.2c. Sapling changes over time (different bar pattern) in absolute density for the It group by species, per plot, per year. Each bar represents the species' absolute value. ▩ =1998; ■ = 2002. Note different scale values in the '*y*' axes.



Continued 5.2c