The influence of food and vegetation on bird distribution in tropical deciduous forest and dry oak woodland in western Mexico

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THE INFLUENCE OF FOOD AND VEGETATION ON BIRD DISTRIBUTION IN TROP[ICAL DECIDUOUS FOREST AND DRY OAK WOODLAND IN WESTERN MEXICO

A dissertation submitted to the University of Durham for the Degree of Doctor of Philosophy, March 1996

Pablo Corcuera Martínez del Río

ABSTRACT

Bird species densities, richness and diversity were estimated on 117 plots in a dry forest and oak woodland in western Mexico. The counts were performed during autumn 1990 and 1991 and spring 1991 and 1992. The plant composition and stratification were measured on each plot. Arthropod densities were estimated for most trees and shrubs during the two autumns.

The relationship between bird species diversity and the plant associations was inspected by means of a canonical ordination. The plant variables explaining the species richness, diversity, total density and evenness were obtained by means of multiple regressions. The two methods were complementary and the results suggest that food abundance might be related with species richness and total number of individuals.

An ordination of the sampling plots, based on the bird species counts, separated the main plant associations. Nevertheless, there were no discreet sets of birds corresponding to each associations. Bird species distribution was individualistic with loose groups of species sharing different associations. The plant variables with highest correlation coefficients in the ordinations corresponded to the vegetation type and in general they were not used directly by the birds.

Birds were grouped into guilds according to foraging strategies and the plant species preferences were estimated. Even though food does not seem to control the bird species distribution for non-insectivorous species, birds favour those plants offering the most appropriate food type for each guild.

The influences of food on the distribution and plant choice was estimated more closely for the insectivorous guilds. In addition to a significant correlation between gleaning insectivores and lepidopteran larvae densities in the first year, insectivores had a significant preference for those plants with highest lepidopteran larvae and homopteran densities.

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I declare that this dissertation is the result of my own work. The work was carried out in the Department of Biological Sciences, University of Durham, the Hacienda of Estipac in Jalisco, Mexico, and the Department of Biological Sciences, Universidad Autónoma Metropolitana-Iztapalapa, Mexico. No part of this dissertation has been submitted for any degree or diploma or qualification at any other Institution other than the University of Durham, England.

1. General introduction

In contrast to other vertebrates, birds can be seen and counted in the field relatively easily. Due to their conspicuousness, their habitat preferences as well as their use of food resources can be readily assessed. Due to this characteristic, birds are an ideal group to help understand some basic ecological aspects at the community level.

Historically, David Lack was one of the first biologists interested in the ecology of closely related bird species. He summarized his ideas in a catalogue of cases published in 1971 (Lack 1971). Simultaneously, Evelyn Hutchinson, developed the mathematics of the niche theory (1965) which was centered on the competitive exclusion principle.

Robert MacArthur, one of the most influential ecologist in the sixties, further developed the niche-competition hypothesis and together with his disciples attempted to formally develop and model the principles of resource partitioning in natural communities (Cody and Diamond 1975). Birds were central to the development of these theories (Cody 1974, Diamond 1975, Wiens 1973).

It was encouraging at first to find that some patterns found in nature could be predicted in simple terms. Simple measures of vegetation structure, for example, could predict the bird species diversity in temperate woodlands

(MacArthur and MacArthur 1961, Recher 1969). Likewise, ecologically similar species either occupied different geographical localities (Diamond 1975) or differed in certain morphological structures which enforced them to explore the resources in different ways (Brown and Wilson 1956, Hutchinson 1959), therefore avoiding competition. However, it was soon realized that the relationship between species diversity and foliage height diversity were not necessarily related (Tomoff 1974, Wilson 1974, Nocedal 1984) and that trophic structure differences, predicted by the character displacement theory (Brown and Wilson 1956), could be explained by statistical null models based on random distributions (Simberloff 1984). Furthermore, the omnipresence of competition as the main organizing force in ecological communities collapsed as the field evidence began to accumulate (Wiens 1977).

The controversy about the importance of competition in nature antagonized biologists and there was a general disillusion concerning the study of animal communities (Strong *et al.* 1984). Furthermore, the accumulation of new evidence has made ecologists realize that the biology of bird communities is less well known than what was thought some years ago (Wiens 1989).

There has been a parallel line of research centered in the descriptions of bird species distribution in time and space. These studies have been pragmatic and perhaps less concerned about theoretical arguments.

Bond (1957) showed that bird communities are not discreet, and therefore, supported the fact that animal communities follow the individualistic school promoted by Gleason (1926).

The development of multivariate statistics programs further contributed to these studies and became a powerful tool to describe the distribution of species either in time or space. Multivariate statistics have been particularly helpful to relate environmental factors to the distributional patterns.

The importance of vegetation on bird species diversity, richness and/or composition has been an important field in bird ecology since the studies conducted by Bond. Some of these studies are reviewed by Wiens (1989).

Birds may respond to physiognomic (general aspect of the vegetation), compositional (plant species present and their relative cover) and structural (foliage height diversity) factors. This thesis attempts to understand which vegetation factors better explain the bird species distribution. It would be expected of physiognomical aspects to be more important at regional levels but that either structure or composition would play a more important role at local levels (Hutto 1985).

A number of studies have found that certain plant species explain, to a certain degree, the distributional patterns found within a certain vegetation type (Sabo and Whittaker 1979, Holmes and Robinson 1981, Rice *et al.* 1983, Robinson and Holmes 1984, Bibby *et al.* 1989, Fuller and Henderson

1992). The obvious question is why are such plants so important. Some of them may offer protection from predators or may be suitable as nesting sites. They may also offer better food resources.

From a theoretical point of view, Fretwell (1972) has explored the importance of food in animal communities. Others have shown that certain plants do offer better food resources and therefore attract a large number of birds (Hutto 1985, Peck 1989). It is perhaps more interesting that birds seem to be able to recognize those plants with higher densities of their preferred food (Heinrich and Collins 1983, Holmes and Robinson 1984).

Considering the importance food may have in the organization of animal communities (Lack 1954), relatively few studies have estimated food abundance and measured its impact on the organization and distribution of bird species.

This work is focused on the bird species distribution on a dry forest in western Mexico. It explores the relationship between the vegetation and the bird species diversity, composition and guild structure. The relationship between food and the bird community is also addressed. In particular, the foraging preferences and distribution of insectivorous guilds is analyzed in relation to the arthropod densities on the different plant species.

The first chapter explains the way in which the vegetation was characterized.

The cover of each plant species was measured in each sample plot. The total vegetation cover at various height intervals was also measured in order to estimate the foliage height diversity. In addition, the plant species were grouped into growth forms and the cover of each of them was obtained.

The arthropod density for each plant was estimated and the results are presented in chapter 3.2. Arthropod densities were estimated as a measure of food availability for insectivorous birds.

Chapter 3.3 introduces the bird species found in the study sites as well as their migratory status and relative densities. It also explores the bird species diversity components and their relationship with the vegetation.

The use of diversity indices aims to answer why there are more species in some communities, why some habitats have a few dominant species while in others species have similar densities and which variables help explain temporal and spatial differences in diversity. Magurran (1988) has also emphasized on the importance diversity can have on conservation.

Bird species diversity has been claimed by some to respond to the vegetation structure in some temperate woodland. Other authors have found that certain plant species explain species diversity more accurately. The importance of both, the structural and floristic factors on bird species richness, diversity, total densities and equitability is explored in this study.

The bird species distribution in the four seasons during which the study was conducted is explained in chapter 3.4. Distribution analyses *per se* are interesting since they help to understand the problem on the nature of the communities. Are communities closed and discreet and self organized, or do the different species respond individually to environmental factors? The problem about distribution is particularly important in the light of the species interaction debate that has been the most important issue in community ecology in the last years (Giller 1984, Strong *et al.* 1984, Diamond and Case 1986). Chapter 3.4 explores the way in which the bird species are distributed and attempts to identify those plant variables related to the distribution.

In order to understand the influence of food on the bird community, the birds were first grouped into guilds (Root 1967). Chapter 3.5 explains how these guilds were determined. In the same chapter, plant preferences by each guild were assessed. The importance of each favoured plant is also discussed.

The last section (chapter 3.6) is focused on the relationship between the insectivorous guilds and the arthropod densities on the plant species. First, the densities of the main arthropod groups is explored in relation to the bird guild density. Finally, the insectivorous guilds plant preferences are addressed.

2. Methods

This chapter explains the methods used to estimate bird densities, plant composition, vegetation stratification and arthropod densities and to quantify bird foraging bahaviour. It also gives a brief description of the classification and ordination techniques used throughout the study.

2.1. Birds

A survey of the birds living in deciduous forests and woodlands of the Tapalpa Sierra and the Villa Corona municipally was made during April 1990. As a result from the preliminary survey, twelve sites representing the main vegetation types were chosen mainly due to their accessibility and these were studied in detail. The location of the sites as well as of the study area is shown in Figures 1.1 and 1.2. The bird species present in the study sites, as well as their relative abundance are shown in Appendix 3.1.

2.1.1. Bird Counts

Several techniques were considered to estimate the number of birds in the study area. The large amount of time needed for some quantitative methods (i.e. spot mapping) and their inadequacy outside the breeding season, made them inappropriate for the present research purposes. On the other hand, the rugged terrain and the high density of the vegetation in the area impeded or even made impossible the use of transect methods. Although not without limitations, which will be discussed later, a circular-plot technique (DeSante 1981) was considered to be the most suitable method and was implemented. Between september-december 1990 and march-april 1991, 117 plots at twelve sites were visited at least three times each. In september-december 1991 and march-april 1992, 67 plots in seven sites were visited to estimate the second year bird densities and foraging behaviour.

It has been estimated that between 80-90% of the birds present in coniferous forests and semitropical rain forests are heard and not seen (Reynolds, Scott and Nussbaum 1980). Both forest and woodland in the study area have dense vegetation and because of this, the percentage of birds seen is near 90%. Due to the difficulty in identifying the distance of a call or sound accurately, a practice period was necessary. The purpose of the first visit was therefore to get used to the bird songs and calls and to determine the distance at which the bird could be heard. Each time a new song/call was heard, the distance was estimated and then, if the bird could be seen, a rangefinder was used and the estimated distance was compared to the real one. After the first few days, there was a clear improvement in the distance estimations as well as in bird identification by sound.

For the counts, 10 stations (plots), were established at equal intervals of 200m within each of eleven sites and seven plots on an additional site. Hutto *et al.* (1986) say that bird counts based on stations with different radius are not comparable (see discussion). Because of this and the difficulty in determining the distance of every bird's call it was decided to use a fixed radius.

The size of the radius used was a compromise. If a small radius is used, all the birds within the circle will be detected but the number of detections will be small. On the other hand, if a large radius is used, not all species will be detected (particularly the least conspicuous birds will tend to be highly under represented) (Hutto, *et al.* 1986). Since detectabilities in different plot sizes vary from one vegetation type to another (and from one observer to another), a particular radius has to be subjectively chosen. A 25 m radius has been used in a similar but denser vegetation by Hutto (1986). In the present study, a 30 m radius was considered appropriate and Hutto agreed with this choice (pers. comm.)

The duration of counts should be long enough so that all the birds present are recorded but short enough so that the probability of counting the same bird more than once is minimized (Reynolds *et al.* 1980). A 10 minute period seemed adequate as new species were seldom detected after this length of time.

Distance between plots and number of replicates are the other aspects which have to be considered when conducting bird counts. Distance between plots should be long enough so that counts in each one are statistically independent, but since the number of samples has to be considered, very long distances may be impractical. Reynolds *et al.* (1980) have estimated that for common birds, from 15 to 21 stations are needed to have reliable density estimates for similar vegetation types to those included in this study. Because of the rugged topography and the difficulty of finding large enough patches of relatively homogeneous vegetation in each study site, only ten stations were designated for each site (each one was visited at least twice). On the other hand Hutto (pers. comm.) suggested that only six or seven samples of the same vegetation, but in different locations, were sufficient to estimate relative densities. Since a classification of the vegetation resulted in eight main vegetation units which included plots of different localities, bird densities can be estimated according to these units. Furthermore, the sample units may be entered individually in multivariate programs (*sensu* Aart *et al.* 1975) if they are statistically independent (i.e. the distance between them is long enough). The advantages and disadvantages for each approach will be discussed in the bird ordination chapter.

2.1.2. Bird foraging maneouvres

Each time a bird was seen in a sample unit, its activity was recorded as a "spot" observation. If the bird moved to another plant species or foraging substrate, the activity was recorded again. In order to make the analyses, the foraging activities were grouped in four categories: foraging maneouvre, foraging height, substrate of attack and plant species in which the bird was seen foraging. Substrate attack was placed in a different category since the plant species used by a bird may be used only as a perch to obtain food from another source (i.e. instead of eating an insect standing on that plant, the bird might look for insects living in mistletoe fruits or insects living on lichens).

Height was recorded as an estimate of the mean height at which each species was seen foraging and by watching the position on the foraging substrate in five categories: ground, low, middle, three-quarters and high. After preliminary analyzes, it was noticed that the position was more meaningful in grouping the guilds and therefore it was decided to remove mean height from the analysis. Sabo and Holmes (1983) suggest that some bird species scale the foraging height according to the relative foliage strata. Accordingly, the four substrates used here correspond to the forest/woodland floor, the shrub layer the mid tree canopy and the upper canopy.

The foraging manoeuvres were modified from Holmes *et al.* (1979) and Rabenold (1978) as follow: 1. Glean, in which a stationary item is picked from a substrate by a standing bird. 2. Hop, in which a bird jumps from one branch to another to obtain food. 3. Flycatch is an attack in which the bird flies into the air to catch a flying prey. 4. Hawk which is a short sally, usually within the foliage. 5. Hover is a manoeuvre in which a stationary item is picked by a flying bird. 6. Probe is a technique in which a bird searches for a subsurface prey (i.e. in coarse bark). 7. Drill, in which a bird hammers the surface in search of buried prey.

The target was defined according to type of substrate which was being attacked by the bird. These categories included the diameter of the trunk or branch if it was being used and then categorized in trunk, medium (c.20-80mm in diameter) and large (>80mm). Smaller branches were often difficult to discern from the foliage and therefore <20mm diameter branches and leaves were categorized as foliage. The other categories of this group of variables were flower, fruit, flying insect, ground, mistletoe and lichen (some bird species foraged only in branches with lichens). The last category included the plant species which were used by the birds. These categories were modified from Sabo and Whittaker (1979), Sabo and Holmes (1983) and Holmes *et al.* (1979). As in other studies (Sabo and Holmes 1983), the frequencies of use for every group of variables belonging to each of the four categories were transformed to percentages.

In order to formally determine the guilds, Holmes *et al.* 1979, Landres and MacMahon 1983 and Recher and Holmes 1985 have used multivariate classifications. Multivariate ordinations are useful to reduce a complex data set to a few axes expressing the major underlying relationships. To associate the resources used by the guilds in the four study seasons, ordinations have been used by Holmes *et al.* 1979, Sabo and Whittaker 1979, Sabo and Holmes 1983, Poulin *et al.* 1995. In this study an R type matrix (Ludwig and Reynolds 1988) was constructed; in it the bird species are represented by rows and the foraging strategies are represented by columns. Both classifications and ordinations were used to group the species in guilds. In the first case, both the euclidean and cosine distances were used for the classification (Norusis 1988, Ludwig and Reynolds 1988). Because it is independent of linearity, Sabo and Whittaker (1979) used reciprocal averaging for their niche ordinations. Detrended correspondence analysis (DECORANA) was used here because it was derived from reciprocal averaging (RA) and therefore is also independent of the curvilinear distribution of the data set (Gauch 1982). Sabo and Holmes (1983) indicate that DECORANA has resulted in more accurate information retrieval from artificial matrices than either principal component analysis and reciprocal averaging.

In addition to traditional ordinations, canonical correspondence analysis (CANOCO) is an useful ordination technique because the algorithm includes a regression analysis between the main axes and the environmental variables (chapter 2). Poulin *et al.* (1995) related the abundances of the guilds (a first data set) found in their study sites with the environmental variables (a second data matrix). In this study CANOCO has been used in a similar way. Since the correlation coefficients between the ordination axes and the variables are provided by the algorithm, the statistical significant variables can be readily identified.

2.2. Vegetation

Plant composition, stratification and structure were estimated for each of the 117 stations used for bird counts.

2.2.1. Plant Composition

Plant composition was estimated during november and december 1990. A 2mm diameter rod was used for plants less than 2.0 m tall. The rod was positioned perpendicular to the ground and the names of all the plant species touching it were recorded. This procedure was repeated 40 times for each of the 117 plots. For higher vegetation an optical square marked with two perpendicular axes was used (adapted from Montaña and Ezcurra 1980). Every plant species present in the intersection was recorded. A species-area (or number of touches in this case) curve was drawn for ten random stations (Grieg-Smith 1983) and they all tended to stabilize (i.e. very few new species occurred after 40 replicates) indicating that 40 replicates per stations were sufficient (Figures 1a and 1b).

2.2.2. Vegetation cover and stratification

The same procedure as for plant composition was used to measure the density of the vegetation but this time, regardless of the species, the height of any plant touching the rod or present in the intersection of the lines drawn

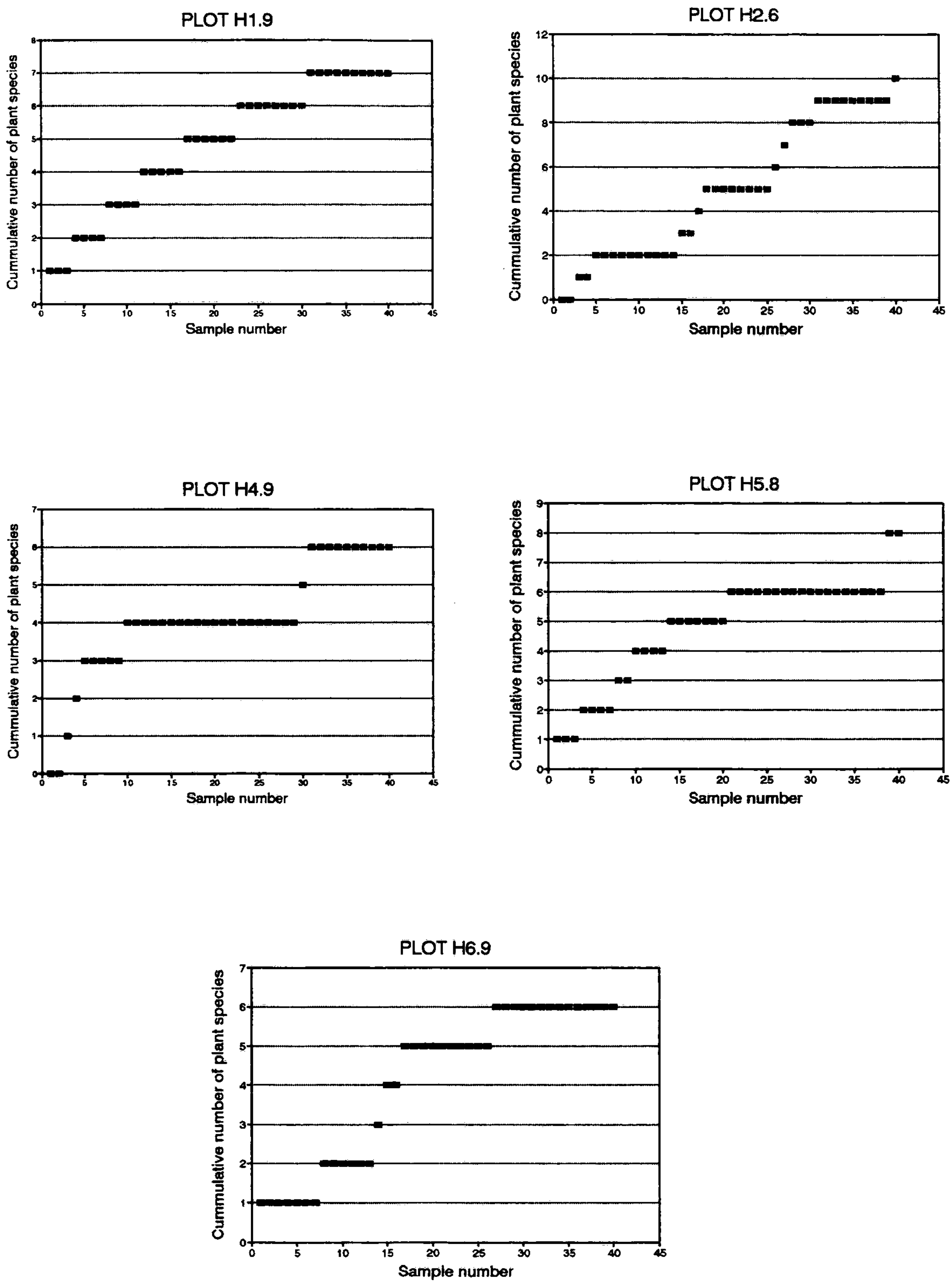


Figure 1. Cummulative frequencies of plant species in 40 samples with a 2mm diameter rod for five random plots.

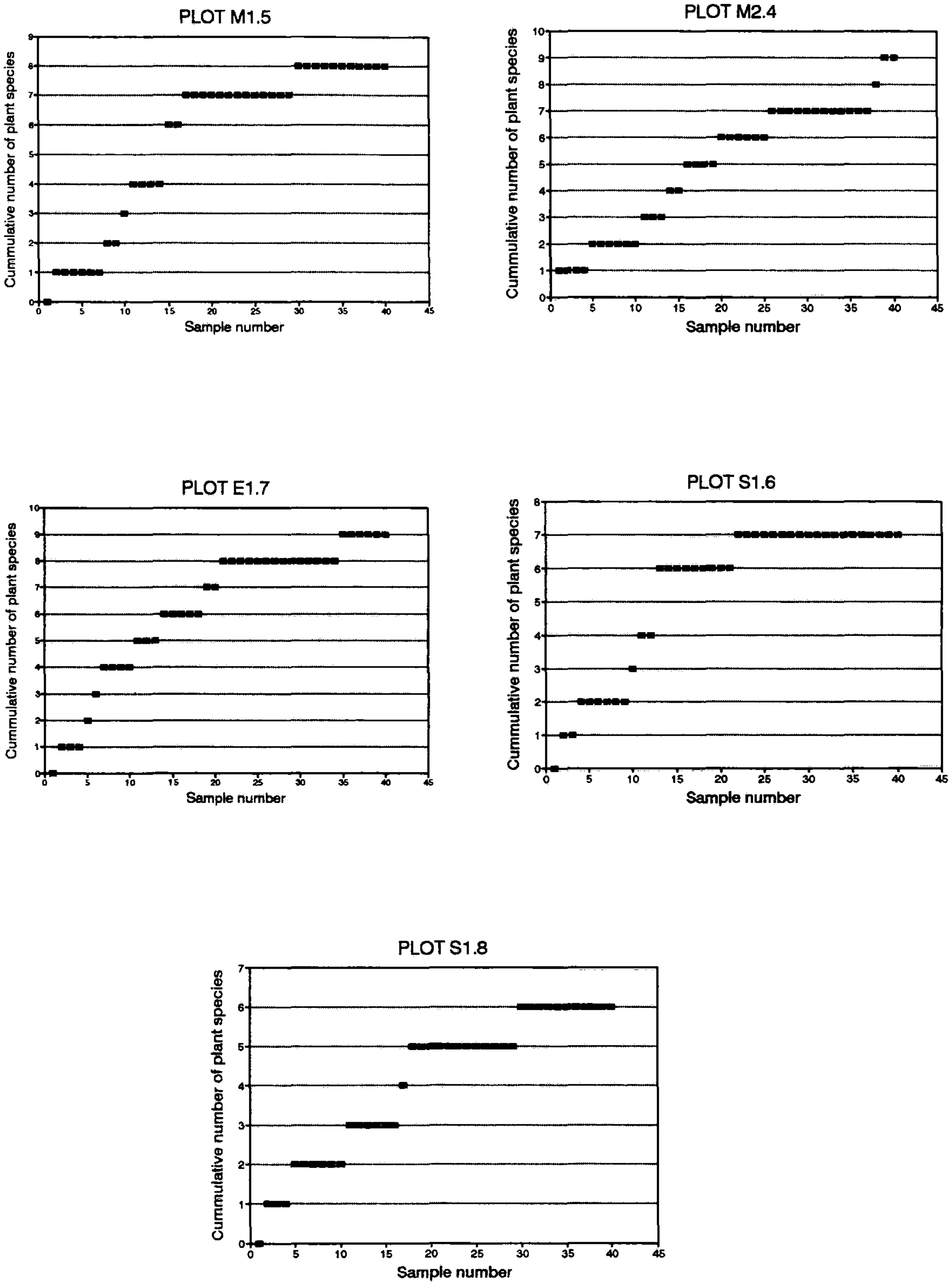


Figure 2. Cummulative frequencies of plant species in 40 samples with a 2mm diameter rod for five random plots.

on the optical square was recorded. Total cover was determined by the number of times all plants were recorded.

Stratification was determined by recording vegetation in each of the following vegetation layers: half meter intervals to 3.0m and then, 3.0-4.5m, 4.5-6.0m and >6.0m. Diversity and evenness indices were then used to obtain the foliage height diversity, following a similar approach used by MacArthur and MacArthur (1961). Diversity was determined with the Shannon-Wiener diversity index. Evenness was determined with the Pielou index (Ludwig and Reynolds 1988, Magurran 1988).

2.2.3. Growth forms

Modifications to the plant growth form classification proposed by Whittaker (1975) for general vegetation and Tomoff (1974) for desert plants (so that they were more suitable to the present's project study sites) have been applied. Eleven plant growth forms were used:

a. Small leaved thorny shrubs (SLTS)
b. Broad leaved shrubs (BLS)
c. Small leaved thorny trees (SLTT)
d. Small leaved semideciduous trees (SLST)
e. Broad leaved deciduous trees (BDT)
f. Small leaved evergreen trees (SLET)

g. Broad leaved semideciduous trees (BLST)

h. Cacti (CRA)

i. Herbs (HERB)

j. Vines (SARSA)

m. Bursera trees (COPAL)

Relative cover of each form was obtained by adding the plant covers of the species belonging to each category.

2.3. Arthropods

At least six specimens of each of the most common tree/shrub species in each of six sites were sampled for arthropods. The sites represent two huizachales, two mature forests and two woodlands and the procedure was repeated twice in autumn 1990 and spring 1991. In autumn 1991, another site on the interface between forests and woodlands was also included, but was only sampled once. Since many plants are common in more than one site, more than six replicates of invertebrates from many plants were collected. At the same time, it was ensured that all trees and shrubs present in the area were included each season.

Sampling was restricted to invertebrates found on small branches and foliage. Each sample was obtained by cutting a small branch, immediately placing it inside a muslin bag and sprayed with insecticide. A more appropriate procedure would have been to place the bag over the branch before cutting it but because of the thorns present in most legumes (which become entangled with the bag material) it was more reliable to cut the branches first, giving less time for the animals to escape. After more than 10 minutes the branch was removed from the bag, and placed over a white sheet and all the invertebrates found collected and preserved in a 70% alcohol solution. Later, each individual was measured and identified. Individuals from the orders Thysanura, Collembola, Psocoptera, Neuroptera, Thrycoptera, Pseudoscorpiones, Acarina and Gasteropoda were not identified to a lower taxonomic level and only the Geometridae, from the lepidopterans was sorted to the family level. Most coleopterans, heteropterans, homopterans and spiders were identified to their respective families.

2.4. Multivariate analyses

2.4.1. Classification

Classification places the sample units into groups according to their affinities so that the relationships between the groups are revealed. The similarities between all pairs of observations (each observation -or sample unit- corresponding to the species and its abundance for each sample unit sampled) are calculated, resulting in a dichotomy in which the sample units which have the highest similarities are grouped together (Davis 1986).

For this study, Two Way Indicator Species Analysis (TWINSPAN) was used for most classifications. In the first instance, TWINSPAN identifies the direction of variation by ordinating the samples. It then divides the ordination to give a crude dichotonomy and identifies the species preferential to either side of the division. The differential species then form a basis for a "refined" ordination which is further divided at the most appropriate point. Indicator species are derived from the "refined" ordination (Hill 1979a).

2.4.2. Ordination

Ordination allows communities to be organized in a system of coordinates so that the most similar appear closest together (Davis 1986).

For the ordination of the habitats, Detrended Correspondence Analysis (DECORANA) was used (Hill 1979b). The main difference between DECORANA and conventional ordination methods is that it avoids the tendency of the second (and higher axes) to be correlated to the first axis (the "arch effect") (Hill 1979b). Furthermore, in some ordination techniques, such as reciprocal averaging and principal component analysis, pairs of points which are separated by the same distance appear closer together if they lie at the extreme of the axis than if they are near the middle. This distortion is avoided in DECORANA because a local mean standard deviation is calculated at different intervals along the axis. The results are then used to rescale the points in the graph (Hill 1979b).

2.4.3. Canonical Correspondence Analysis

Typically, ordination techniques such as principal components and correspondence analysis follow two steps. The first one is based on the ordination of samples based on species abundances, and produces a few main axes which usually explain the largest variation between sample units. In the second step, regressions are performed between the axes and the environmental variables (Gauch 1982, Ludwig and Reynolds 1988). A difficulty with this procedure is that the main axes may well not be those which are better related with the environmental variables (Ter Braak 1986, 1988). Canonical correspondence analysis (Ter Braak 1988) forces the ordination axes to be significantly correlated to the environmental variables (the resulting restricted scores are linear combinations of the environmental variables) and was the technique used in this study. A further advantage is that CANOCO (community ordination by partial detrended canonical correspondence analysis) and the ordination and classification programs (DECORANA and TWINSPAN respectively -Hill 1979a, 1979b), used for the habitat determination in this study, are based on correspondence analysis and the three can readily be compared.

3. Results

3.1. Vegetation

3.1.1. The vegetation types in the study area

The two main vegetation types in the study sites are included in what Rzedowski (1978) described as Deciduous Tropical Forest ("Bosque Tropical Caducioflio") and *Quercus* Woodland ("Bosque de *Quercus*"). The first type, which on a global scale belongs to the tropical dry forests, is the prevailing vegetation of the Pacific coast of Mexico and covers 12.4% (Arizmendi, *et al.* 1990) of Mexico (Figure 1.1). Flores-Villela and Gerez (1988) estimate that some 3.4% of these ecosystems are subject to perturbation. Oak woodlands are typical of mountainous regions of this country and comprise some 5.5% of its surface.

Although the main emphasis in this study has been in the forests, some plots in an oak woodland were included for comparative purposes and because they represent one extreme of a gradient starting with thorn scrublands or "huizachales" (see below) which can be regarded as a particular type of dry forests.

On a global scale, dry forests represent a variety of vegetation types and a

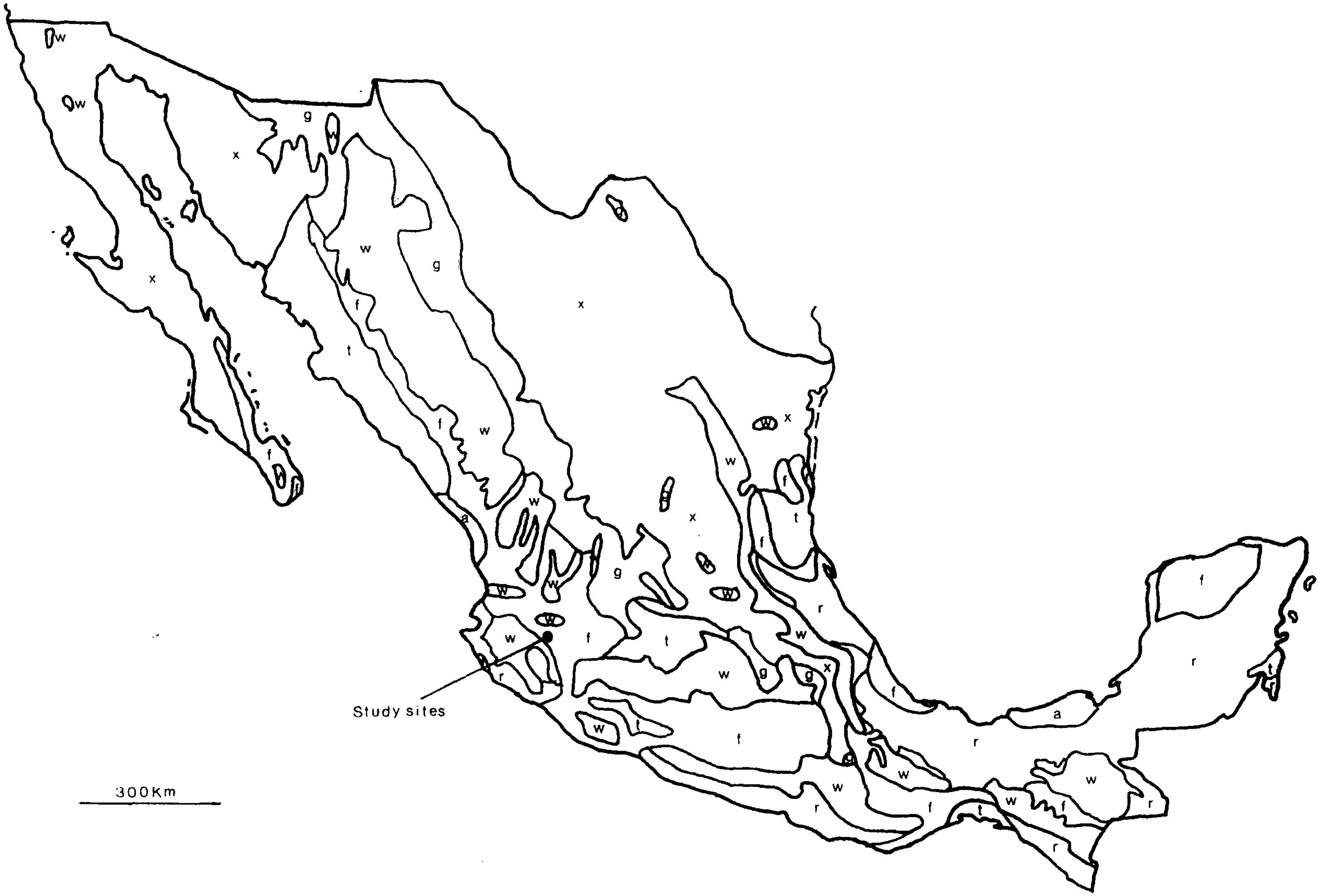


Figure 1.1. Main vegetation types in Mexico. r = tropical semi-deciduous and evergreen forest; f = dry forest; t = thorn forest; x = arid tropical scrub and desert; g = grassland; w = conifer and oak woodland; a = aquatic vegetation.

general panorama of their main characteristics will be presented next.

In a comprehensive review, Murphy and Lugo (1986), following the Holdrige life zone classification, mention that 42% of the tropical and subtropical landmass on earth is dominated by dry forests. Dry forest develops where mean annual temperature is higher than 17°C, mean annual rainfall is 250-2000mm and annual ratio of potential evapotranspiration to precipitation exceeds unity (Murphy and Lugo 1986). This ample range suggests that rainfall seasonality - timing, frequency and duration of dry periods- is often as important as the total amount of rain per year for their development. More particularly, dry forests near the latitudinal limits of the tropics, where this study was conducted, have mainly one intense rainy season but the dry season might last as long as eight months (Murphy and Lugo 1986). Clearly such a marked contrast between the main two periods (the dry and the rainy seasons) is a predominant event which determines the establishment of a characteristic set of organisms and has a major influence on such activities as growth and reproduction. It also limits the access of those species whose distribution is constrained by moisture limitations.

Another important aspect which influences dry forests structure and function is year to year rain variability. Murphy and Lugo (1986) estimate that the coefficient of variation for dry forests is around 30% in contrast to a 15% coefficient found in temperate regions.

Perhaps this unpredictability has some influence on life cycles although soil may also have an effect on the proportion of phenological stages at a given time (Murphy and Lugo 1986). It is true that, physiognomically, the contrast between the two seasons is striking but even during the driest months there are some species with green foliage. Also, although there is a tendency for many plants to start flowering towards the end of the dry season -when annual temperature is highest- this is by no means a generality. In fact there appears to be a marked phenological variation between species and even among individuals of the same species (Murphy and Lugo 1986, personal observation).

Structurally, these ecosystems are less complex than rain forests. Tree height is lower and their richness as well as their productivity is less. Table 1.1 shows a comparison of some structural and functional characteristics between dry and wet tropical forests.

In Mexico, dry forests grow in areas where mean annual temperature is 20-29°C and, perhaps more important in determining its distribution, where the extreme minimum is generally not less than 0°C (Rzedowski 1978). Annual precipitation is usually from 600 to 1200mm, although in some areas it may be as low as 300mm whilst in others as high as 1800mm. This phenomenon results in a marked dry period lasting mainly from December to May (Rzedowsky 1978) in which most arborescent plants shed their leaves (Plates 1 and 2). It must be emphasized again that this is not a generalized phenomenon and some of the

Table 1.1. A comparisson of some structural and functional characteristics between tropical dry and wet forests (adapted from Murphy and Lugo 1986).

	Forest type	
Trait	Dry[a]	Wet[b]
Structural traits		
Number of tree species	35-90	50-200
Canopy height (m)	10-40	20-84
Number of canopy strata	1-3	3 or more
Leaf area index (m^2/m^2)	3-7	5-8
Ground vegetation cover	low-high	<10%
Basal area of trees (m^2/ha)	17-40	20-75
Plant biomass (t/ha)		
Stems and branches	38-266	209-1163
Leaves	2-7	7-10
Roots	1-45	11-135
Total	78-320	269-1186
Functional traits		
(tons/ha yr)		
Aboveground	5-16	10-22
Roots	2-5	3-6
Total	8-21	13-28
Growth periodicity	1-2 pulses annually	Continuous-intermittent
Foliage persistence	Deciduous & evergreen	Primarily evergreen
Reproductive phenology	Seasonal & aseasonal	Less seasonal

[a] Annual rainfall 500-2000mm and strongly seasonal
[b] Annual rainfall >2000mm; little or moderate seasonality

most notable exceptions are the trees of the genus *Prosopis* (Plate 3) which are conspicuous because of their green foliage during the dry season in most dry and even arid environments in Mexico (personal observation).

Edaphologically, deciduous tropical forests are developed mainly in shallow/stony soils. In alluvial and deeper soils, vegetation becomes thorn forests, dominated by the thorny shrub *Acacia cymbispina* (Rzedowsky 1978), which are morphologically more xeromorphic (Plates 4 and 5). *A. cymbispina* is known as "huizache" in Mexico and the dry forests in which it dominates are known as "huizachales". This species represents 22.6% of the total vegetation cover of the thorn forest in the study area, in contrast to only 3% of the total cover of the sites represented by what will be referred subsequently as "mature forests". On the other hand, small deciduous legume trees represent only 4.7% of the plant cover in huizachales but 17.1% in mature forests.

Floristically, the dominant species of dry forests are legumes and this is true for either species richness or number of individuals. In the study area they constitute c.38% of the total cover in thorn forests and c.25% in mature forests. *Bursera* trees, although typical of mexican deciduous tropical forests as well (Toledo, unpublished manuscript), have a lower cover in the present study sites (1.7% in thorn forests and 2.8% in mature forests).

Arizmendi and her associates (1990) comment that dry forest reserves in Mexico

Plates 1 and 2. Mature dry forest in the rainy (1) and the dry (2) season.

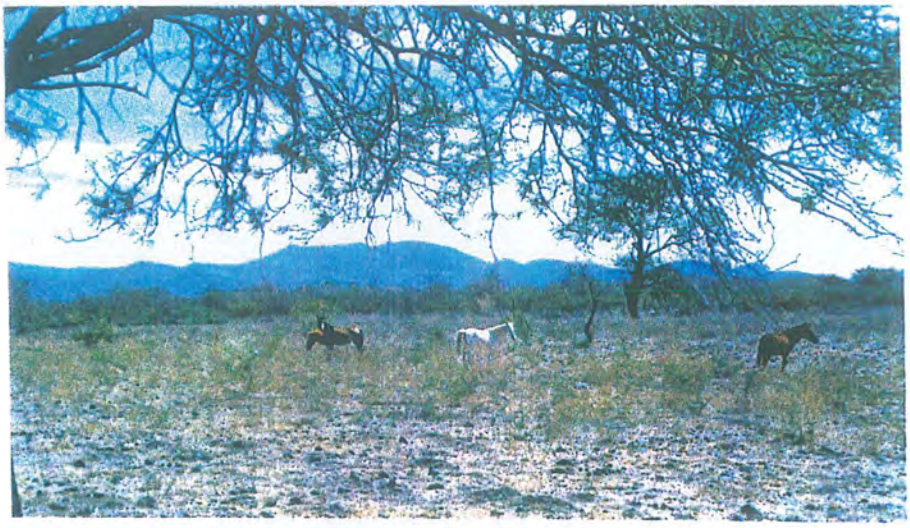


Plate 3. *Prosopis juliflora* during dry season.

Plates 4 and 5. Thorn forest or "huizachal" in the rainy (4) and the dry (5) season.

comprise only 50% of the total bird species occurring in these ecosystems. Furthermore, Rzedowsky (1978) and Flores-Villela and Gerez (1988) have warned that the extensive destruction of these vegetation types is occuring due to farming, logging and replacement by grasslands for cattle grazing. Arizmendi *et al.* (1990) add that the Pacific coast of Mexico, where most of these forests grow, has been very attractive for tourism and resorts have proliferated enormously during the last 20 years. Resort developers have not acknowledged the threat to wildlife which tourism can have if not checked.

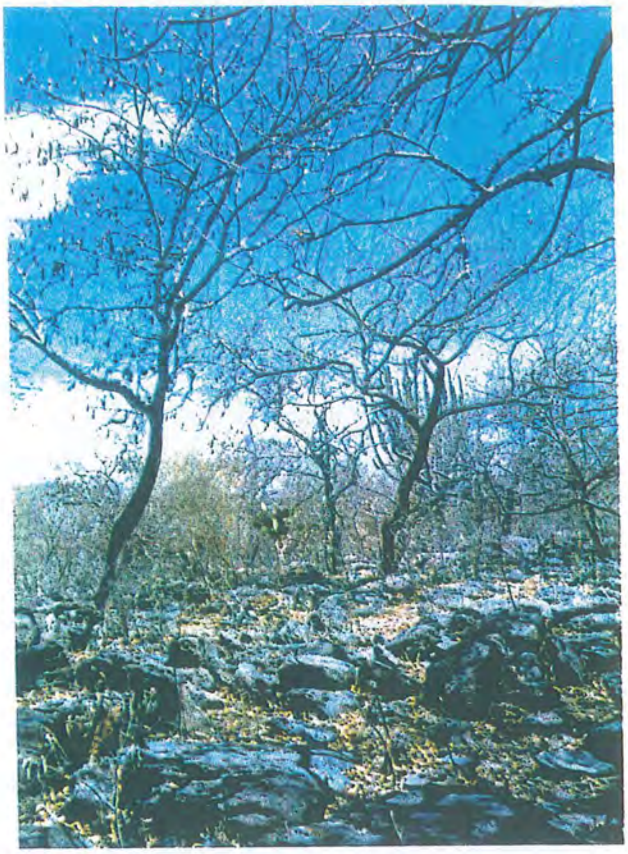
In the area surrounding the study sites, the original vegetation was drastically transformed for cattle grazing during the Spanish rule. Later on, the land was mainly used for sugar cane growth. On the other hand, the study sites are situated in relatively large patches which still remain relatively intact: mature forests cover approximately 1920 hectares, thorn forests are well represented in two patches covering approximately 1000 and 865 hectares respectively, while oak woodlands cover some 1460 Ha.

The main reason human activities have not had a pronounced influence on these areas is due to their topography and soils, which makes them difficult to cultivate because of the high content of volcanic rock and rock fragments (lithosol -Plates 6 and 7). Nevertheless, there are few areas which have not suffered from cattle and goat grazing and selective wood gathering. (Plates 8 and 9). More recently, patches have been cleared for agriculture because of human demographic pressures, (Plates 10 and 11). Moreover, anecdotal evidence suggests that with intensive goat and cattle grazing, mature dry forests suffer a transition to a vegetation type more similar to that of a thorn forest.

Oak woodlands are typical of mountainous regions in Mexico, comprising some 5.5% of its surface. Since in general they exist in good agricultural areas, their conservation situation is precarious (Rzedowski 1978). Precipitation is mainly from 600 to 1200 mm/yr whilst temperature varies from 12 to 20°C. Minimum temperatures of less than 0°C during winter are frequent in this vegetation type. Oaks are not generally used commercially because of their small size.

Some areas originally with this vegetation type have been used mainly for seasonal agriculture in the area of the study sites. Elsewhere in the country, the main cause for its destruction is clearing for cattle grazing. Oak woodlands in the study area are deciduous. Ten sample units in one site representing the edge between the forest and the woodland were included in the present study as well (Plate 13). The contrast between the dry and the rainy season in oak woodlands is shown in Plates 13 and 14.

From the 27 plant species recorded, 12 are shared by both vegetation types. These 12 plant species represent 55.5% of the total plant cover in the forests and 57.6% in the woodlands.



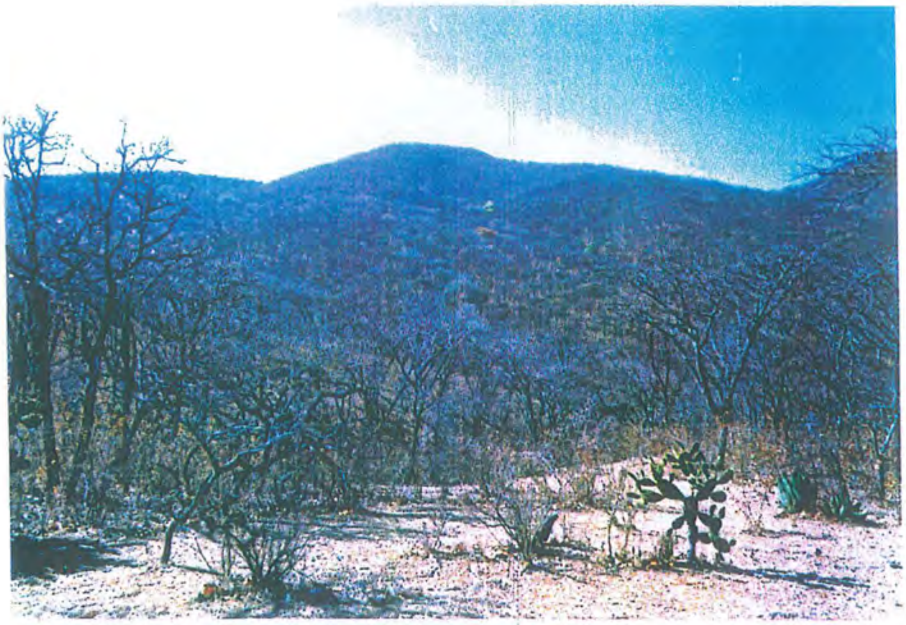
Plates 6 and 7. Lithosols in mature forest (6) and in huizachal (5).

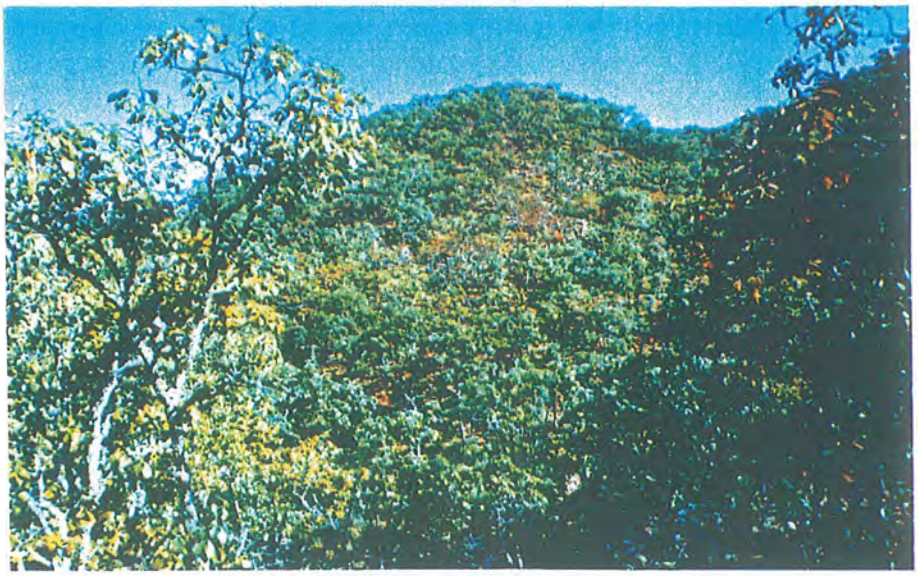
Plate 8. Selective wood gathering.

Plate 9. Typical cattle in this area of Mexico.

Plates 10 and 11. Clearings for seasonal agriculture. Notice the steep slope of clearing in Plate 10.

Plate 12. One of the edge sample units. The bigest tree is an oak. At its right stands an "osote" *(Ipomoea sp.)*, typical of dry forests in Mexico.





Plates 13 and 14. Oak woodland in dry (13) and rainy (14) season.

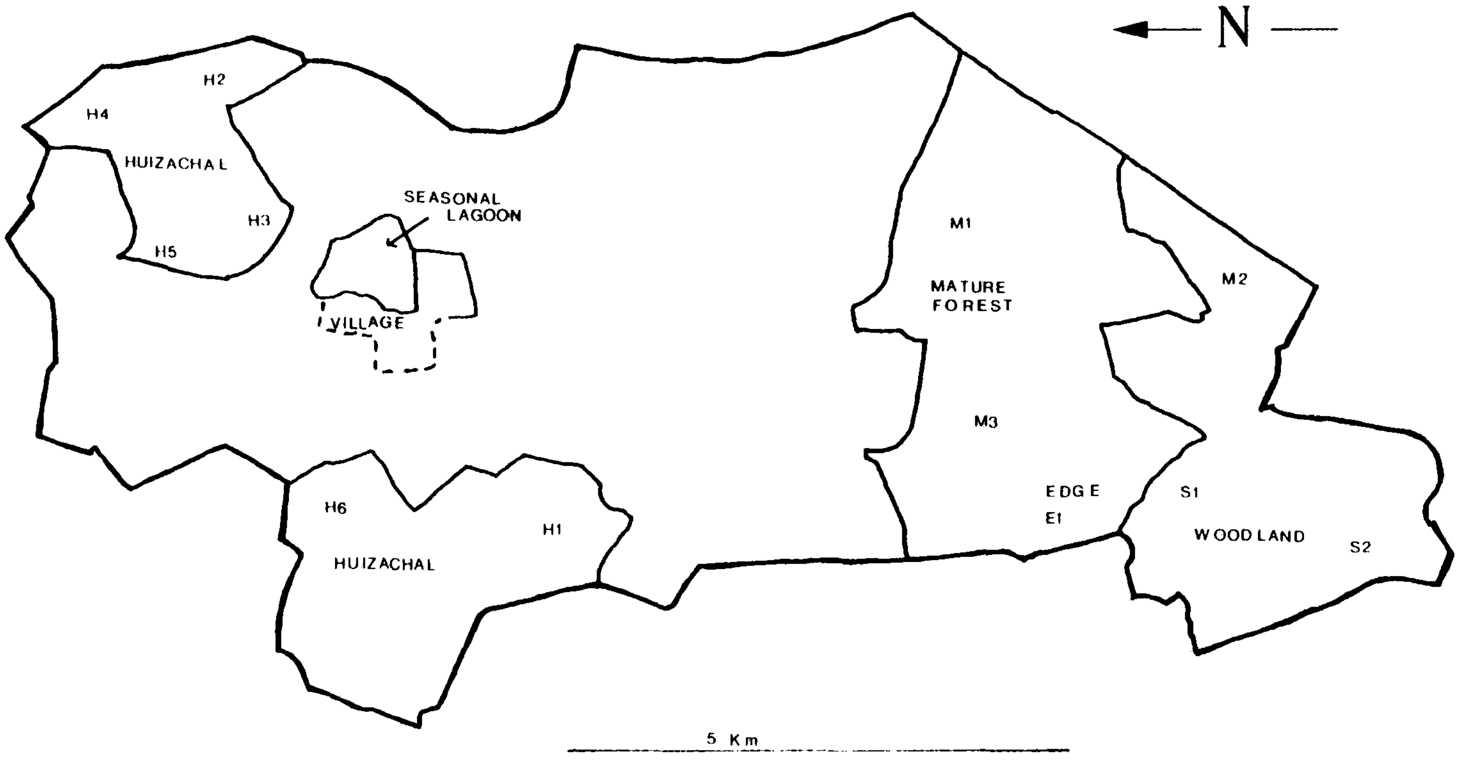


Figure 1 2. Vegetation types in study sites. H - huizachales; M mature forests; E · edge; S oak woodlands.

The study sites are located in the state of Jalisco. They are situated at approximately 20°20'N and 103°35'W (Figure 1.2). Mean height is 1640m a.s.l., with the lowest altitude being at 1355m and the highest at 1995m. Mean temperature is 20.3°C (Figure 1.3) and mean precipitation is 826mm, giving a 2.4 T/P ratio. Most of the rain falls between mid-June to mid-September (Figure 1.4) and there are from 6 to 8 dry months each year (data was gathered at the nearest meteorological station, which stands within the altitudinal range of the study sites and is at 15Km from the study site). It should be added that spring 1992 was anomalous in the sense that january had the highest precipitation in at least the past 18 years, due to El Niño effect (Figure 1.5).

3.1.2. Classification of the vegetation.

3.1.2.1. The study sites.

Twelve sites, representing the main vegetation types were chosen. Two of them are woodlands (sites S1 and S2), other three mature forests (sites M1-M3) and six, thorn forests or huizachales (sites H1-H6) which although structurally different, share most of their species with mature forests (there are only two species which belong exclusively to huizachales and none belonging exclusively to mature forests). The last site (E1) is located between the forests and the woodlands and represents the interface between the two main vegetation types. In each site, 10 plots were sampled to assess relative cover per plant species

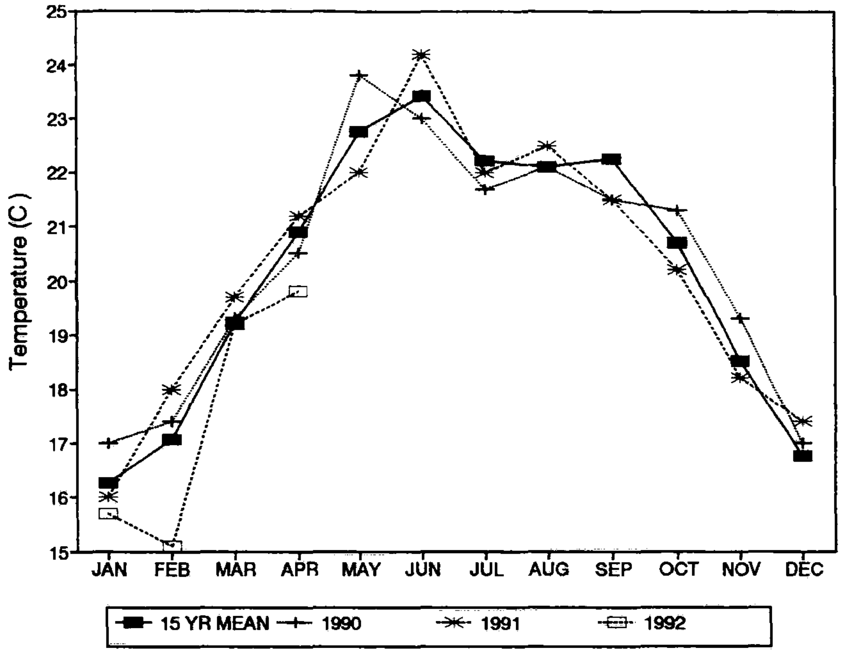


Figure 1.3. Mean annual temperature for last 15 years, 1990, 1991 and 1992.

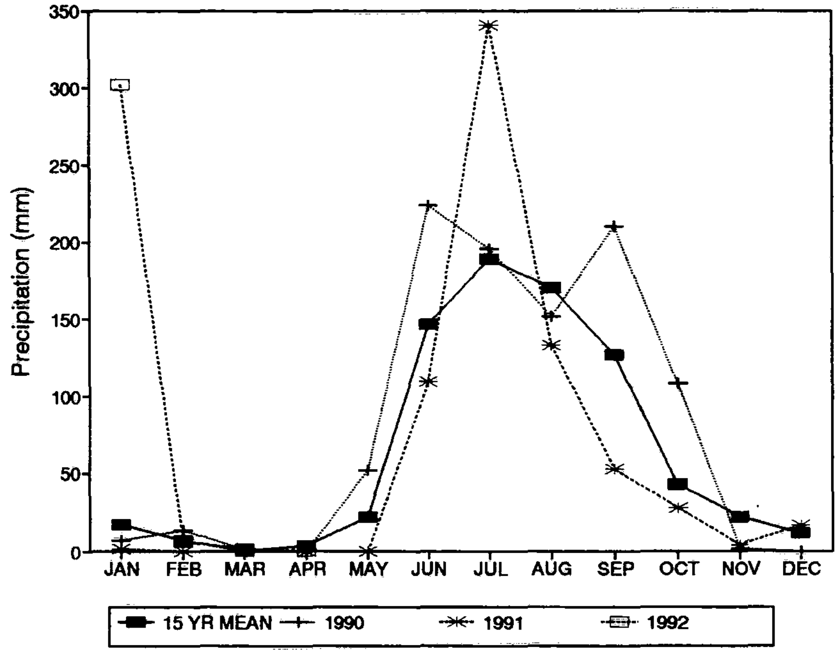


Figure 1.4. Mean annual precipitation for the last 15 years, 1990, 1991 and 1992.

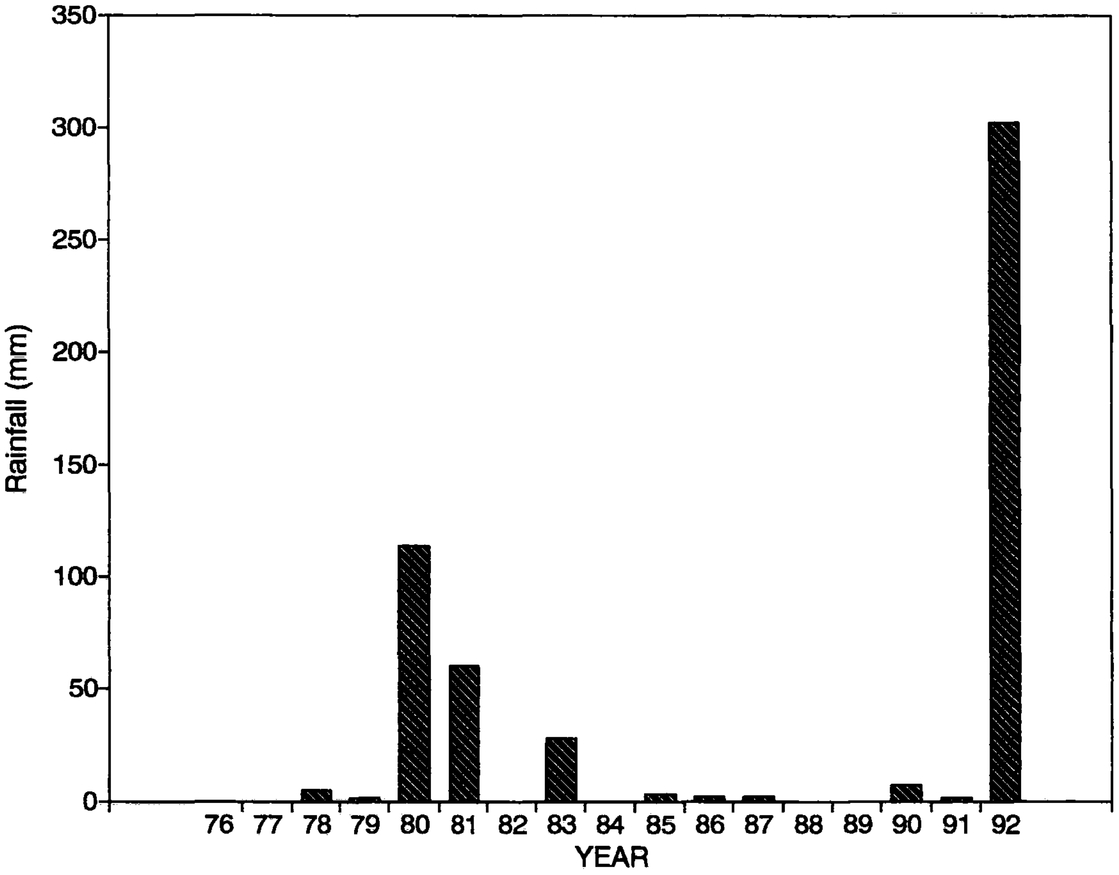


Figure 1.5. Mean january rainfall from 1976 to 1992 in the Villa Corona Municipally, Jalisco. High precipitation in 1992 resulted from El Nino effect.

(composition) and the number of existing vegetation layers (stratification). Plant species were also grouped in growth-forms as explained in the methods.

A first classification was made with TWINSPAN using the means of the 10 sample units of each site for the abundance level of each plant species. An ordination, using DECORANA was performed as well. Ter Braak (1988) mentions that eigenvalues higher that 0.3 are common in plant community data sets when detrended correspondence analysis is used. The ordination of the study sites resulted in relatively high eigenvalues (0.59 for the first axis and 0.12 for the second) suggesting a meaningful separation between the vegetation types. Figure 1.6 shows the results of these tests. The two straight lines represent the classification results where the first division isolated the mature forests and huizachales (M1-3 and H1-6) from the woodlands (S1 and S2) together with the interface site (E1), while the second separated the mature forests (M1-3) form the huizachales (H1-6). The same analysis was also performed using all the measured variables and the final classification was the same.

The measurements for each of the variables per site can be seen in Table 1.2 and the main qualitative differences between vegetation types will be considered.

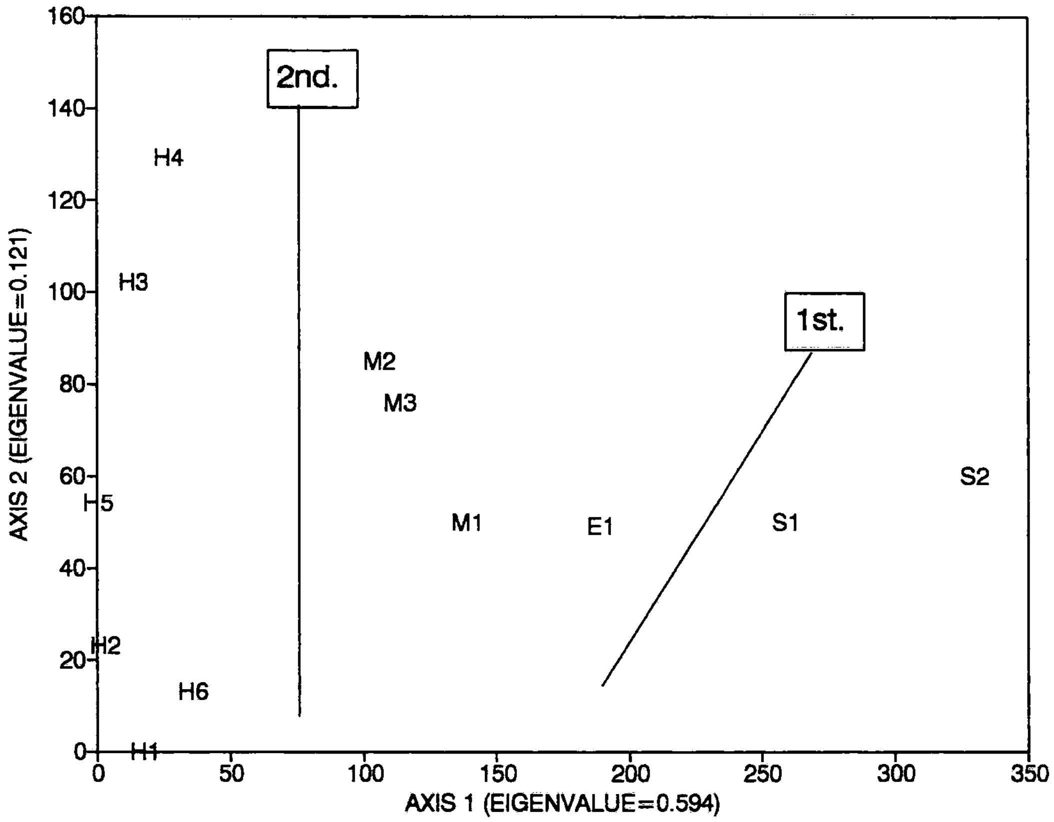


Figure 1.6. Ordination of the study sites according to plant composition. Sites H1-H6 are thorn forests (huizachales), sites M1-M3 are mature forests. Site E1 represents the interface between forests and woodlands and S1 and S2 are woodlands. A classification using TWINSPAN separated the forests and the interface from the woodlands. A second division separated huizachales from mature forests.

3.1.2.2. Composition.

The most obvious differences in plant composition between woodlands (S1 and S2) and forests (M1-3 and H1-6) is the complete absence of oaks in the dry forests and the absence of the thorny shrubs *Acacia cymbispina* and *Acacia macilenta* and of the broad leaved shrubs *Annona* sp. and an unidentified *Apocynaceae* from the woodlands. Other species absent from both woodland sites are the small leaved evergreen tree *Prosopis juliflora*, the small leaved semideciduous tree *Conzattia sericea* and the broad leaved deciduous trees *Guazuma ulmifolia*, *Heliocarpus* sp. *Ceiba* sp. and *Celtis caudata*. *Ipomoea* sp. another broad leaved tree, together with the small shrub *Croton ciliato-glandulosae* is also typical of dry forests and both were found only in a few plots of one of the woodland sites (S1). Mature forests share with the woodlands a high cover of herbs as well as the small leaved thorny trees *Mimosa galeottii* and *Acacia pennatula*.

Floristically, the main differences between huizachales and mature forests is the low cover of the thorn shrubs *Acacia cymbispina* and specially *Acacia macilenta* which tends to be the dominant species in huizachales. The evergreen leguminous tree *Prosopis juliflora* is also typical of huizachales. On the other hand, mature forests have a higher cover of herbs, *Heliocarpus* sp. which is a deciduous tree, and the leguminous semideciduous tree *Lysiloma acapulcensis*. The later has only a high cover in site H6 which, although being a huizachal, its

Table 1.2. Plant species cover and composition diversity in the 12 sites of the study area.

	DRY FORESTS											
PLANT	HUIZACHAL						FOREST			V.I.	WOOD	
COVER	H1	H2	H3	H4	H5	H6	M1	M2	M3	E1	S1	S2
Prosopis juliflora	18	7	27	38	5	5	0	0	0	1	0	0
Randia sp.	15	7	14	13	1	27	13	1	4	0	0	0
Annona sp.	0	0	7	5	0	1	15	18	7	0	0	0
Conzattia sericea	0	3	0	6	0	4	80	38	39	45	32	3
Bursera sp.	12	9	4	11	1	11	11	10	23	13	36	0
Quercus castanea	0	0	0	0	0	0	0	0	0	17	37	6
Guazuma ulmifolia	10	24	83	93	43	13	8	66	87	0	0	0
Herbs	0	11	31	44	16	2	95	86	87	161	159	76
Acacia macilenta	5	25	23	0	11	13	0	0	0	0	0	0
Acacia cymbispina	120	95	65	42	175	70	10	14	22	28	0	0
Apocynaceae	1	4	4	2	0	12	0	1	0	0	0	0
Agave sp.	0	0	0	0	0	0	0	0	0	7	7	0
Byrsonima sp.	22	14	29	43	2	33	11	5	3	2	4	0
Opuntia sp.	19	18	13	3	11	6	21	18	27	9	7	2
Ipomoea sp.	64	27	11	2	24	10	26	28	45	58	20	0
Stenocereus sp.	5	3	1	2	1	1	2	1	0	0	1	0
Ceiba acuminata	1	5	0	0	2	0	3	2	3	0	0	0
Quercus crassifolia	0	0	0	0	0	0	0	0	0	2	108	194
Vines	6	11	34	29	31	9	11	14	11	2	1	0
Heliocarpus sp.	7	18	16	51	4	20	82	91	27	1	0	0
Acacia pennatula	1	2	2	0	4	9	14	18	31	42	60	18
Ficus sp.	2	5	1	3	1	0	0	2	1	0	0	0
Lysolima acapulcensis	1	5	0	0	1	44	32	21	16	11	40	3
Mimosa galeoti	40	4	5	0	0	41	19	12	11	1	4	6
Mimosa sp.	12	23	1	1	0	9	3	1	0	0	0	0
Celtis caudata	1	6	4	17	0	1	0	0	0	0	0	0
Croton sp.	49	57	4	96	93	100	27	94	68	24	9	0
Cover*	408	378	376	501	421	437	480	537	508	421	522	308
S	21	22	20	19	18	22	19	21	18	17	15	8
H’	2.30	2.55	2.43	2.39	1.82	2.51	2.47	2.43	2.46	2.03	2.07	1.09
E	0.76	0.82	0.81	0.81	0.63	0.81	0.84	0.80	0.85	0.72	0.76	0.52

*Number of single touches per species from 40 rod/prism intersections.

V.I.= Vegetation interface

S = No.spp.

H’= Shannon-Wiener diversity index.

E = Pielou evenness index.

Cont. Table 1.2. Life-form and plant stratification cover.

	DRY FORESTS											
	HUIZACHAL						FOREST			V.I.	WOOD	
LIFE-FORMS	H1	H2	H3	H4	H5	H6	M1	M2	M3	E1	S1	S2
SLTS	125	120	88	42	186	83	10	14	22	28	0	0
BLS	38	24	53	63	3	72	38	25	13	2	4	0
SLTT	41	8	7	6	4	54	113	67	81	87	96	27
BLDT	82	79	114	163	72	44	119	187	161	59	20	0
SLST	13	28	1	1	1	53	35	22	16	11	40	3
OAK	0	0	0	0	0	0	0	0	0	19	145	200
LAYERS												
0-0.5	38	47	60	33	61	65	39	56	46	58	64	42
0.5-1.0	50	41	70	99	89	54	70	100	82	109	101	32
1.0-1.5	46	49	65	89	80	54	73	70	62	85	57	35
1.5-2.0	126	106	139	185	147	134	112	86	99	73	65	34
2.0-2.5	78	75	67	68	64	50	70	53	98	48	50	13
2.5-3.0	41	37	37	35	37	47	39	53	53	18	47	21
3.0-4.5	55	59	68	73	42	48	122	112	103	63	73	45
4.5-6.0	31	30	13	19	7	23	76	85	48	22	74	53
> 6.0	5	20	4	8	1	6	40	43	34	9	69	79
TOTAL COVER	470	464	523	609	528	481	641	658	625	485	600	355
H'	2.01	2.09	1.97	1.93	1.90	2.01	2.12	2.15	2.13	2.01	2.17	2.09
E	0.92	0.95	0.90	0.88	0.87	0.92	0.96	0.98	0.97	0.92	0.99	0.95

V.I.= Vegetation interface
SLTS = Small leaved thorny shrub.
BLS = Broad leaved shrub.
SLTT = Small leaved thorny tree.
BLDT = Broad leaved deciduous tree.
SLST = Small leaved semideciduous tree.
OAK = Oaks.
S = Species richness
H'= Shannon-Wiener diversity index.
E = Pielou evenness index.

soil has a higher percentage of rock material than the rest of the thorn forests and in that sense is more similar to mature forests.

3.1.2.3. Structural factors.

When the plant species are grouped in growth form categories (see methods), the main characteristics of dry forests are the high cover values for broad leaved shrubs (BLS) and broad leaved deciduous trees (BLDT). Huizachales are distinctive because their high cover of small leaved thorny shrubs (SLTS) while mature forests, together with woodlands, have the highest densities of small leaved thorny trees (SLTT). Woodlands are characterized by the presence of oaks (OAK) (Table 1.2).

Since huizachales are dominated by thorny shrubs, it is hardly surprising that they have the highest vegetation density in the 1.5-2.0m layer. Mature forests have the highest 3.0-4.5m vegetation layer, corresponding to small trees while woodlands, characterized by somewhat taller oak trees have the highest < 6.0m cover.

Mature forests have the highest total cover as measured by the total number of plant contacts although not always for cover based on composition (i.e. site M1, a mature forest, has a lower composition cover than sites H1, a huizachal and S1, an oak woodland) (Table 1.2). The reason for this is that every touch of the sampling rod by any plant, regardless of its species, was recorded while for the composition only one touch per species was noted, (as explained in the Methods). Mature forests, together with woodlands, have higher foliage diversity and evenness values compared to the edge and thorn forest sites.

3.1.3. Determination of the main plant associations

Although the results of the former analyses correspond to a first appraisal of the general plant physiognomy, the results are not discriminating enough on a closer examination. Site E1 (the vegetation interface) was grouped together with the woodlands, even though it differs in two important ways: 1) *Acacia cymbispina* ("huizache") is not present in woodlands but is common in both, dry forests and the interface, 2) vegetation in the highest strata (>4.5m) is abundant in the woodlands but not so in the vegetation interface (Table 1.2). Furthermore, vegetation in most sites is not as homogeneous as it would appear at first sight. Depending on the substrate, most huizachales have patches in which thorn shrubs are almost absent and which structurally resemble the mature forests rather than the vegetation surrounding them. These vegetation patches are usually in small hills -hereafter called "mogotes" which is the local name- where igneous rocks predominate. Finally, some patches in mature forests, perhaps due to former use have a low plant cover if compared with the vegetation surrounding them.

It has been shown that patchiness can have a significant effect on bird distribution (Sherry and Holmes 1985; Wiens 1989). Since many ecological studies are performed with the assumption that the study areas are environmentally homogeneous, some authors (see Wiens 1989) have emphasized on the importance of incorporating heterogeneity into community studies. The following paragraphs show how the main vegetation types occurring in the study sites were identified.

First, the 117 sample units were classified so that each sample unit could be characterized according to the main vegetation associations. Both TWINSPAN and cluster analyses were used. For the classification, both the squared euclidean distance and the cosine similarity measures were used. The reason for this is that the first, although popular in ecology, squares each species difference between sample units, therefore giving too much importance to the larger differences (Ludwig and Reynolds 1988). The chord or cosine method, by using the following expression, gives more importance to the relative proportions of the species:

$$Simm(X,Y)=\sum\frac{(X_iY_i)}{\sqrt{\sum(X_i^2)\sum(Y_i^2)}}$$

Simm(X,Y) = cosine distance beteen plots X and Y,

X_i = value for variable i in case X, and

Y_i = value for variable i in case Y

The cluster analysis of the vegetation sample units, using either of the methods separated the oak woodlands from the rest of the sites. A second division divided the interface from the woodlands and, less neatly, the mature forests form the thorn forests. A further subdivision, although not very clear, is based on the relative abundance of trees in huizachales. The analysis seemed to performed better when using the cosine similarity coefficient. The squared differences, by giving too much importance to the bigger differences, tends to leave more "clusters" represented by single plots.

TWINSPAN seemed to be the best technique for the classification; it accurately separates the forests form the woodlands together with the edge in the first division and then the woodlands form the edge and the forests form the huizachales in the second one.

Although this first classification showed that plant composition is effective in classifying reasonable vegetation subunits, many studies have shown that structural factors can have a distinct influence on the distribution of the bird species (MacArthur and MacArthur 1961, Willson 1974, Tommoff 1975, Nocedal 1984, Rice *et al.* 1983, Sabo 1980, Urban and Smith 1989). Therefore, both the structural as well as the floristic variables were used to perform the same multivariate analysis.

Since the groups of variables were measured in different units (i.e. diversity indices, total cover per vegetation layer and individual plant cover), the values were standardized so that each variable could be measured in units of standard deviation:

$$Z_i = \frac{(X_i - \overline{X})}{s}$$

where:

Z_i = standard normal form for each observation

X_i = value for each observation

X = mean value of variable

s = standard deviation of variable

The main reason why it was decided to standardize the vegetation data set was because of the use of a semiquantitative technique such as TWINSPAN; it would be very difficult and inappropriate to assign pseudospecies levels for the classification as a whole when the variables included in the data set not only differ in their measurement units but also in their magnitude. Since TWINSPAN does not accept negative values, the lowest value for each variable (corresponding to these original zeros) was substracted from all the other values. There is some controversy over the use of transformations for other multivariate techniques (Pielou 1984) classifications were therefore performed with the original as well as the standardized data set for the cluster analysis.

After running the cluster analyses programs, it became apparent that standardization is effective mainly for the semiquantitative TWINSPAN classification. The results from the cluster analyses were easier to interpret when using the original data.

When TWINSPAN was used with the original data, huizachales were first separated from mature forests and woodlands and then the mature forests from the edge and the forests. Further subdivisions were more ambiguous. On the other hand, when using the standardized data, the resulting clusters were clearly distinguished. Values for the standardized data ranged from zero to seven (very few samples had values of >7) and the pseudospecies chosen were 0.25, 0.75, 1.5 and 3.0. A dendrogram based on the analysis (Figure 1.7) shows that a first division separated the woodlands, the edge and the mature forests from the rest of the forests and the huizachales. A second division clustered together the woodlands and the edge with the mature forests on one side and the rest of the forests and huizachales on the other. Finally, a third division ended in eight main vegetation types: oak woodlands, mixed woodlands, the vegetation interface and an open mature forest with high *Conzatia sericea* covers (coatales) on one side and on the other, two huizachales (in one of which *Prosopis juliflora* was more abundant), a mature forests and the "mogotes". The labels at the sides of each subdivision in the dichotomy in Figure 1.7 are the indicator variables; i.e. those variables which TWINSPAN uses to characterize the groups at each dichotomy. The first dichotomy was based on the presence or significantly

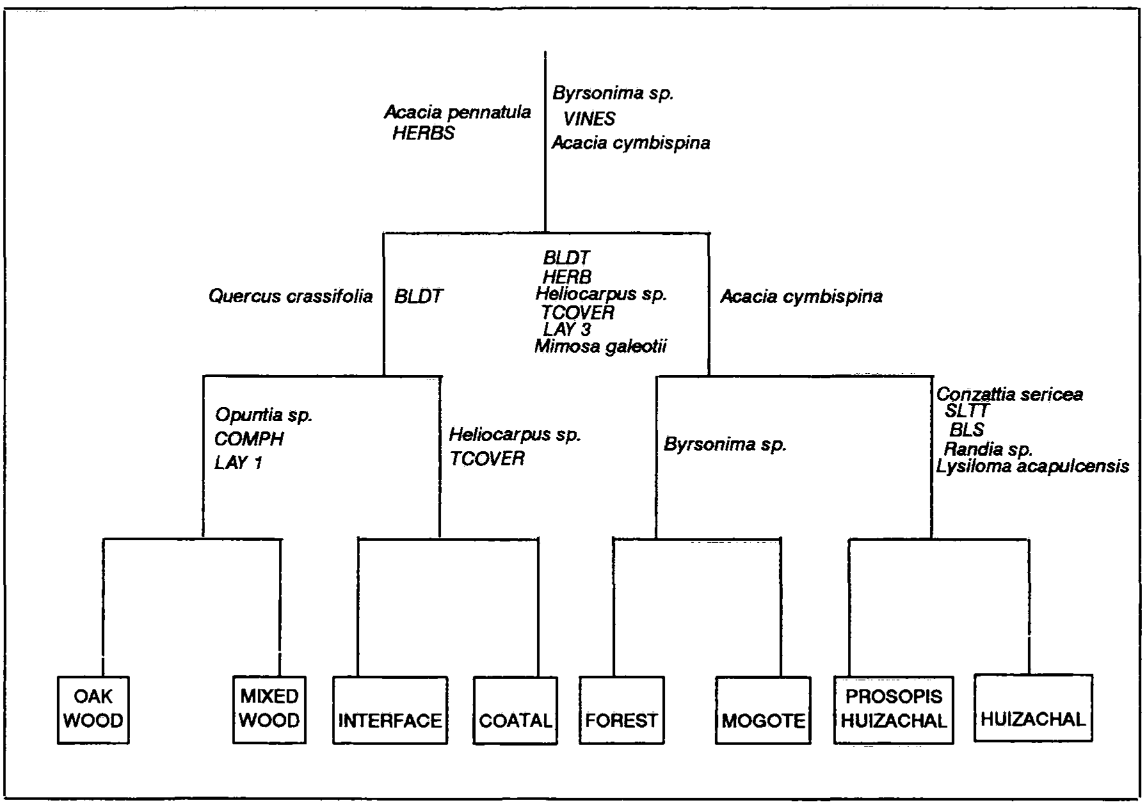


Figure 1.7. Classification of sample units according to plant variables. Names on sides of dendrogram are plant species and vegetation variables used by TWINSPAN as indicators for corresponding subdivisions. BLDT = broad leaved deciduous trees; BLS = broad leaved shrubs; SLTT = small leaved thorny trees; LAY1 = 0-1.0m plant cover; LAY3 = >2.5m plant cover; TCOVER = vegetation cover; COMPH = plant composition diversity.

higher cover of herbs, *Acacia pennatula* and small leaved thorny trees in the woodlands-edges-forest group and of *Byrsonima* sp., and broad leaved shrubs on the huizachal-mogote group. The interface and the woodlands were separated from the mature forests mainly because of the presence of both *Quercus* species on the former and the higher covers of *Guazuma ulmifolia*, composition diveristy, *Croton ciliato-glandulosae* and broad leaved deciduous trees on the forests. The huizachales were separated form the mogotes and the mature forest by the presence of *Acacia cymbispina* in the thorn forests and of *Heliocarpus* sp., total cover and cover of the >2.5 vegetation layer on the other group. In the third subdivision, woodlands and the edge were considered dissimilar by higher values of *Quercus castanea* on the first one and of *Ipomoea* sp. on the second. Both forests differed on the relative covers of *Acacia pennatula* on one of them and of *G. ulmifolia* and *Annona* sp. on the other. Huizachales differed by the higher abundance of small leaved thorny trees, *Conzattia sericea*, *Randia* sp., composition diversity, broad leaved shrubs, *Ipomea* sp. and stratification diversity on one of them. Finally, the mogotes differed from the altered forest by the higher cover of *Byrsonima* sp., the deciduous tree "mora" and the lower cover of *Mimosa galeotii*.

Although the indicators are some of the variables which make two groups dissimilar, usually there are more which are also statistically different. Comparisons between each pair of the resulting eight clusters were performed by means of t-tests in order to identify the additional variables characteristics of

Table 1.3. Means and standard errors of plant variables in the TWINSPAN classification clusters.

	HUIZACHAL		PROSOPIS HUIZACHAL		MOGOTE		FOREST		COATAL		INTERFACE		MIXED WOODLAND		OAK WOODLAND	
PLANT	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
PRJU	0.4	0.2	2.8	0.8	0.6	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
RASP	1.8	0.4	0.1	0.1	3.0	0.8	0.7	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0
ANSP	0.0	0.0	0.1	0.1	0.5	0.2	1.6	0.6	1.1	1.0	0.3	0.2	0.0	0.0	0.0	0.0
COSE	0.1	0.1	0.0	0.0	1.0	0.5	4.9	1.1	6.6	1.3	2.8	0.7	4.2	1.1	0.4	0.2
BUSP	1.0	0.3	0.2	0.2	1.9	0.6	1.3	0.4	2.5	1.3	1.0	0.5	2.8	1.0	0.0	0.0
CRSP	6.9	1.0	9.5	1.2	6.3	0.9	6.6	0.8	5.6	1.7	5.5	1.3	1.0	0.3	0.0	0.0
QUCA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.9	0.7	0.4
GUUL	0.8	0.3	3.9	1.0	8.8	2.1	8.4	1.2	7.8	2.2	2.2	0.9	0.6	0.6	0.0	0.0
HERB	0.2	0.1	1.5	0.4	4.2	1.1	8.4	0.9	8.1	1.6	11.4	1.9	17.0	1.2	11.7	4.8
ACMA	1.1	0.4	0.9	0.6	2.4	1.6	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ACCY	9.7	1.0	15.1	1.8	2.0	0.5	1.7	0.4	0.8	0.5	3.1	1.1	0.7	0.6	0.0	0.0
APOC	0.9	0.5	0.1	0.1	0.6	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AGSP	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.8	0.3	0.0	0.0
SESP	0.0	0.0	0.1	0.1	0.2	0.2	0.9	0.4	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0
BYRS	2.5	0.5	0.8	0.3	4.7	0.6	0.6	0.1	0.6	0.4	0.1	0.1	0.3	0.2	0.0	0.0
OPSP	0.9	0.2	1.2	0.3	0.5	0.4	2.7	0.5	2.0	0.7	1.1	0.3	0.8	0.2	0.0	0.0
IPSP	4.1	0.9	1.4	0.5	0.5	0.2	3.1	0.6	4.4	1.0	5.8	1.0	2.5	0.9	0.0	0.0
STSP	0.2	0.1	0.1	0.1	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
CEAC	0.1	0.0	0.3	0.2	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0
QUCR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.8	2.6	21.4	3.1
VINE	0.7	0.2	2.3	0.6	2.9	0.5	1.4	0.3	1.0	0.4	0.2	0.1	0.1	0.1	0.0	0.0
HESP	0.8	0.3	1.0	0.4	7.5	1.7	7.8	1.5	6.1	2.0	0.2	0.1	0.0	0.0	0.0	0.0
ACPE	0.4	0.2	0.1	0.1	0.4	0.3	1.1	0.5	2.8	0.9	2.8	0.4	6.3	0.8	2.0	1.0
FISP	0.1	0.0	0.1	0.0	0.6	0.4	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LYAC	2.3	0.8	0.0	0.0	0.5	0.4	3.0	0.6	2.3	1.1	0.3	0.1	3.5	0.7	0.4	0.4
MIGA	1.5	0.5	0.2	0.2	3.5	2.4	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
MISP	3.9	0.9	0.1	0.0	0.9	0.7	0.8	0.3	2.4	1.0	0.5	0.3	0.3	0.1	0.9	0.4
CECA	0.1	0.0	0.4	0.3	1.3	0.4	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
COVER	41.0	1.7	42.2	1.9	55.3	2.7	56.1	1.6	55.3	3.2	37.5	1.2	52.2	2.9	37.4	7.2
COMPH	2.7	0.1	2.2	0.1	3.0	0.1	3.2	0.0	3.0	0.1	2.5	0.1	2.5	0.1	1.4	0.1
COMPE	0.8	0.0	0.7	0.0	0.9	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.8	0.0	0.7	0.0
BLS	4.3	0.8	1.0	0.4	8.3	0.7	2.9	0.6	1.9	1.0	0.3	0.2	0.3	0.2	0.0	0.0
SLTT	4.5	0.9	0.1	0.1	2.4	1.1	6.8	1.4	11.9	2.0	6.1	0.9	10.8	0.8	3.3	1.1
BLDT	5.7	1.0	6.7	1.1	17.0	2.9	19.5	1.6	18.4	2.5	8.3	1.2	3.2	1.1	0.0	0.0
LAY1	10.5	0.8	13.8	1.4	10.0	0.7	12.4	1.2	11.8	1.5	15.5	1.0	17.6	1.0	5.2	1.1
LAY2	24.1	1.4	28.1	1.4	32.7	2.6	25.1	1.4	25.0	2.7	20.1	1.1	18.5	1.2	8.2	1.0
LAY3	13.1	1.7	10.5	1.3	24.5	3.7	29.8	2.0	29.9	3.8	8.4	1.7	23.4	3.3	20.6	1.4
LAYH	2.7	0.1	2.6	0.0	2.8	0.0	2.9	0.0	2.8	0.0	2.6	0.1	2.9	0.0	2.7	0.1
LAHE	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0

Mnemonics for plan names composed from first two genus and first two species words
COMPH = plant composition diversity
COMPE = plant composition evenness
BLS = Broad Leaved Shrubs.
SLTT = Small Leaved Thorny Trees.
BLDT = Broad Leaved Deciduous Trees.
LAY1 = 0-0.1m plant layer
LAY2 = 1.0-2.5m plant layer
LAY3 = >2.5 plant layer
LAYH = foliage height diversity
LAYE = foliage height evenness

Table 1.4. T-test significance levels for plant variables between pairs of TWINSPAN plant associations. Symbol position indicates cluster on which plant varible was more abundant.

Plant variables	MOGOTE	FOREST	HUIZACHAL	PROSOPIS HUIZACHAL	COATAL	INTERFACE	MIXED WOODLAND	OAK WOOD
P. juliflora	+			*				
Randia sp.			**					
Annona sp.				+				
C. sericea		*	+				**	
Bursera sp.			*				*	
Croton sp.							+	
G. ulmifolia				**	*		+	
Herbs		**		***				
A. macilenta	+							
A. cymbispina	*						+	
Apocynaceae						+		
Agave sp.			+			+	*	
Senecio sp.				+				
Byrsonima sp.	***		*				+	
Opuntia sp.							**	
Ipomoea sp.			*			**	**	
Stenocereus sp.								+
C. acuminata		*						
Q. crassifolia								***
Vines				*				
Heliocarpus sp.		***			*		+	
A. pennatula						*	+	
L. acapulcensis			+					
M. galeoti			**			**		
Mimosa sp.			**			+		
C. caudata	+							
Composition H	**		***				***	
Composition E						***		
BLS			***				+	
SLTT			**			**	*	
BLDT					*		**	
0.0-1.0m				*			**	
1.0-2.5m							**	
>2.5m			*					
Lay H			**		**			
Lay E					*			

Presence in only one cluster is indicated by "+"
P<0.05=*; P<0.01=**; P<0.001=***

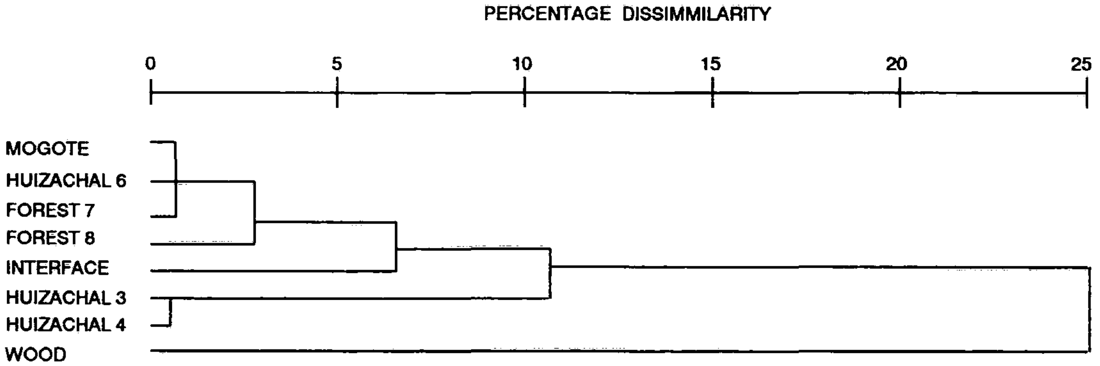
each group. Table 1.4 shows the significance levels of these differences, while Table 1.3 presents the means and standard errors of the variables present in each TWINSPAN group.

An ordination using DECORANA gave higher eigenvalues when using the standardized data (0.201, 0.086 and 0.049 for the first three axes with the raw data, against 0.236, 0.144, 0.093 and 0.078 with the standardized data). It must be noted that eigenvalues were lower when all the variables were included as compared with the floristic data set alone. The reason for this is that when using only composition, many sample units do not share the same plants, and so they tend to be more dissimilar. When the rest of the variables are included, all of the plots have similar values for each of these new variables. Since all of them have more variables (with small ranges between their values) to share, they are more alike. Nevertheless, it is interesting to note that although eigenvalues are lower, the microhabitat classification seems to be more accurate.

The cluster analyses performed better when the original data set were used: when the standardized data was used, too many sample units were not classified in clusters and were left isolated. When using the original set, both the squared euclidean dissimilarity and, particularly the cosine similarity index, resulted in eight clusters -at the 15% similarity level- which were similar to the groups obtained with TWINSPAN. Figure 1.8 presents a dendrogram with the

Figure 1.8. Simmilarity matrix and dendrogram between eight clusters representing the main vegetation types in the study area. The cosine simmilarity coefficient was used.

	WOOD	INTERFACE	HUIZ 3	HUIZ 4	MOGOT	HUIZ 6	FOREST
INTERFACE	0.928						
HUIZACHAL 3	0.828	0.917					
HUIZACHAL 4	0.846	0.948	0.979				
MOGOTE	0.896	0.955	0.949	0.967			
HUIZACHAL 6	0.873	0.947	0.947	0.966	0.980		
FOREST 7	0.904	0.971	0.939	0.950	0.978	0.979	
FOREST 8	0.899	0.947	0.886	0.917	0.962	0.977	0.975



resulting clusters, as well as the cosine similarity coefficients obtained from the means of the variables of each of the eight groups. It can be seen that woodlands were first isolated from the rest of the microhabitats. Two of the huizachales were then segregated form the edge and the mature forests. The mature forests were finally isolated from the mogote and a further huizachal.

The main difference between the results of TWINSPAN and the (cosine) cluster analysis was that the former identified an interface and a mixed wood (which also shares species with dry forests), while the cluster analysis added a further huizachal. In the first case, when the interface was compared with the rest of the forests, t-tests indicated significantly higher cover of small leaved thorny trees ($P<0.05$), particularly of *Acacia pennatula* ($P<0.01$) and lower covers of broad leaved shrubs ($P<0.001$) and broad leaved deciduous trees ($P<0.01$), particularly *Heliocarpus* sp. ($P<0.001$).

The additional huizachal from the cluster analysis differs from the other thorn forests by having a lower huizache cover (*Acacia cymbispina*) ($P<0.001$) and of the other thorny shrub, *Conzatiia sericea* ($P<0.05$). It also has higher covers of broad leaved trees ($P<0.001$), particularly of *Heliocarpus* sp. ($P<0.001$) and *Guasuma* sp. ($P<0.01$) which are more typical of mature forests. Structurally it has higher total vegetation cover ($P<0.001$) and higher values for composition diversity ($P<0.001$) and equitability ($P<0.01$). It also has a more abundant canopy layer ($P<0.001$) and a higher stratification diversity index ($P<0.001$).

Although there are no rigorous statistical tools yet devised to test for significance for multivariate statistics (Norusis 1988), there are some ways of testing for differences between resulting clusters.

One way of testing for the actual significance between the means of classification groups is to calculate Wilkis' lambda which is the ratio of the within-groups sum of squares to the total sum of squares. The value obtained can then be transformed to a variable which has an approximate chi-square distribution (Norusis, 1988). The resulting value can then tested for significance. Differences between means of huizachales, mogote and forests and huizachales, and edge and woodlands were highly significant for both TWINSPAN and the cluster analysis ($\alpha < 0.001$ in all cases). Furthermore, the two methods agreed on the fact that the difference between the two mature forest groups was not significantly different (clusters 5 and 6 of TWINSPAN where $\alpha = 0.057$, and clusters 7 and 8 of the cluster analysis where $\alpha = 0.086$).

Since both classification methods yielded similarly reasonable results, it is difficult to judge which performed better. In order to select one of them, perhaps more subjective methods may be appropriate. The main aspect which became apparent when a list of the sample units was arranged according to both classification results, was that TWINSPAN ordered the plots in an intuitively more logical way. For example, there was a tendency of arranging more sample units of the same vegetation type belonging to the same site together. Another additional advantage of TWINSPAN is that the mogotes were better isolated (the cluster analysis grouped some sample units, which were clearly located in mogotes, with one of the thorn forests). A final argument in favour of TWINSPAN is that since DECORANA and particularly CANOCO are the more suitable ordination techniques for the purpose of this study, it would be more appropriate to use their complementary classification method, which is TWINSPAN (Gauch 1982).

Summarizing, three different data sets were used: 1. the composition or floristic matrix, 2. the complete variable matrix, 3. the complete standardized variable matrix. All of these were evaluated with three different methods: cluster analysis with the square euclidean dissimilarity coefficient, cluster analysis with the cosine similarity coefficient and TWINSPAN. In all cases the woodlands were clearly separated from the forests and the edge from both main vegetation types. The mature forests were also separated from huizachales and two sets of thorn forest were identified. Interestingly, it was only when using all the variables that the mogotes emerged as a discrete group, particularly when TWINSPAN was used with the standardized data set. Since the clusters obtained by TWINSPAN were those which better represented the structural and compositional differences between the individual plots, these will be used for the rest of the analyzes in the study.

3.2. Arthropod densities on the plant species

3.2.1. Introduction

Various techniques have been used in order to estimate the food availability for insectivorous birds. Raitt and Pimm (1976) used a D-vac while Holmes and Robinson (1981) visually counted the arthropods present on the vegetation. Hutto (1985) used sticky boards hung at different plant height intervals and sweep-nets and light-traps and pitfall traps were used by Poulin *et al.* (1994).

Peck (1989) used muslin bags in which the terminal branches of the tree species were enclosed and subsequently sprayed with insecticide. The arthropods present in each branch were then removed, identified and counted. Since most insectivorous birds in this study search for prey among the foliage, the same technique was used here.

In the first year, arthropods on each plant species were sampled twice during September and November. A preliminary analysis showed that arthropod densities on the plant species were very similar in the two sample dates. It was concluded that sample size and technique were adequate to obtain reliable estimates and therefore, the data for the first year was pooled and compared with the 1991 results. Details of the sampling method are explained in the methodology section. Agaves and cacti were omitted due to their morphology;

the sample techniques would have made the results-non comparable with those of the other plants.

Collections were made also during spring (the dry season) but most plants shed their leaves at this time of the year and very few arthropods were obtained to make reliable comparisons. Only the results from autumn will be presented.

All arthropods collected were identified to Order and most spiders, beetles and heteropterans were identified to their Family. A list of the arthropod groups found on each plant species and in each year is presented in Appendices 2.1 and 2.2.

Heinrich and Collins (1983) found that brightly coloured hairy, bristly or spiny caterpillars are avoided by birds and therefore these groups (which represented less than 6% of the total lepidopteran larvae) were excluded from the analyses.

In some cases, groups of young individuals, probably hatched from a clump of eggs, were captured. These events were difficult to deal with, because these groups usually consisted of very large numbers of individuals and their occurrence had a large effect on the results. For example, groups of young spiders just out of the web nest were found. Since these groups usually consisted of very large numbers which then disperse rapidly, and are not representative of what is typically found on a particular plant species, they were represented by one individual. On one plant, a group of ant larvae was found in large numbers and since this was an isolated incident, they were also represented by one individual.

For each plant species, the total invertebrate density was tested for normality using the Kolmorogov-Smirnov test. It was found that the distribution deviated from normality in some plant species and therefore the original data were log transformed. The test was repeated and no further deviation from normality was detected.

The t-test was used to confirm significant differences between arthropod densities in the first and second year. Analyses of variance were used to detect differences in density between plant species of the same year. The data were transformed to perform the statistical analysis, the abundance tables include the geometric mean and logarithmic standard deviations.

3.2.2. Results

3.2.2.1. Total arthropod densities

3.2.2.1.1. Autumn 1990

Figure 2.1 shows the mean numbers of invertebrates per plant species in

Table 2.1. Autumn 1990 and 1991 geometric mean and logarithmic standard deviation of arthropods per sample (plant branch).

Plant species	Plant codes	Geometric mean 1990	sd	N	Geometric mean 1991	sd	N
Ceiba acuminata	Cac	4.3	0.27	7	2.1	0.18	6
Apocynaceae	Apo	4.7	0.18	9	1.8	0.30	6
Celtis caudata	Cca	1.1	0.32	5	5.6	0.32	6
Vines	Vin	4.4	0.18	9	3.0	0.27	5
Quercus crassifolia	Qcr	5.4	0.25	21	3.5	1.03	8
Randia sp.	Rsp	5.9	0.20	6	3.4	0.36	5
Bursera sp.	Bsp	3.2	0.24	22	6.4	0.37	23
Ipomoea sp.	Isp	5.1	0.16	9	6.0	0.24	17
Mimosa sp.	Msp	6.7	0.29	17	5.3	0.25	12
Ficus sp.	Fsp	9.1	0.28	8	3.1	0.25	6
Conzattia sericea	Cse	7.5	0.30	27	6.4	0.25	12
Prosopis juliflora	Pju	7.3	0.19	22	6.6	1.55	14
Quercus caudata	Qca	8.6	0.23	22	6.3	1.49	12
Lysiloma acapulcensis	Lac	6.0	0.27	33	9.6	0.21	12
Mimosa galeottii	Mga	7.7	0.23	44	8.1	1.43	24
Acacia cymbispina	Acy	8.8	0.25	44	7.2	0.23	24
Byrsonima sp.	Byr	7.1	0.47	16	11.4	0.30	12
Acacia macilenta	Ama	6.8	0.29	22	13.7	0.40	6
Acacia pennatula	Ape	11.3	0.24	33	11.0	0.20	17
Heliocarpus sp.	Hsp	10.6	0.36	39	12.6	0.14	11
Guasuma ulmifolia	Gul	8.3	0.29	44	16.8	0.21	12
Senecio sp.	Ssp				15.8	0.17	18
Croton sp.	Ccg				11.3	0.18	11
Compositae herb	Her				6.4	0.26	12
Annona muricata	Ann				17.7	0.18	12

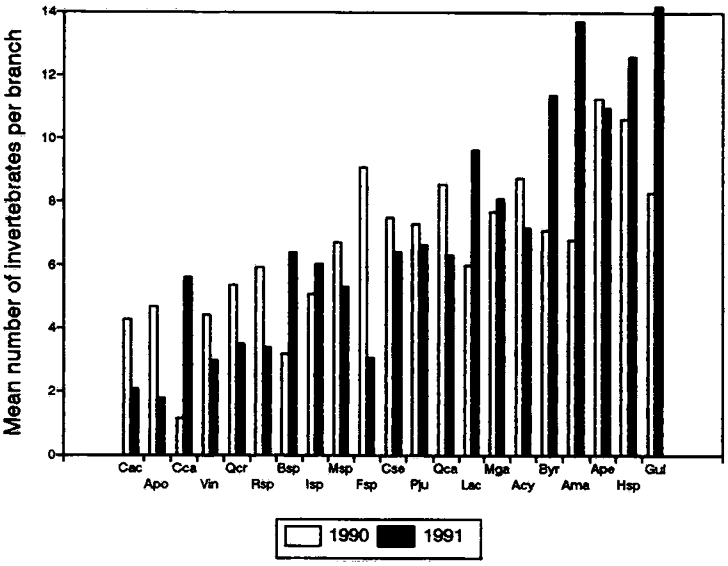


Figure 2.1. Arthropod densities (geometric mean) of plant species sampled in autumn 1990 and 1991. See Table 2.1 for plant species codes.

autumn 1990 and Table 2.1 shows the mean, standard deviation and the sample size. Homogeneity of variances was tested with Cochran's C and the result was not significant. The ANOVA results indicate that there were significant differences between the number of invertebrates supported by the different plant species ($F=6.24$, d.f. 20, 459, $P<0.005$).

The Duncan range test was used to detect differences between all pairs of species, Table 2.2 shows these differences. *Acacia pennatula* (=11.3), *Heliocarpus* sp. (=10.6), *Ficus* sp. (=9.1), *Acacia cymbispina* (=8.8), *Quercus castanea* (=8.6) and *Guazuma ulmifolia* (=8.3) supported the largest density of invertebrates; *Celtis caudata* (=1.1) had the lowest densities, followed by *Bursera* sp. (=3.2) and the vines (=4.4). *Ficus* sp. and *Quercus castanea* had significantly higher densities than *Celtis caudata*, *Bursera* sp. and the vines, while *Acacia pennatula*, *Heliocarpus* sp. and *Guazuma ulmifolia* had higher densities than on most other plants (Table 2.2). *Celtis caudata* had significant less arthropods than all other plants. Similarly, *Bursera* sp. and the vines also supported lower densities than most other plants, while *Ceiba acuminata*, which had a low mean density (=4.3), was only significantly lower than that of *Acacia cymbispina*, *Heliocarpus* sp. and *Acacia pennatula*.

3.2.2.1.2. Autumn 1991

In addition to the plant species sampled in 1990, three herbs (*Croton ciliato-*

glandulosae, an unidentified *Compositae* herb and *Senecio* sp.) and one shrub, (*Annona* sp.) were also sampled in autumn 1991. The analysis of variance showed that the arthropod densities between plant species differed significantly (F=7.1, d.f. 24, 275, P<0.005).

The mean, standard deviation and sample size of the 1991 data are shown in Table 2.1. The significant differences between the plant total arthropods are presented Table 2.3. The herbs *Senecio* sp. and *Croton ciliato-glandulosae* (=15.8 and =11.3), the broad leaved trees *Guazuma ulmifolia* (=16.8) and *Heliocarpus* sp. (=12.6), the broad leaved shrubs *Byrsonima* sp. (=11.4) and *Annona* sp. (=17.7) together with *Acacia macilenta* (=13.7) and *Acacia pennatula* (=11.0) (small leaved legumes) supported large invertebrate densities. *Annona* sp., *Senecio* sp. and *Heliocarpus* sp. supported significantly higher invertebrate numbers than most other plants.

The *Apocynacea* shrub (=1.8), *Ceiba acuminata* (=2.1), the vines (=3.0), *Randia* sp. (=3.4) and *Quercus crassifolia* (=3.5) had the lowest invertebrate densities. *Ceiba acuminata* and the *Apocynacea* shrub in particular, differed from most other plants (Table 2.3).

3.2.2.2. Comparison between autumn 1990 and autumn 1991

Table 2.1 shows the invertebrate density mean, the standard deviation and the

	Cca	Cac	Bsp	Vin	Asp	Isp	Qcr	Lac	Msp	Cse	Gul
Cac	*										
Bsp	*										
Vin	*										
Asp	*										
Isp	*										
Qcr	*		*								
Rsp	*										
Lac	*	*	*								
Msp	*	*	*								
Byr	*	*	*								
Pju	*	*	*								
Mga	*	*	*	*							
Cse	*	*	*	*							
Gul	*	*	*	*							
Qca	*	*	*	*							
Acy	*	*	*	*	*	*	*	*			
Fsp	*	*	*	*							
Hsp	*	*	*	*	*	*	*	*			
Ape	*	*	*	*	*	*	*	*	*	*	*

Table 2.2. Significant differences ($P<0.05$) between the total pooled arthropod densities on plants sampled in autumn 1990. Mnemonics are for plant species and the codes are given in Table 2.1. The Duncan range test was used.

	Asp	Cac	Vin	Fsp	Rsp	Qcr	Msp	Bsp	Cca	Isp	Qca	Her	Mga	Pju	Cse	Acy	Gul	Lac
Msp	*	*																
Bsp	*	*																
Cca	*																	
Isp	*	*																
Qca	*	*																
Her	*	*																
Pju	*	*																
Cse	*	*	*	*														
Acy	*	*	*	*														
Gul	*	*	*	*	*	*												
Lac	*	*	*	*	*	*		*										
Ccg	*	*	*	*	*	*	*	*										
Ape	*	*	*	*	*	*	*	*		*								
Byr	*	*	*	*	*	*	*	*		*								
Hsp	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		
Ama	*	*	*	*	*	*	*	*		*	*	*						
Ssp	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	
Asp	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*

Table 2.3. Significant differences ($P<0.05$) between the total arthropod densities on plants sampled in autumn 1991. Mnemonics are for plant species and the codes are given in Table 2.1. The Duncan range test was used.

sample size for each plant species sampled in 1991. It also includes the same statistics for the 1990 data for comparative purposes. Figure 2.1 is a histogram of these densities for both years.

A regression analysis showed that there was a significant relationship between the invertebrate density in both years ($R^2 = 0.22$, 19 d.f., $P < 0.05$). Figure 2.2 shows the relationship in graphic form. The regression line was: $Y = 0.58 + 0.34 (X)$, s.e. ± 0.15. The slope shows that even though most plants with low densities in 1991 had higher densities in 1990 and most plants with high densities in 1991 had lower densities in the first year, in both autumns the relative densities were similar; *Acacia macilenta*, *Heliocarpus* sp., *Acacia pennatula* and *Guazuma ulmifolia,* for example, had the highest invertebrate densities, while the *Apocynaceae* shrub, *Ceiba acuminata* the vines and *Quercus crassifolia* had the lowest densities.

It is clear that some plants supported higher arthropod densities, while others had consistently lower densities in both years. Nevertheless, there were some significant differences between the abundance on some plants between the two autumns. *Celtis caudata* ($t = 2.56$, 9 d.f., $P < 0.05$), the *Byrsonima* shrub ($t = 2.54$, 25 d.f., $P < 0.05$) and *Lysolima acapulcensis* ($t = 2.11$, 43 d.f. $P < 0.05$) had 84%, 62% and 62% more arthropods in 1991, while *Ficus* sp. ($t = 2.71$, 12 d.f., $P < 0.05$), had 75% more arthropods in 1990. Although the densities were significantly different, *C. caudata* and *Bysronima* sp. supported average

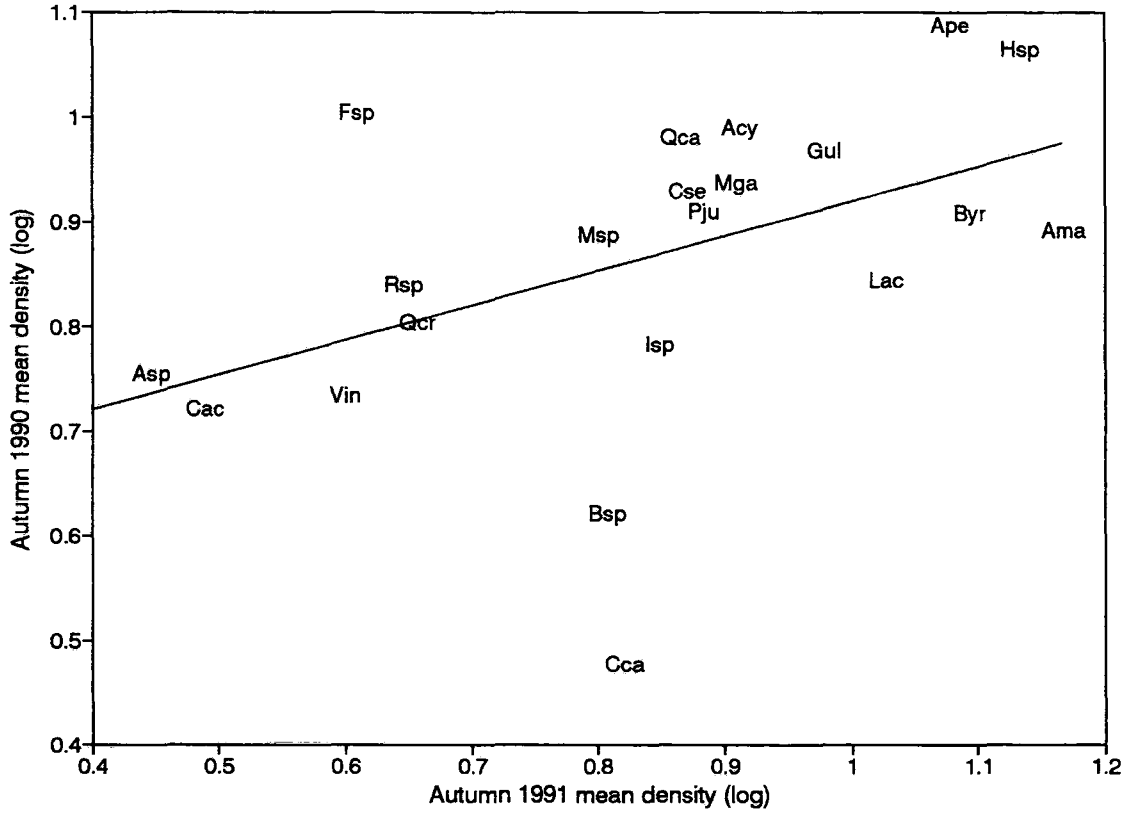


Figure 2.2. Regression between mean total arthropod densities per branch on the plant species sampled in autumn 1990 and 1991.

abundances in both years. In fact, the only plant which strongly differed between years was *Ficus* sp.

Among the plants sampled only in 1991, *Annona muricata*, *Croton ciliato-glandulosae* and *Senecio* sp., supported high invertebrate densities, while the unidentified *Compositae* herb had low densities (Table 2.1).

3.2.2.3. Arthropod taxonomic groups

Appendix 2.1 and 2.2. show the identified arthropod groups and their average density per plant species in both autumn 1990 and 1991. There were four clases of arthropods in 1990 and one mollusc. In the second year no isopods were found and only clases orders of arthropods were found. A few gasteropods were also found in this year.

In autumn 1990, the class Arachnidae consisted of the orders Araneae, Pseudoscorpionidae and Acarina while the crustaceans were represented by the order Isopoda. The insects were represented by 16 orders out of which 47 families were identified. Most of them belonged to heteropterans, homopterans and coleopterans (Appendix 2.1).

In the second year the same orders of Arachnidae were found. Insects were represented by 12 orders, out of which 55 families were identified (Appendix

2.2).

Table 2.4 shows the densities of the arthropod groups having more than 1% of the total density in the plant samples in both autumn 1990 and 1991. In both years the spiders from the families *Saltacidae* and *Thomisidae*, the curculionid beetles, the cicadellid bugs and the lepidopteran larvae were among the most numerous groups. The mites, and dermapterans were also common, together with the heteropteran family *Miridae* and the spiders *Oxypidae*, *Phylodromidae*, and *Linyphiidae*. The major compositional change between years was the scarcity of ants in the second year compared with 1990 (4% in 1990 and 1% in 1991).

Arthropods were also grouped in nine main groups: *Araneidae*, *Heteroptera*, *Coleoptera*, *Lepidoptera* larvae, *Homoptera*, *Formicidae*, *Thysanoptera*, *Hymenoptera* and *Diptera*. Spiders were the most numerous groups in both years, representing 27% and 40% of the total density in 1990 and 1991 (Table 2.5).

Spiders were followed in density by bugs and beetles. The heteropterans included 17% and 12% in 1990 and 1991 of the total sample, while the beetles included 10% of the total invertebrates caught in both years. Homopterans and lepidopteran larvae were the only other two groups which formed more than 5% of the total catch. Lepidopteran larvae formed 8% of the arthropods in 1990

Table 2.4. Geometric mean densities of arthropod groups per plant species in 1990 and 1991. Only those groups having more than 1% of the total catch are shown. Codes for plant species are given in Table 2.1.

Autumn 1990	Rsp	Cse	Bsp	Qca	Gul	Vin	Ama	Acy	Asp	Pju	Cca	Byr	Isp	Cac	Qcr	Hsp	Fsp	Lac	Msp	Ape	Mga	Asp	Ccg	Ssp	Her	Total	%
Tingidae	0.0	0.2	0.4	0.8	0.9	0.1	0.1	0.3	0.4	0.0	0.0	3.7	0.4	0.4	0.6	3.6	0.1	0.6	0.1	0.9	1.1	-	-	-	-	14.7	10.5
Larvae	0.0	0.6	0.1	0.9	0.3	0.4	0.9	1.1	0.2	0.6	0.0	0.1	0.3	0.4	0.1	0.2	0.1	0.5	0.7	1.9	0.8	-	-	-	-	10.3	7.4
Saltacidae	0.6	0.6	0.1	0.4	0.4	0.5	0.5	0.8	0.1	0.7	0.0	0.2	0.2	0.1	0.2	0.5	0.4	0.2	0.6	0.4	0.3	-	-	-	-	7.9	5.7
Clubionidae	0.9	0.6	0.3	0.9	0.4	0.4	0.1	0.4	0.5	0.1	0.0	0.7	0.2	0.1	0.2	0.3	0.4	0.2	0.2	0.3	0.4	-	-	-	-	7.7	5.5
Curculionidae	0.1	0.1	0.2	0.2	1.0	0.1	0.3	0.4	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.3	0.1	0.5	0.2	0.7	0.8	-	-	-	-	5.5	3.9
Formicidae	0.1	0.1	0.0	0.0	0.5	0.4	0.4	0.4	0.3	0.4	0.0	0.2	0.3	0.8	0.2	0.1	0.2	0.1	0.2	0.2	0.0	-	-	-	-	4.9	3.5
Linyphiidae	0.1	0.6	0.1	0.3	0.3	0.2	0.2	0.3	0.2	0.3	0.1	0.2	0.1	0.0	0.2	0.1	0.3	0.2	0.0	0.3	0.4	-	-	-	-	4.8	3.4
Cicadellidae	0.3	0.5	0.1	0.3	0.1	0.0	0.2	0.2	0.0	0.1	0.0	0.0	0.3	0.0	0.2	0.1	0.0	0.3	0.0	0.6	0.4	-	-	-	-	3.8	2.7
Oxypidae	0.1	0.3	0.1	0.2	0.0	0.1	0.2	0.2	0.0	0.2	0.0	0.1	0.2	0.2	0.1	0.2	0.3	0.1	0.6	0.2	0.1	-	-	-	-	3.4	2.5
Thomisidae	0.0	0.2	0.0	0.0	0.2	0.1	0.5	0.3	0.1	0.2	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.2	0.4	0.3	0.2	-	-	-	-	3.0	2.1
Acarina	0.2	0.1	0.1	0.1	0.1	0.2	0.3	0.2	0.3	0.2	0.0	0.0	0.1	0.1	0.0	0.1	0.0	0.2	0.1	0.1	0.3	-	-	-	-	2.8	2.0
Dermaptera	0.0	0.0	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.0	0.2	0.3	0.3	0.1	0.4	0.1	0.0	0.1	0.0	-	-	-	-	2.7	1.9
Phylodromidae	0.0	0.2	0.2	0.0	0.2	0.1	0.0	0.2	0.4	0.1	0.0	0.1	0.1	0.0	0.1	0.3	0.3	0.0	0.0	0.2	0.2	-	-	-	-	2.7	1.9
Miridae	0.3	0.1	0.2	0.1	0.0	0.0	0.1	0.1	0.2	0.2	0.0	0.0	0.1	0.0	0.0	0.2	0.3	0.1	0.0	0.2	0.2	-	-	-	-	2.4	1.7
Reduviidae	0.3	0.1	0.1	0.0	0.0	0.0	0.2	0.1	0.0	0.5	0.0	0.0	0.0	0.0	0.1	0.0	0.3	0.1	0.1	0.1	0.1	-	-	-	-	1.9	1.4
Blattidae	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.2	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.4	0.0	0.4	0.0	0.0	-	-	-	-	1.8	1.3
Coccoidea	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.1	0.0	-	-	-	-	1.7	1.2
Membracidae	0.0	0.5	0.0	0.2	0.1	0.0	0.3	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	-	-	-	-	1.6	1.1
THYSANOPTERA	0.3	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.6	0.0	0.0	0.0	0.0	-	-	-	-	1.6	1.1
Autumn 1991	Rsp	Cse	Bsp	Qca	Gul	Vin	Ama	Acy	Asp	Pju	Cca	Byr	Isp	Cac	Qcr	Hsp	Fsp	Lac	Msp	Ape	Mga	Asp	Ccg	Ssp	Her	Total	%
Saltacidae	0.1	1.4	0.6	0.9	1.7	0.5	1.6	1.4	0.3	0.5	1.4	1.7	1.6	0.1	0.4	3.0	0.3	1.1	0.9	1.9	0.4	5.7	0.9	3.2	1.3	33.0	17.4
Cicadelidae	0.0	0.2	0.1	0.1	0.5	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.2	0.5	0.4	0.2	0.1	1.7	0.1	0.8	0.6	2.6	1.8	0.6	0.1	10.7	5.6
Larvae	0.5	0.5	0.1	0.0	0.1	0.0	0.9	0.6	0.0	0.4	0.0	0.3	0.0	0.4	0.3	0.2	0.0	1.7	0.7	2.1	0.5	0.1	0.1	0.2	0.1	9.7	5.1
Thomisidae	0.3	0.2	0.1	0.1	0.5	0.0	2.7	0.6	0.1	0.3	0.1	0.3	0.3	0.0	0.0	0.3	0.1	0.2	0.4	0.3	0.2	0.4	0.5	0.8	0.7	9.4	5.0
Tingidae	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.3	2.1	0.3	0.0	0.0	3.6	0.2	0.1	0.0	0.5	0.0	0.2	0.1	0.1	0.0	7.7	4.0
Linyphiidae	0.1	0.4	1.1	0.2	0.1	0.0	0.1	0.5	0.3	0.4	0.0	0.7	0.0	0.1	0.0	0.5	0.0	0.1	0.3	0.2	0.2	0.9	0.1	0.7	0.1	7.0	3.7
Acarina	0.9	0.1	0.1	0.1	0.3	0.1	0.2	0.3	0.1	0.9	0.6	0.7	0.0	0.0	0.1	0.1	0.0	0.1	0.3	0.0	0.6	0.2	0.0	0.2	0.2	6.1	3.2
Curculionidae	0.0	0.0	0.1	0.0	0.1	0.0	4.1	0.0	0.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.1	0.4	0.0	0.1	0.0	0.3	0.0	6.1	3.2
Peucetia sp.	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.7	0.0	0.1	3.2	0.1	0.0	5.2	2.8
Phylodromidae	0.1	0.0	0.1	0.0	0.3	0.0	0.6	0.2	0.0	0.1	0.3	0.4	0.3	0.1	0.0	0.1	0.1	0.1	0.3	0.0	0.4	0.1	0.1	0.2	0.0	3.9	2.1
Miridae	0.0	0.0	0.0	0.1	0.5	0.0	0.4	0.1	0.0	0.2	0.1	0.1	0.0	0.0	0.1	0.5	0.0	0.0	0.1	0.0	0.5	0.2	0.5	0.2	0.0	3.7	2.0
Dermaptera	0.0	0.0	0.1	0.0	0.4	1.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.7	0.1	3.2	1.7
Oxypidae	0.0	0.1	0.2	0.1	0.1	0.1	0.4	0.3	0.1	0.1	0.1	0.2	0.1	0.0	0.0	0.1	0.1	0.0	0.3	0.2	0.0	0.2	0.1	0.1	0.0	3.0	1.6
Bruchidae	0.1	0.0	0.5	0.1	0.1	0.0	0.0	0.1	0.0	0.3	0.5	0.1	0.1	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.1	0.2	0.0	0.2	0.1	2.9	1.5
Lygeidae	0.0	0.5	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.2	0.2	2.7	1.4
Reduviidae	0.0	0.1	0.1	0.1	0.1	0.0	0.0	0.2	0.1	0.7	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.0	1.8	1.0

Table 2.5. Geometric mean densities of arthropod groups per plant species in autumn 1990 and 1991. Codes for plant species are shown in Table 2.1.

Autumn 1990	Rsp	Cse	Bsp	Qca	Gul	Vin	Ama	Acy	Asp	Pju	Cca	Byr	Isp	Cac	Qcr	Hsp	Fsp	Ape	Lac	Msp	Mga	Ann	Ccg	Ssp	Her	Tot	%
Araneida	2.3	3.1	1.0	2.3	1.8	1.4	1.9	2.9	1.6	1.8	0.0	1.8	1.0	0.7	1.2	1.9	2.1	2.2	1.2	3.2	1.9	-	-	-	-	37.2	26.5
Hemiptera	0.9	0.5	0.8	1.1	1.1	0.2	0.4	0.7	0.6	0.9	1.1	3.7	0.9	0.4	0.8	4.4	0.8	1.6	1.0	0.3	1.5	-	-	-	-	23.4	16.7
Coleoptera	0.6	0.5	0.3	1.3	1.5	0.1	0.4	0.5	0.0	0.2	1.0	0.5	0.3	0.1	0.8	1.0	0.6	1.6	0.8	0.7	1.1	-	-	-	-	13.9	9.9
Larvae	0.0	0.6	0.1	0.9	0.3	0.4	1.0	1.1	0.2	0.8	0.0	0.1	0.3	0.4	0.1	0.2	0.1	1.9	0.5	0.7	0.8	-	-	-	-	10.6	7.5
Homoptera	0.3	1.2	0.3	0.7	0.3	0.2	0.7	1.0	0.1	0.7	0.0	0.2	0.4	0.0	0.4	0.2	0.3	0.8	0.6	0.2	0.5	-	-	-	-	9.2	6.5
Formicidae	0.1	0.1	0.0	0.0	0.5	0.4	0.4	0.4	0.3	0.4	0.0	0.2	0.3	0.8	0.2	0.1	0.2	0.2	0.1	0.2	0.0	-	-	-	-	4.9	3.5
Thysanoptera	0.3	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	2.3	0.0	0.0	0.1	0.0	0.0	0.6	0.0	0.0	0.0	0.0	-	-	-	-	3.7	2.6
Hymenoptera	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.6	0.1	0.1	0.0	0.0	-	-	-	-	1.4	1.0
Diptera	0.0	0.1	0.1	0.0	0.1	0.3	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.1	0.0	0.0	-	-	-	-	1.2	0.9
Autumn 1991	Rsp	Cse	Bsp	Qca	Gul	Vin	Ama	Acy	Asp	Pju	Cca	Byr	Isp	Cac	Qcr	Hsp	Fsp	Ape	Lac	Msp	Mga	Ann	Ccg	Ssp	Her	Tot	%
Araneida	1.2	3.7	3.6	1.8	5.8	0.8	6.1	3.8	1.0	1.6	2.4	5.0	2.4	0.5	0.4	4.5	0.7	3.9	1.7	2.9	1.6	8.8	6.6	6.6	2.6	80.2	39.8
Hemiptera	0.0	1.8	1.6	1.2	1.0	0.1	0.7	0.4	0.1	1.0	0.3	2.5	0.9	0.0	0.3	4.7	0.5	0.7	0.4	0.3	0.8	0.8	1.6	2.2	0.4	24.4	12.1
Coleoptera	0.1	1.5	1.7	0.3	1.0	0.1	4.3	0.3	0.3	0.3	0.8	0.2	0.6	0.1	0.5	0.8	0.6	1.0	0.5	0.1	0.4	0.9	1.1	1.3	1.2	20.2	10.0
Homoptera	0.0	1.6	1.1	0.4	0.8	0.0	0.4	0.3	0.0	0.4	0.4	0.1	0.3	0.5	0.7	0.3	0.2	1.0	1.9	0.1	0.7	2.9	2.9	0.9	0.3	18.2	9.0
Larvae	0.3	1.5	1.2	0.4	0.1	0.0	0.9	0.6	0.0	0.4	0.0	0.3	0.0	0.4	0.3	0.2	0.0	2.1	1.7	0.7	0.5	0.1	1.1	0.2	0.1	13.0	6.5
Hymenoptera	0.0	1.1	1.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.0	0.7	1.1	0.3	0.3	5.4	2.7
Diptera	0.0	1.0	1.1	0.1	0.1	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.1	0.0	0.0	0.3	0.1	0.0	0.1	0.1	3.4	1.7
Formicidae	0.0	1.0	0.0	0.1	0.2	0.3	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.0	0.0	0.1	2.5	1.2
Thysanoptera	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.9	0.5

Arthropod group	Constant	Slope	Standard error
Heteroptera	0.12	0.77	0.12
Homoptera	0.01	0.38	0.17
Lepidopteran larvae	0.07	0.67	0.14

Table 2.6. Significant regression equations between arthropod groups on the plant species in autumn 1990 and 1991.

and 7% in 1991; homopterans were 7% in the first year and 9% in the second (Table 2.5). The other groups in 1990, in order of density, were *Formicidae* (4%), *Thysanoptera* (3%), *Hymenoptera* (1%) and *Diptera* (1%). In 1991, Caterpillars were followed by *Hymenoptera* (3%), *Diptera* (2%), *Formicidae* (1%) and *Thysanoptera* (<1%). If the 1990 percentages are compared between the plants sampled in both years (i.e. without the additional plants sampled in 1991), the relative proportions do not change (*Araneidae* 37%, *Heteroptera* 13%, *Coleoptera* 10%, *Homoptera* 7%, lepidopteran larvae 7%, *Hymenoptera* 2%, *Diptera* 2%, *Formicidae* 2% and *Thysanoptera* <1%).

Those groups representing more than 5% of the total densities were analyzed in more detail. The others, because of their low numbers, were not amenable to statistical analyses.

3.2.2.4. Densities of the main arthropod groups in the vegetation

Kolmogorof-Smirnov tests of normality showed that with the exception of spiders, the arthropod densities on each plant species differed from normality in many cases. On the other hand, when comparisons between the two sample dates of autumn 1990 were analyzed, it became clear that the distribution of the arthropod groups in some plant species became normal if the data were pooled (after it was log-transformed). It appears therefore, that larger sample sizes would result in normal distributions. Furthermore, the results when using non-parametric statistics (Mann-Whitney and Kruskal Wallis) were almost identical to the results of the parametric tests (t-test and analysis of variance). The geometric mean was therefore used as a density indicator and parametric statistics were used to detect arthropod density differences between the plant species.

Figures 2.3. and 2.4 show the number of heteropterans, homopterans, coleopterans, lepidopteran larvae and spiders in autumn 1990 and 1991.

Heteroptera

In both years heteropterans were particularly abundant on *Heliocarpus* sp. (=4.4 in 1990 and =4.7 in 1991) and *Byrsonima* sp. (=3.7 and =2.5). They were infrequent on the vines (=0.2 and =0.1), *Acacia macilenta* (=0.4 and =0.7), *Mimosa* sp. (=0.3 and =0.3) and the *Apocynacea* shrub (=0.6 and =0.1) (Figure 2.3). The only significant differences between heteropteran densities in 1990 and 1991 were for *Celtis caudata* ($t=2.56$, 9 d.f., $P<0.05$) and for *Acacia pennatula* ($t=2.19$, 48 d.f., $P<0.05$). *C. caudata* had 1.1 mean individuals per branch in 1990 and 0.3 in 1991 while *A. pennatula* had 1.6 in 1990 and 0.7 in 1991.

The regression of the mean heteropteran densities per plant species between both years, shown in Figure 2.5, was highly significant ($R^2=0.69$, 19 d.f., P<0.001). The relationship is shown in Table 2.6.

Densities between plants were different (F=8.79, d.f. 20, 458, P<0.001 for 1990 and F=4.58. d.f. 24, 275, P<0.001 for 1991). Table 2.7 shows the significant differences in heteropteran densities of all plants sampled in 1990 and 1991 according to the Duncan range test. In both years, *Heliocarpus* sp. (=4.4 in 1990 and =4.7 in 1991) and *Byrsonima* sp. (=3.7 and =2.5) supported significantly higher densities than most other plants, while *Ceiba acuminata* (=0.4 in the first year and none in the second) and the vines (=0.2 and =0.1) had low densities. In addition, *Randia* sp. had no individuals in 1991 and low densities in 1990 (=0.9) and the *Apocynaceae* shrub had low densities in both years (=0.6 in 1990 and =0.1 in 1991).

Homoptera

Comparisons between homopteran densities in the vegetation (Figure 2.3) showed that *Bursera* sp. had significantly higher densities in 1991 (=0.29 in 1990 and =1.06 in 1991, representing a 78% change; t=2.11, d.f. 43, P<0.05;), while *Acacia cymbispina* had highest densities in 1990 (=0.98 and =0.29, corresponding to a 77% change; t=3.02, d.f. 64.6, P<0.01). *Ceiba acuminata* had no homopterans in 1990 and =0.51 in 1991.

The regression between the 1990 and the 1991 data, was significant ($R^2=0.21$,

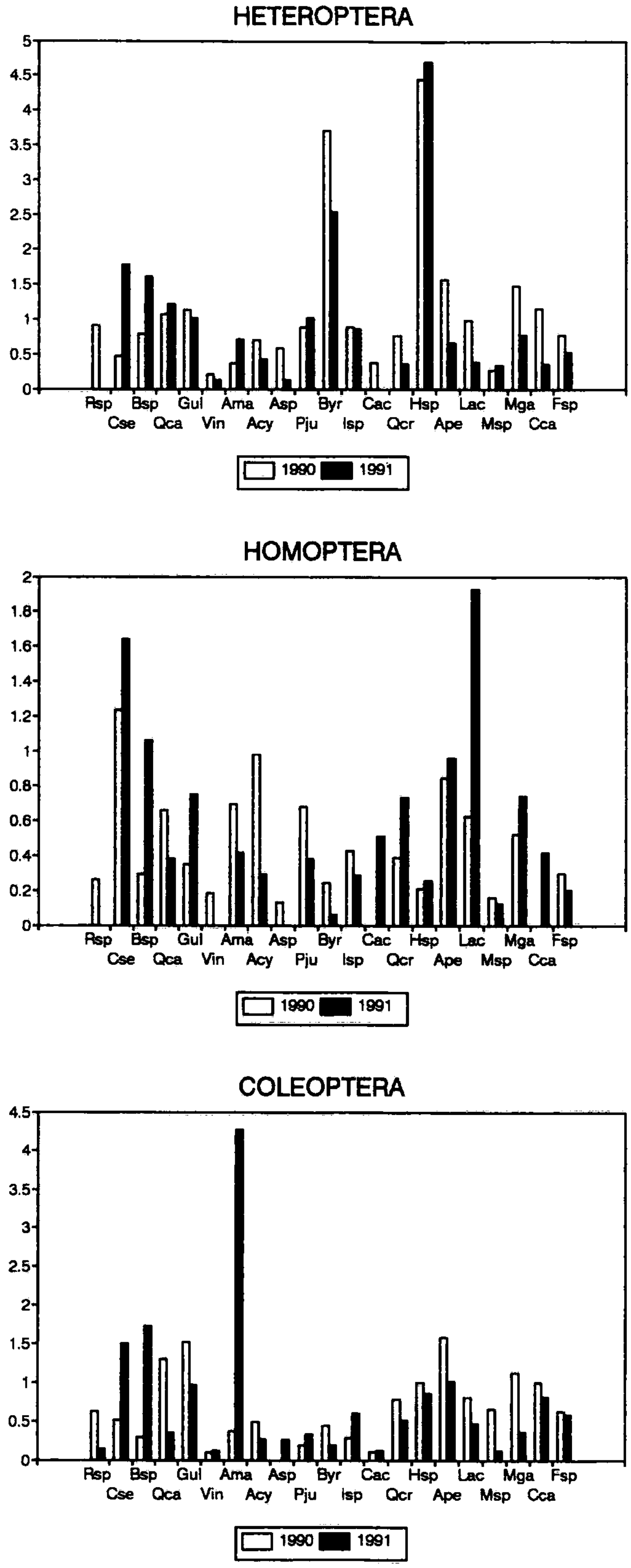
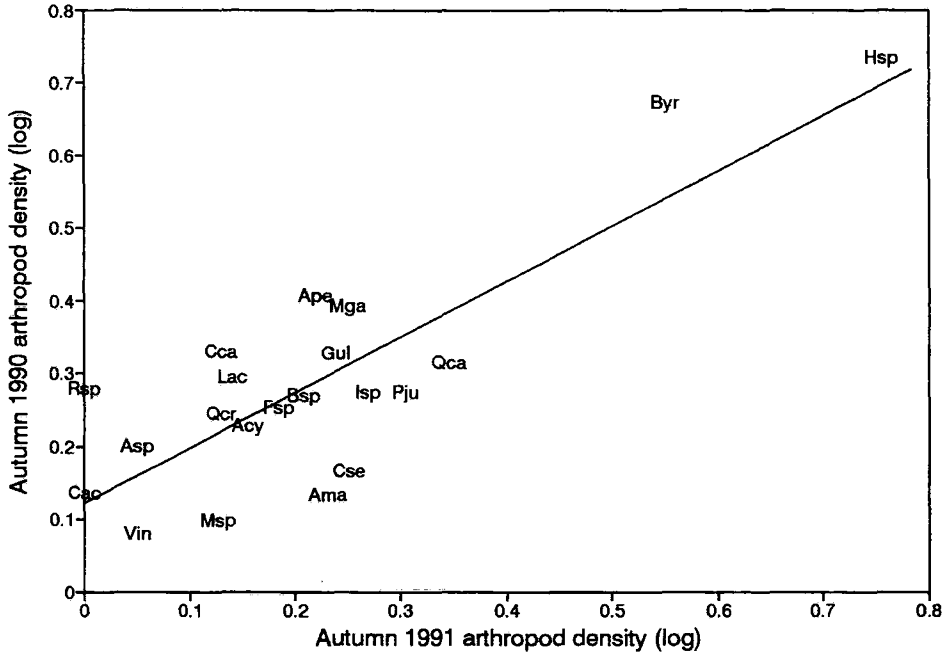


Figure 2.3. Mean number of arthropod groups per plant species in autumn 1990 and autumn 1991. Codes for plant species are given in Table 2.1.

HETEROPTERA



HOMOPTERA

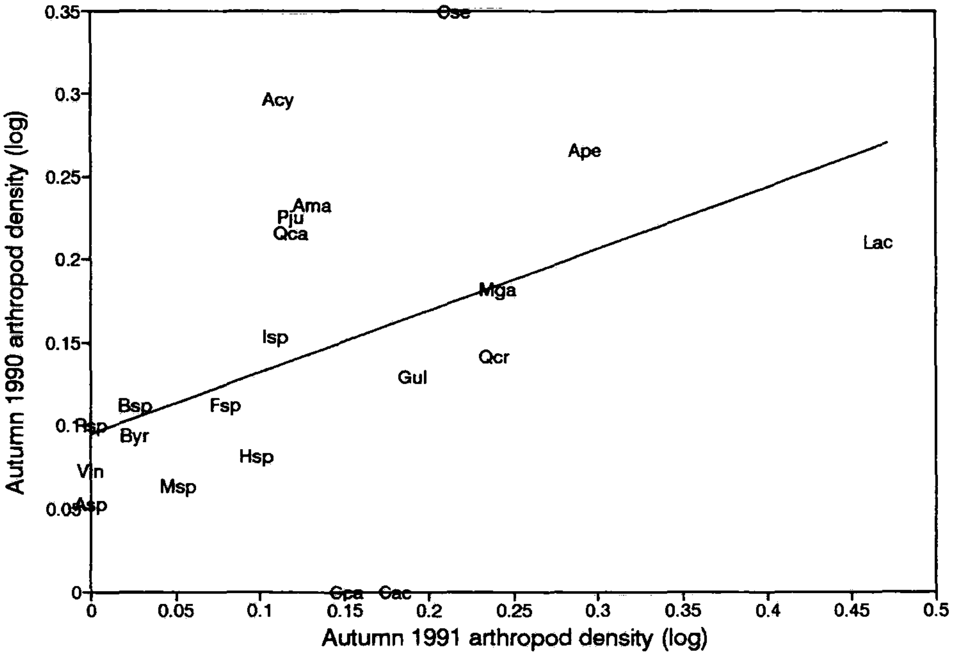


Figure 2.5. Regressions between the mean number of arthropod groups on the plant species in autumn 1990 and 1991. Codes for the plant species are shown in Table 2.1.

Table 2.7. Significant differences between arthropod densities on the plant species according to the Duncan range test (P<0.05). Plant codes are shown in Table 2.1.

HETEROPTERA 1990

	Hsp	Byr	Ape	Mga	Gul	Qca	Lac
Ape	*	*					
Mga	*	*					
Cca	*	*					
Gul	*	*					
Qca	*	*					
Lac	*	*					
Rsp	*	*					
Pju	*	*					
Isp	*	*					
Bsp	*	*					
Fsp	*	*					
Qcr	*	*					
Acy	*	*	*				
Asp	*	*					
Cse	*	*	*	*	*		
Cac	*	*					
Ama	*	*	*	*	*		
Msp	*	*	*	*	*		
Vin	*	*	*	*	*	*	*

HETEROPTERA 1991

	Cca	Hsp	Byr	Ssp
Ssp	*	*		
Qca	*	*		
Pju	*	*		
Isp	*	*	*	*
Cse	*	*	*	*
Mga	*	*	*	*
Ann	*	*	*	*
Gul	*	*	*	*
Ama	*	*		
Ape	*	*	*	*
Bsp	*	*	*	*
Ccg	*	*	*	*
Fsp	*	*	*	*
Acy	*	*	*	*
Her	*	*	*	*
Lac	*	*	*	*
Qcr	*	*	*	*
Msp	*	*	*	*
Asp	*	*	*	*
Vin	*	*	*	*
Cac	*	*	*	*
Rsp	*	*	*	*

HOMOPTERA 1990

	Cse	Acy	Ape
Lac	*		
Mga	*		
Isp	*		
Qcr	*	*	
Gul	*	*	*
Fsp	*		
Bsp	*	*	
Byr	*	*	
Hsp	*	*	*
Vin	*	*	*
Msp	*	*	*
Asp	*	*	
Cca	*	*	
Cac	*	*	*

HOMOPTERA 1991

	Ann	Lac	Ccg	Ape	Ssp	Mga	Qcr	Cse
Ape	*	*						
Ssp	*	*						
Mga	*	*	*					
Qcr	*							
Cse	*	*	*					
Gul	*	*	*					
Ama	*	*	*					
Pju	*	*	*					
Qca	*	*	*					
Her	*	*	*					
Acy	*	*	*	*	*			
Isp	*	*	*	*	*			
Hsp	*	*	*					
Fsp	*	*	*					
Msp	*	*	*	*	*			
Bsp	*	*	*	*	*	*		*
Byr	*	*	*	*	*			*
Cca	*	*	*	*	*			
Cac	*	*	*	*	*			
Asp	*	*	*	*	*			
Vin	*	*	*	*	*			
Rsp	*	*	*	*	*			

19 d.f., $P<0.05$) indicating that homopterans had similar relative densities on the plant species in both years (Figure 2.5). The regression equation is shown in Table 2.6.

The differences between the densities on individual plants were significant for autumn 1990 ($F=3.53$, d.f. 20, 458, $P<0.001$). *Conzatia sericea* (=1.24) and *Acacia cymbispina* (=0.98) had the highest *Homoptera* densities. The differences between these and most other plant species were significant (Table 2.7). On the other hand, *Ceiba acuminata* in which no homopterans were found, differed only form those plants with the highest densities (*Quercus castanea* with =0.66, *Acacia cymbispina* with =0.98, *Prosopis juliflora* with =0.68, *Acacia pennatula* with =0.85 and *Conzanttia sericea* with =1.24).

The differences between plants were also significant for autumn 1991 ($F=5.8$, d.f. 24, 275, $P<0.001$). *Croton ciliato-glandulosae* and *Annona* sp. (not sampled in 1990) supported the highest densities (=2.9 hompoterans per branch in both cases) and were significantly different from most other plants (Table 2.7). *Lysolima acapulcensis* also supported high densities (=1.9) and the Duncan range test indicates that there were no significant differences between the densities of homopterans on this species and those supporting the highest numbers. On the other hand, there were significant differences between this species and the plants supporting lower homopteran densities (Table 2.7).

Coleoptera

Coleopterans were found to be dense in *Quercus castanea, Guazuma ulmifolia, Acacia pennatula* and *Mimosa galeoti* in 1990 (the means were =1.3, =1.5, =1.6 and =1.1 respectively) (Figure 2.3). The vines (=0.1), Prosopis juliflora (=0.2), Bursera sp. (=0.3) and *Ipomoea* sp. (=0.3) had the lowest numbers.

Coleopteran densities between plants differed significantly (F=5.17, d.f. 20, 458, P<0.001). The Duncan range test resulted in significant differences between the five plants supporting more individuals (*Heliocarpus* sp. with =1.0 coleopterans per branch, *Mimosa galeotti* with =1.13, *Quercus castanea* with =1.31, *Guazuma ulmifolia* with =1.53 and *Acacia pennatula* with =1.58) and those plants having low densities (Table 2.8).

The vines (which had the lowest densities with =0.1 individuals per branch) in 1990 differed significantly from plants having medium to high coleopteran densities. *Ceiba acuminata* and *Prosopis juliflora* which also had low densities (=0.1 and =0.2 respectively), differed significantly from those plants having the highest number of individuals. *Mimosa* sp. (=0.66) and *Ipomoea* sp. (=0.29) which had intermediate densities differed from plants with both extremes in coleopteran densities (Table 2.8).

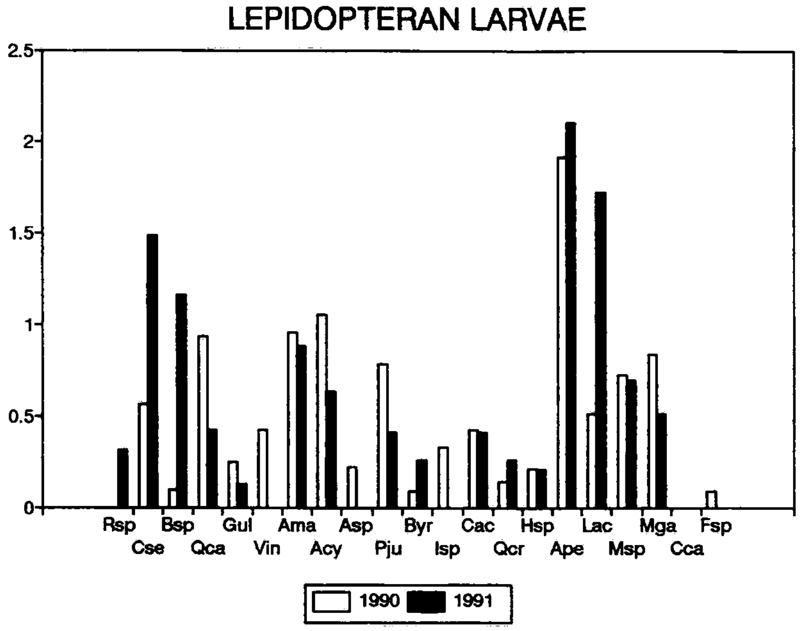
Coleopteran densities in 1991 were also different between plants (F=3.4, d.f.

24, 274, $P<0.001$). The Duncan range test tests indicate that beetles were particularly dense on *Acacia macilenta* (=4.28) and differed significantly from the rest (Table 2.8). *Senecio* sp. (=1.3) and the herbs (=1.2), followed by *Acacia pennatula,* also had high densities (=1.0) and differed from those having the low densities (*Acacia cymbispina* with =0.3, *Byrsonima* sp. with =0.2, *Mimosa* sp. with =0.1, the *Apocynaceae* shrub with =0.3, the vines with =0.1 and *Ceiba acuminata* with =0.1). On the other hand, *Bursera* sp., with the second highest density (=1.73), differed only from *A. macilenta*.

The regression between the pooled 1990 and the 1991 coleopteran densities on the plant species was not significant. In particular, *Acacia macilenta* had 92% higher densities in 1991, resulting in a significant difference ($t=2.6$, 5.3 d.f., $P<0.01$), while *Quercus castanea, Guazuma ulmifolia* and *Mimosa* sp. had 79%, 61% and 84% higher densities in 1990 ($t=2.53$, 32 d.f., $P<0.05$ for *Q. castanea,* $t=2.02$, 53 d.f., $P<0.05$ for *G. ulmifolia* and $t=2.26$, 23 d.f., $P<0.05$ for *Mimosa* sp.). The other plant specie sampled in both years had similar relative densities (Figure 2.3).

Lepidopteran larvae

In 1990, the lepidopteran larvae were particularly dense on *Acacia pennatula* (=1.9) (Figure 2.4). They were also common in *Acacia macilenta* (=1.0), *Acacia cymbispina* (=1.1), *Mimosa galeoti* (=0.8) and *Quercus castanea*



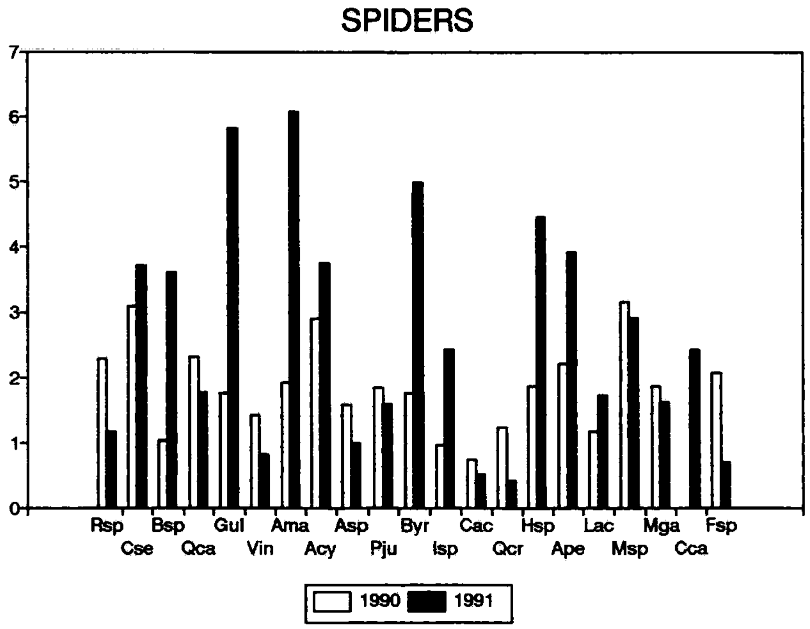


Figure 2.4. Mean number of arthropod groups per plant species in autumn 1990 and autumn 1991. Codes for plant species are given in Table 2.1.

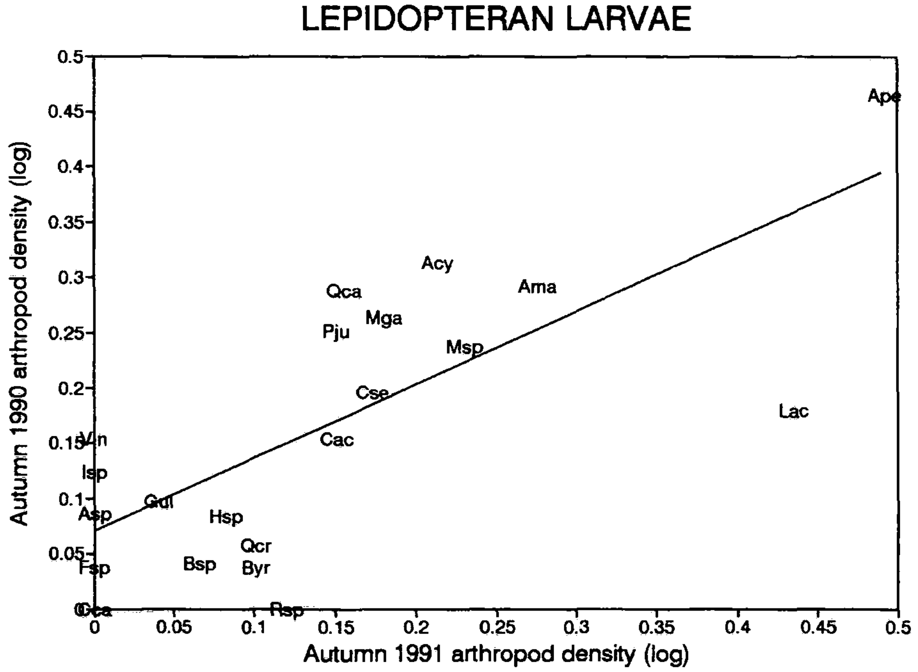


Figure 2.6. Regression between the mean number of arthropod groups on the plant species in autumn 1990 and 1991. Codes for the plant species are shown in Table 2.1.

Table 2.8. Significant differences between arthropod densities on the plant species according to the Duncan range test ($P<0.05$). Plant codes are shown in Table 2.1.

COLEOPTERA 1990

	Ape	Gul	Qca	Mga	Hsp	Lac	Qcr
Lac	*	*					
Qcr	*						
Msp	*	*					
Cse	*	*	*	*			
Acy	*	*	*	*	*		
Byr	*	*	*				
Ama	*	*	*	*	*		
Bsp	*	*	*	*	*		
Isp	*	*	*	*	*		
Pju	*	*	*	*	*	*	
Cac	*	*	*	*	*		
Vin	*	*	*	*	*	*	*

COLEOPTERA 1991

	Ama	Ssp	Her	Ape
Ssp	*			
Her	*			
Ape	*			
Ann	*			
Hsp	*			
Bsp	*			
Gul	*			
Isp	*			
Fsp	*			
Qcr	*			
Cse	*	*		
Lac	*			
Mga	*	*		
Cca	*			
Qca	*	*		
Pju	*	*		
Acy	*	*	*	*
Byr	*	*	*	*
Rsp	*	*		
Ccg	*	*	*	*
Msp	*	*	*	*
Cac	*	*	*	
Vin	*	*		
Apo	*	*	*	*

LEPIDOPTERAN LARVAE 1990

	Ape	Acy	Ama	Qca	Mga	Pju	Msp	Cse
Acy	*							
Ama	*							
Qca	*							
Mga	*							
Pju	*							
Msp	*							
Cse	*	*						
Lac	*	*						
Cac	*							
vin	*	*						
Isp	*	*						
Gul	*	*	*	*	*	*		
Asp	*	*						
Hsp	*	*	*	*	*	*		
Qcr	*	*	*	*	*	*	*	
Bsp	*	*	*	*	*	*	*	*
Fsp	*	*	*	*				
Byr	*	*	*	*	*	*	*	
Cca	*	*	*	*				
Rsp	*	*	*	*	*			

LEPIDOPTERAN LARVAE 1991

	Ape	Lac	Ama	Msp	Acy	Mga	Cse
Ama	*						
Msp	*	*					
Acy	*	*					
Mga	*	*					
Cse	*	*					
Qca	*	*					
Cac	*	*					
Pju	*	*					
Qcr	*	*					
Byr	*	*					
Ssp	*	*			*		
Hsp	*	*					
Bsp	*	*	*	*	*		
Gul	*	*	*	*	*		
Ccg	*	*	*	*	*		
Ann	*	*	*	*	*		*
Her	*	*	*	*	*		
Cca	*	*	*	*	*		
Fsp	*	*	*	*	*		
Isp	*	*	*	*	*	*	*
Asp	*	*	*	*	*		
Vin	*	*	*	*	*		
Rsp	*	*	*		*		

(=0.9). *Conzattia sericea* (=0.6) and *Lysolima acapulcensis* (=0.5) also had relatively high densities and with the exception of *Q. castanea*, these plants include all of the small leaved legumes found in the study sites.

There were significant differences between the 1990 densities on the plant species (F=6.0, d.f. 20, 458, $P<0.001$). Table 2.8 shows the Duncan range test significant differences between them. *Acacia pennatula*, the plant with higher larvae densities (=1.92 individuals per branch) differed from the rest of the plants.

A correlation indicates that there was a significant relationship between the larvae densities in autumn 1990 and 1991 ($R^2=0.55$, 19 d.f., $P<0.005$). Figure 2.6 shows the plot of the regression and Table 2.6 shows the regression equation. All small leaved legumes (*Acacia pennatula, A. macilenta, A. cymbispina, Mimosa* sp., *M. galeotti, Prosopis juliflora, Consattia sericea* and *Lysolima acapulcensis*), together with *Quercus castanea* had higher densities than other plants in both years (Figure 2.6). Nevertheless, *Lysolima acapulcensis* had significantly higher lepidopteran larvae densities (77% more) in 1990 ($t=2.81$, 43 d.f., $P<0.01$). The only other major difference was *Ipomoea* sp. which had =0.97 individuals per branch in 1990 but none in 1991.

Differences between the 1991 plants were also significant (F=7.1, d.f. 24, 275, P<0.001) and the Duncan range test showed that small leaved legumes had higher larvae densities than most other plants. Figure 2.6 shows that again, *Acacia pennatula* (=2.11) was the plant with more dense larvae. Small leaved legumes, and in particular, *Lysolima acapulcensis* and *Mimosa* sp. also had high densities and differed even from other small leaved plants of the same family (Table 2.8).

Spiders

Spiders were the most common group in the study area (27% of the total plant invertebrates in 1990 and 40% in 1991). In the first year, they were particularly dense on *Conzattia sericea* (=3.1), *Acacia cymbispina* (=2.9) and *Mimosa* sp. (=3.2), while *Ipomoea* sp. =1.0) and *Ceiba cuminata* (=0.7) had few individuals (Figure 2.4).

An analysis of variance indicated that the differences between the densities on the different plant species were significant (F=2.88, d.f. 20, 458, P<0.001). Differences between spiders on the plant species were detected by the Duncan test and are shown in Table 2.9.

Celtis caudata had no individuals in 1990 and was significantly different from most other plants. *Mimosa* sp. (with =3.15 individuals per branch), *Conzattia sericea* (=3.09), and *Acacia cymbispina* (=2.91) had the highest density and were significantly different from those plants with the lowest densities (*Ceiba acuminata* with =0.74), *Ipomoea* sp. (=0.97), *Bursera* sp. (=1.03), *Lysolima acapulcensis* (=1.17), *Quercus crassifolia* (=1.23), and the vines (=1.42).

In the second year, spiders were also frequent in *Conzattia sericea* (=3.72), *Acacia cymbispina* (=3.76), and *Mimosa* sp. (=2.92) and scarce in *Ceiba acuminata* (=0.51) and *Quercus crassifolia* (=0.41) (Figure 2.4). Nevertheless, *Bursera* sp. and *Ipomoea* sp. which had low densities in 1990, had 78% and 72% higher numbers in 1991 resulting in significant differences (t=2.99, 43 d.f., $P<0.05$; t=2.30, 31 d.f., $P<0.05$). *Acacia macilenta*, *Heliocarpus* sp., and *Acacia pennatula* had also higher densities in the second year (76%, 71% and 64% respectively) which were significant (t=3.37, 20 d.f., $P<0.005$; t=2.34, 48 d.f., $P<0.05$; t=-2.23, 48 d.f., $P<0.05$). Moreover, a correlation between the densities of both years was not significant, suggesting that spider distribution was different between years.

There were significant differences between the densities on the plant species in autumn 1991 (F=6.2, d.f. 24, 275, $P<0.001$). The significant differences between spider densities on the plant species are shown in Table 2.10. The Duncan range test results indicate that the seven plants with highest densities (*Acacia macilenta* with =6.08, *Guazuma ulmifolia* with =5.82, *Byrsonima* sp. with =4.99, *Heliocarpus* sp. with =4.47, *Acacia pennatula* with =3.91,

	Cca	Cac	Isp	Bsp	Lac	Qcr	Vin	Asp	Gul	Byr	Pju	Hsp
Bsp	*											
Lac	*											
Qcr	*											
Vin	*											
Asp	*											
Gul	*											
Byr	*											
Pju	*											
Hsp	*											
Mga	*											
Ama	*											
Fsp	*											
Ape	*		*	*	*							
Rsp	*											
Qca	*			*								
Acy	*	*	*	*	*	*	*		*			
Cse	*	*	*	*	*	*	*		*			*
Msp	*	*	*	*	*	*	*					

Table 2.9. Significant differences between spider densities on plant species sampled in autumn 1990. The Duncan range test was used (P<0.05).

	Ann	Ssp	Ama	Ccg	Byr	Hsp	Ape	Acy	Gul	Msp	Cse	Her	Bsp	Isp
Ape	*													
Acy	*	*												
Gul	*													
Msp	*	*												
Cse	*	*		*										
Her	*	*												
Bsp	*	*		*										
Isp	*	*		*										
Qca	*	*	*	*	*	*	*	*						
Lac	*	*	*	*	*	*	*	*						
Mga	*	*	*	*	*	*	*	*						
Pju	*	*	*	*	*	*	*	*						
Rsp	*	*	*	*	*	*	*	*						
Asp	*	*	*	*	*	*	*	*	*					
Cca	*	*	*	*	*	*	*	*	*	*	*		*	
Vin	*	*	*	*	*	*	*	*	*		*			
Fsp	*	*	*	*	*	*	*	*	*	*	*		*	
Cac	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Qcr	*	*	*	*	*	*	*	*	*	*	*	*	*	*

Table 2.10. Significant differences between spider densities on plant species sampled in autumn 1991. The Duncan range test was used (P<0.05).

Acacia cymbispina =3.76, and *Conzattia sericea* =3.72) differed significantly with those having the lowest densities (*Quercus castanea* with =0.41, *Ceiba acuminata* with =0.51, *Ficus* sp. and the vines with =0.7) but did not differ between themselves. Plants with intermediate numbers (*Ipomoea* sp. with =2.44, the Compositae herb with =2.6, *Mimosa* sp. with =2.92, *Bursera* sp. with =3.61, and *Conzattia sericea* with =3.72 individuals per branch) differed significantly from the other plants having high and low densities.

3.2.3. Discussion

The arthropod densities on the plant species were remarkably similar in two preliminary sample dates conducted in autumn 1990 and in the pooled 1990 and the 1991 samples. Although the method used in this study was adequate for some arthropod groups, the branches are disturbed at the moment of cutting them and the densities of the more active arthropods, such as flies and hymenopterans, were probably underestimated.

The lepidopteran larvae, the homopterans and the heteropterans, together with the total arthropod biomass had very similar distribuions in both years. The results suggest that certain plant species support higher arthropod biomass, while others seem to be favoured by particular arthropod taxonomic groups.

The total arthropod densities were particularly high in *Guazuma ulmifolia,* *Heliocarpus* sp., *Acacia pennatula* and *Acacia macilenta*. *Ceiba acuminata*, the *Apocynaceae* shrub, the vines and *Quercus crassifolia*, on the other hand, had low densities. *Ceiba acuminata* has scarce foliage and is the first to lose its leaves after the rainy season. This may explain the low arthopod densities in this tree. *Quercus crassifolia* has coreaceous leaves which might make them unpalatable for many arthropods, while the vines (belonging to the *Cucurbitaceae* and *Solanaceae* families) have secondary compounds which repels most insects (Gilbert 1980). *Bursera* sp. also had a low arthropod biomass. On the other hand *Bursera* sp. was one of the plant species with higher homopteran and lepidopteran larvae densities in 1991. This tree contains terpenoids (Rzedowski and Ortiz 1982) which may repel insects. The high densities of homopterans and lepidopteran larvae might be due to a few specialists which may have develop a resistance to terpenoids (although this is a hypothesis which would have to be tested in further studies).

Guazuma ulmifolia and *Heliocarpus* sp. are broad leaved trees, while *Acacia pennatula* and *Acacia cymbispina* are small leaved legumes (the first one is a small tree, while the second is a shrub). These four species supported high arthropod densities in both years. Since there is little taxonomic or morphologic resemblance between the first two species and the two acacias, it is difficult to understand why do arthropods favour them without further studies.

Insectivorous birds favour certain arthropod groups (Heinrich and Collins 1983, Robinson and Scott 1982, Poulin *et al.* 1994a) and therefore, the densities of spider, homopterans, heteropterans, lepidopteran larvae and beetles on the plant species were also inspected.

Heteropteran densities were higher in *Heliocarpus* sp. and *Byrsonima* sp. They were low in *Ceiba acuminata* and the vines. *Heliocarpus* sp. and *Byrsonima* are broad leaved plants but the first one is a tree, while the second is a shrub. As with the total arthropod densities, the secondary compounds in the vines and the spareness of foliage in *Ceiba acuminata* may account for low number of heteropterans they support. On the other hand, it is more difficult to answer why heteropterans favour *Heliocarpus* sp. and *Byrsonima* sp.

Homopterans were particularly dense in *Croton ciliato-glandulosae* and *Annona* sp. The first one is a small shrub (<1m), while the second is a medium sized shrub (1-2m) and both are broad leaved. Neither of this plants were sampled in 1990. Together with the lepidopteran larvae, small leaved plants also supported high homopteran abundance. Both, homopterans and the lepidopteran larvae, had higher densities in *Bursera* sp. in 1991. This tree is the only non-legume small leaved tree and therefore, both homopterans and particularly the lepidopteran larvae seem to favour plants with this particular growth form.

Coleopteran distribution differed between years. They were particularly dense on *Heliocarpus* sp., *Mimosa galeotti, Quercus castanea* and *Acacia pennatula* in

1990, while the vines together with *Ceiba acuminata* had the lowest densities. In 1991 *Acacia macilenta* and *Bursera* sp. had the highest densities while *Mimosa* sp. had the lowest.

Spiders were dense on *Conzatiia sericea*, *Acacia cymbispina* and *Mimosa* sp. in both years. As with the coleopterans, a correlation between the 1990 and 1991 densities on the plant species was not significant, suggesting that both coleopterans and spiders, were not as closely associated with any particular plant or group of plant species.

Perhaps the reason densities of spiders on the plant species change between years, is that once they have chosen one plant species (particularly in autumn, when the young ones are emerging), they remain attached to it during the whole season. This would explain why the densities in the two samples of the first year were simmilar. The differences between years on the other hand, suggests that they do not have permanent preferences for specific plants.

Due to the fact that birds favour certain arhtopod groups, and that the plant distribution of the main arthropods is not the same, it is not possible to say which plant species represent better food sources without knowing what birds are looking for. Chapter 3.6 attempts to find a relationship between the birds foraging preferences and the arthropod abundances on the plant species.

3.3. Bird species composition and diversity

3.3.1. Introduction

This section will be focused on the bird species diversity and its relation to the vegetation. The bird species included in this study, as well as their breeding and numerical status in America will also be introduced. The distribution of the bird species will be analyzed in detail in chapter 3.4.

The relationship between vegetation structure and bird diversity has been a well researched aspect in community ecology. MacArthur and MacArthur (1961) started with this field and predicted that the plant foliage diversity could explain bird diversity in North American temperate woodlands. Other workers tried to extrapolate these findings to other vegetation types, such as tropical rain forest (MacArthur 1961), other temperate woodlands in North America (Wilson 1974) and Mexico (Nocedal 1984), deserts (Tommoff 1974) and British plantations (Peck 1989) and found that the two parameters were not always correlated. It was also evident that in different vegetation types, bird diversity was affected by different factors.

Diversity indices are useful for describing by a single value, different characteristics of the community (Wiens 1989). Despite the common use of diversity indices, many ecologists are cautious about their interpretation (James and Rathbun 1981, Ludwig and Reynolds 1988, Wiens 1989). Hutto et al. (1986) go as far as to suggest that almost any method used to count birds tends to over or underestimate the abundances of some species. If this is so, diversity and specially equitability estimates are biased in most studies and the patterns found by many avian ecologists should be examined with care. On the other hand, Urban and Smith (1989) maintain that most ecologists have an intuitive knowledge about richness and equitability and therefore, although not disregarding their limitation, diversity may help to understand the structure of bird communities. Furthermore, many authors who followed the approach originated by MacArthur and MacArthur (1961) found that, even if the relationship between bird species diversity and plant stratification was not strong, the use of diversity indices was helpful to understand the relations between other aspects of the vegetation and the bird community (Wilson 1974, Tomoff 1974, Nocedal 1984, Peck 1989).

This study attempts to find how the vegetation composition and structure influence bird abundance (total number of individuals), richness, diversity and equitability in a tropical deciduous forest in western Mexico.

3.3.2. Results

3.3.2.1. Bird species composition

A list of the bird species present in the study area is shown in Appendix 3.1. The scientific and english names are included, as well as their relative frequency in Mexico (common, frequent and uncommon), breeding status (resident, migrant but breeding in or near the study sites and winter migrant), season in which each species was present (spring, autumn and both seasons) and distribution in America (endemic of Mexico, North America and Mexico, Central America and Mexico and North and South America) (Howard and Moore 1991, Rappole *et al.* 1993, Howell and Webb 1995).

A total of 69 species were found belonging to 20 families. With the exception of *Vermivora celata* and *Piranga ludoviciana*, which are rare, all species are common or frequent in Mexico. There are 49 bird species which are resident in Mexico and 7 more which are migratory but breed in or near the study sites (*Myiarchus cinerascens, Dendroica coronata, Contopus* sp., *Poleoptila caerulea, Archilochus alexandri, Dendroica petechia* and *Icteria virens*). *Dendroica nigrescens, Regulus calendula, Piranga ludoviciana, Passerina cyanea, Vireo solitarius, Selasphoros rufus, Dendroica townsendi, Catharus guttatus, Vermivora ruficapilla, Vermivora celata, Chondestes grammacus, Mniotilta varia* and *Vermivora virginianae* are winter migrants. Of the 49 resident species, *Pheucticus chrysopeplus, Calothorax lucifer* and *Amazilia beryllina* were only present in autumn in the study area, while *Euphonia elegantissima, Carduelis psaltria, Melozone kieneri, Poliptila nigriceps, Certhia americana, Turdus migratorius, Melanotis caerulescens, Salpinctes obsoletus, Passerina caerulea, Toxostoma vociferans, Quiscalus mexicanus, Trogon elegans, Ptilogonis cinereus, Picoides stricklandi* and *Spizella atrogularis* were only present in spring. *Polipoptila caerulea* which breeds near the study area, was very common in autumn but nearly absent in spring and is unlikely to breed in the study sites.

Most species present (67%) have a north American distribution. In addition, eight species are ubiquitous in the American continent (*Pitangus sulphuratus, Contopus sordidulus, Mniotilta varia, Dendroica petechia, Piranga flava, Piranga ludoviciana, Quiscalus mexicanus* and *Carduelis psaltria*). Five species range from Mexico to Central America (*Amazilia beryllina, Eugenes fulgens, Contopus pertinax, Euphonia elegantissima* and *Icterus pustulatus*) and four more are present in Mexico and South America (*Piaya cayana, Pyrocephalus rubinus, Myopagis viridicata* and *Catharus aurantiirostris*). *Picoides stricklandi, Melozone kieneri, Campylorhynchus gularis* and *Melanotis caerulescens* are endemic to Mexico, while *Pheucticus chrysopeplus* and *Ptilogonis cinereus* are from Mexico and Guatemala.

Appendix 3.2 shows the densities (number of birds in ten 30m diameter plots) of each bird species in the three main habitats (dry forest, oak woodlands and the interface between them) in the four seasons of the study period. There were 51 species in autumn and 61 in spring. Forty five species were present in both seasons.

Even though 15 autumn species were present in only one year, the densities of the 36 shared species correspond to 98% of the total densities in 1990 and 95% in autumn 1991. In spring 41 out of the 61 species were found in both years and they represented 98% of the total 1991 densities and 89% of the total 1992 densities.

The two seasons of the first year study (autumn 1990 and spring 1991) shared 31 out of 57 species. The 31 common species represented 61% of the autumn 1990 total bird densities and 83% of the spring 1991 densities. Autumn 1991 and spring 1992 shared 40 species (there were 65 between both seasons) which corresponded to 80% of the autumn densities and 83% of the spring densities.

The bird species diversity and its relationship with the vegetation in the two years of the study period will next be explored. The birds species distribution will be discussed in chapter 3.4.

3.3.2.2. Bird abundance, richness, diversity and equitability in the main habitats

The Shannon-Wiener and the Pielou indices were used to estimate bird species diversity and equitability. Diversity indices have two main components: the number of species or richness and the evenness of abundance among species, any of which influences the index in different degrees. Total abundance of birds, richness, diversity and evenness were obtained for all sample units. The mean values for the main habitats of the study area are shown in Figures 3.1 to 3.8 for autumn 1990 and 1991 and spring 1991 and 1992.

There was a strong similarity in the bird diversity components in each habitat between years. Abundances were high in huizachales and low in forests and woodlands in autumn. The vegetation interface between forests and woodlands also had high abundances. Coatales, on the other hand, had high bird abundances in the first year but low in the second (Figure 3.1). Richness was high in coatales, the vegetation interface and the mixed woodlands, but low in the pure oak woodland, mogotes and forests (Figure 3.2). Diversity was strongly correlated with richness in both years ($r=0.91$, d.f. $=105$, $P<0.001$ in 1990, and $r=0.87$, d.f. $=65$, $P<0.001$ in 1991) and followed the same general pattern (Figure 3.3). Evenness was relatively unchanging but an analysis of variance showed that there were significant differences between habitats ($F=6.85$, 7 d.f., $P<0.001$ for autumn 1990 and $F=2.18$, 7 d.f., $P<0.05$ for autumn 1991). The main difference between years was that woodlands had the

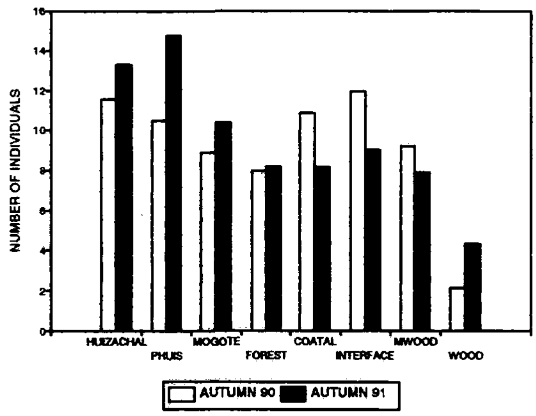


Figure 3.1. Autumn mean number of individuals per habitat.

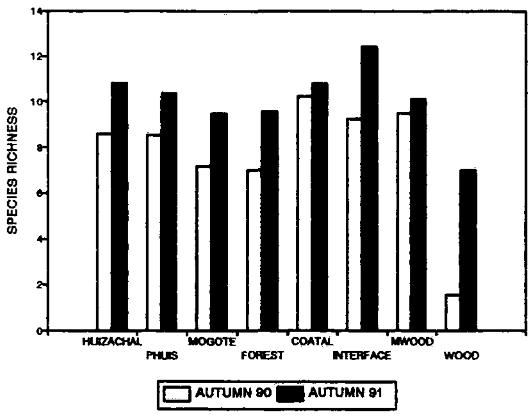


Figure 3.2. Autumn mean number of species per habitat.

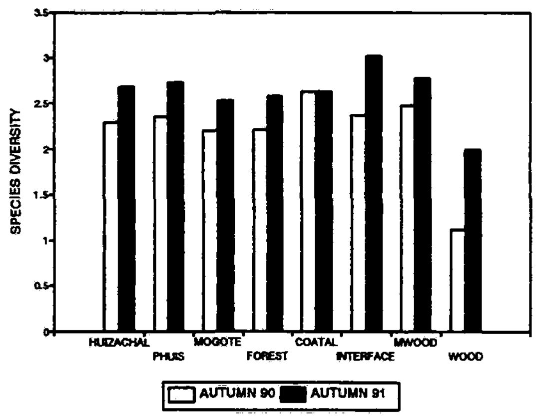


Figure 3.3. Autumn mean diversity per habitat.

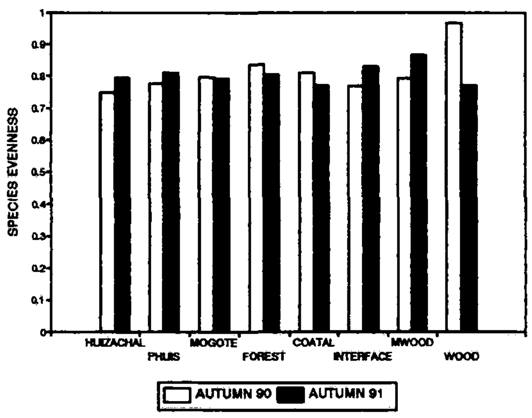


Figure 3.4. Autumn mean evenness per habitat.

PHUIS=Prosopis huizachal, MWOOD=mixed woodland.

highest value in 1990, but the lowest in 1991 (Figure 3.4). There was a negative relationship between evenness and total bird abundance, although a correlation was only significant for the first year ($r=-0.51$, 105 d.f., $P<0.001$ for the first year and $r=-0.20$, 65 d.f., $P=$n.s. for the second). The negative correlation between total abundance and evenness suggests that, at least in the first year, abundance in those habitat with highest number of birds was explained by a few dominant bird species.

In spring, number of individuals, as well as species, were higher in the second year (Figures 3.5 and 3.6). Although there appears to be a strong similarity between the number of individuals per habitat in both years, an analysis of variance indicated that there were no significant differences in abundances between habitats in spring 1992 ($F=1.9$, 65 d.f., $P=$n.s.). Analyzes of variance were used for the other diversity components as well, and they were not significant for diversity ($F=1.69$, 65 d.f.) and evenness ($F=1.25$, 65 d.f.) in spring 1992 either. Richness, the only component which had significant differences between habitats in spring of the second year, was particularly high in the vegetation interface in both years (Figure 3.6). It was lowest in woodlands and had low values in mogotes and forests as well. *Prosopis* huizachales had a relatively high number of species in 1992, but was low in 1991 (Figure 3.6). As in Autumn, abundances were low in mogotes and woodlands in spring 1991. Richness, was also low in mogotes and oak woodlands and high in the vegetation interface and the mixed woodlands.

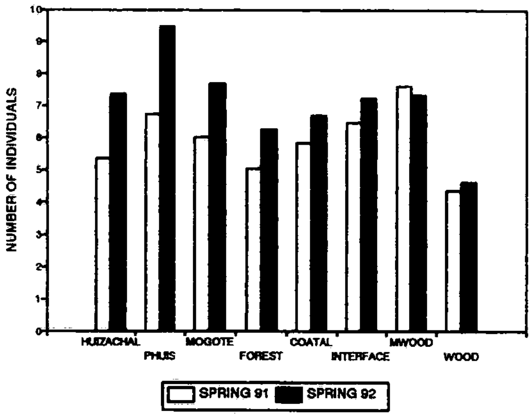


Figure 3.5. Spring mean number of individuals per habitat.

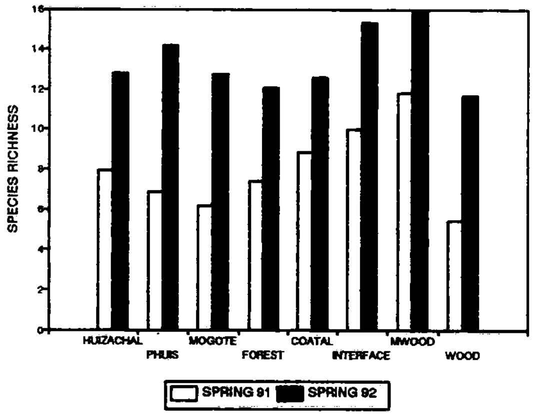


Figure 3.6. Spring mean number of species per habitat.

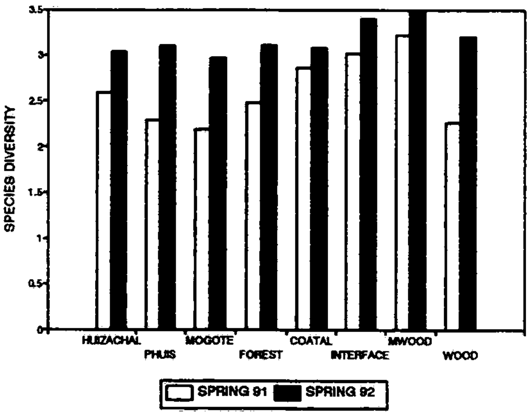


Figure 3.7. Spring mean diversity per habitat.

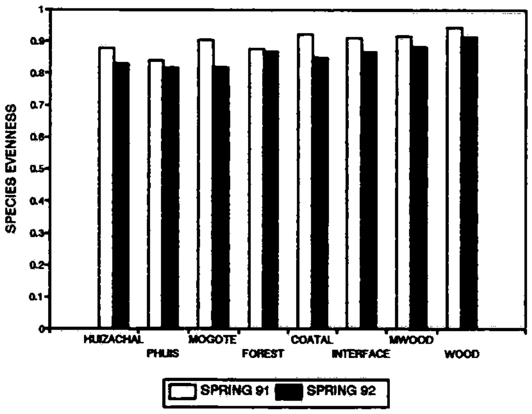


Figure 3.8. Spring mean evenness per habitat.

PHUIS=Prosopis huizachal, MWOOD=mixed woodland.

The similarities of the diversity components between the two years suggests that birds respond to certain characteristics of the different habitats. In the following section, the relationship between the vegetation variables and the bird diversity components will be explored in detail.

3.3.2.3. Ordination analysis

Since the bird species diversity components are not necessarily related with the main plant associations types in a particular area, multivariate techniques were used in order to obtain different meaningful ways in which the vegetation can be organized (i.e. the first axis may be associated with the plant composition, but a second one might be associated with another aspect -such as vegetation structure- to which the birds may show a stronger response). These vegetation gradients (as well as the individual vegetation variables explaining the ordination) were then correlated with the bird species diversity components.

For these purpose two data sets were used in a canonical correspondence analysis (CANOCO) (Ter-Braak 1988) for each year. The first one contained the values of the plant variables for each of the sample units used in this study (107 in autumn 1990 and spring 1991, and 67 in autumn 1991 and spring 1992) and which were used for the habitat classification. The resulting axes from the plant ordination are restricted by CANOCO to be correlated to a second matrix. The second matrix included the values for bird abundances, richness, diversity and equitability for autumn and spring. For consistency with the classification of the habitats made with TWINSPAN (Section 3.1), standardized values for the plant variables were used.

Ordinations were used in an exploratory way in this chapter and are explain in more detail in the methods and the chapter on bird distribution.

Eigenvalues for the first year for the four axes were 0.113, 0.063 and 0.038 and accounted for 39%, 61% and 74% of the accumulated variance of the species-environment relationship. The fourth axis, which explained 10% of the variation is difficult to interpret and was left out from the rest of the analysis.

In the second year, eigenvalues were 0.160, 0.054 and 0.041 for the first three axes and accounted for 50%, 67%, 80% of the accumulated variance. As in the first year, the fourth axis contributed little to the results (less than 8% of the variation).

In order to test the significance between diversities and the main axes, Monte Carlo permutations were employed. For each random data set, CANOCO can calculate permutations for the eigenvalues and for the trace (the sum of all eigenvalues). The later gives an overall test of the significance of the relationship between the environmental variables on the species. Tests for the first axes and the trace were performed, using 99 permutations, and they were significant ($P<0.05$) for the two years.

As a result of high intercorrelations between spring richness, diversity and evenness, the three components had high inflation values in the second year ordination (Ter Braak 1988). Since it is more interesting to analyze the change in richness and evenness (both of which define the diversity index) separately, than to study the changes in a single and more abstract index, diversity was removed for spring 1992. An additional ordination, without this component, resulted in low inflation factors for both richness and evenness.

3.3.2.4. Interpretation of the ordination axes

The plant gradients as depicted by the ordination axes will be explained in this section. A second approach, explained in the next section, attempted to extract those vegetation variables which had a direct influence on the bird community.

Figures 3.9 and 3.11 show the ordination of the sample units numbered according to their corresponding TWINSPAN habitat classification (chapter 3.1) for the first and second year. The first axis in both years represents a gradient that goes from woods ("8" in the diagram) to huizachales ("1" and "2") through the mixed woodland ("7"), the vegetation interface ("6"), and the forests ("4" and "5"). Mogotes ("3"), are actually spread between the huizachales on this

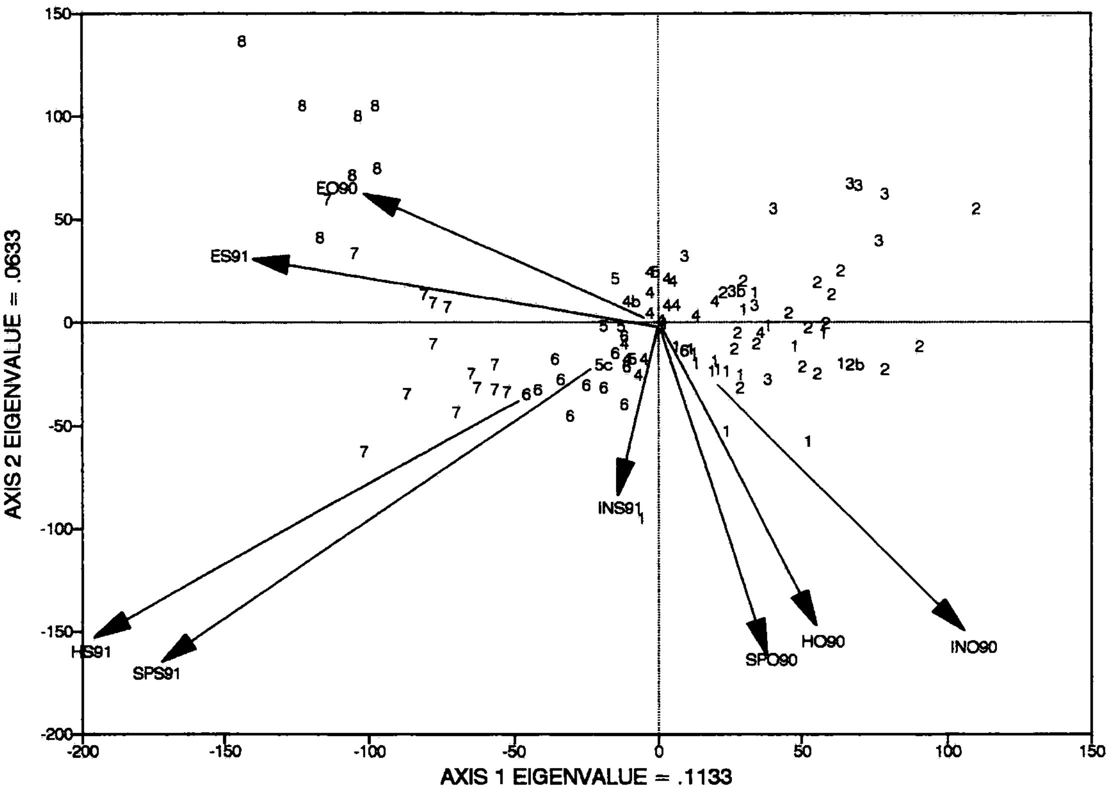


Figure 3.9. First year canonical correspondence analysis (CANOCO) of plant variables with respect to bird diversities (arrows). The diagram displays bird individuals, species richness, diversity and evenness in relation to the vegetation variables used to ordinate the study plots. INO90 = number of individuals in autumn; SPO90 = autumn bird richness; HO90 = autumn diversity; EO90 = autumn evenness; INP91 = number of individuals in spring; SPS91 = spring richness; HS91 spring species diversity; ES91 = spring evenness. Habitats are: 1 = huizachales; 2 = Prosopis huizachales; 3 = mogotes; 4 = forests; 5 = coatales; 6 = vegetation interface; 7 = mixed woodlands; 8 = oak woodlands Letters besides numbers indicate overlapping in the ordination: a = 1; b = 2; c = 3.

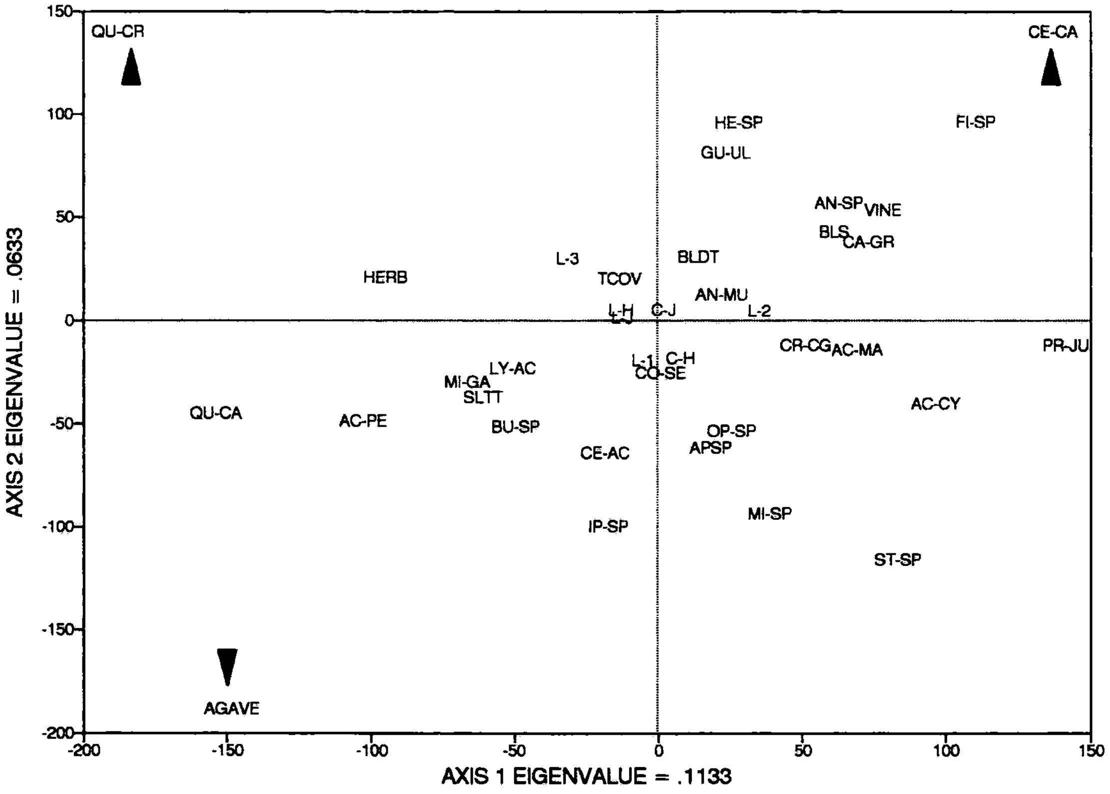


Figure 3.10. Ordination based on canonical correspondence analysis of plant variables. The oaks (QU-CR and QU-CA) and A. pennatula (AC-PE) represent the woodlands, while Ficus sp. (FI-SP), Acacia cymbispina (AC-CY) and Prosopis juliflora (PR-JU) are typical of huizachales. The second axis is exemplified by Heliocarpus sp. (HE-SP), and Guazuma ulmifolia (GU-UL) which are broad leaved trees with dense foliage, on one extreme, and by Mimosa sp. (MI-SP), Ipomoea sp. (IP-SP) and Ceiba acuminata (CE-AC) on the other. Other symbols are: AN-SP = Annona muricata; MI-GA = Mimosa galeotti; CR-CG = Croton sp.; AC-SY = Acacia macilenta; APSP = an Apocynaceae shrub; AGAVE = Agave sp.; AN-SP = Annona muricata; OP-SP = Opuntia sp.; ST-SP = Stenocereus sp.; VINES = vines; LY-AC = Lysiloma acapulcensis; CO-SE = Conzattia sericea; CE-CA = Celtis sp.; TCOV = total cover; BLS = broad leaved shrub; SLTT = small leaved thorny tree; BLDT = broad leaved deciduous tree; L-1 = 0-1.0m vegetation layer; L-2 = 1.0-2.5m layer; L-3 = >2.5m layer; L-H = foliage height diversity; L-E = foliage high evenness. Axes were rescaled to coincide with habitat plot, arrowheads indicate that coordinates for the corresponding variables are outside the limits of the rescaled plot.

axis, although they were segregated in the second axis in the first year (Figure 3.9).

The second axis represents a gradient related to plant physiognomy in the first year. Those plots in which broad leaved trees and oaks dominate are on the positive section (mainly oak woodlands and mogotes but also most of the forests and some huizachales), while those in which small leaved legumes were more abundant had negative scores (mixed woodlands, the vegetation interface, and huizachales) (Figure 3.9). In the second year, the second axis segregated the vegetation interface (in which small leaved plants and shrubs are dominant as well) from woodlands and forests (Figure 3.11).

If the ordination plots for the habitats (Figures 3.9 and 3.11) are overlaid with those for the plant variables ordinations (Figures 3.10 and 2.12 for the first and second year), an accurate association between the habitats and their characteristic plant species can be seen. Both oak species (*Quercus crassifolia* and *Q. castanea*) are associated with woodlands ("7" and "8"). The vegetation interface ("6"), as well as the mixed woodlands ("7") are respectively associated with *Acacia pennatula, Lysiloma acapucensis* and *Mimosa galeotti.* The later two, together with *Bursera* sp. are also frequent in coatales ("5"). Broad leaved deciduous trees have high covers in forests ("4") and broad leaved shrubs have the highest covers in mogotes ("3"). Finally, *Acacia cymbispina, A. macilenta* and *Prosopis juliflora*, which are small leaved legumes are typical of huizachales

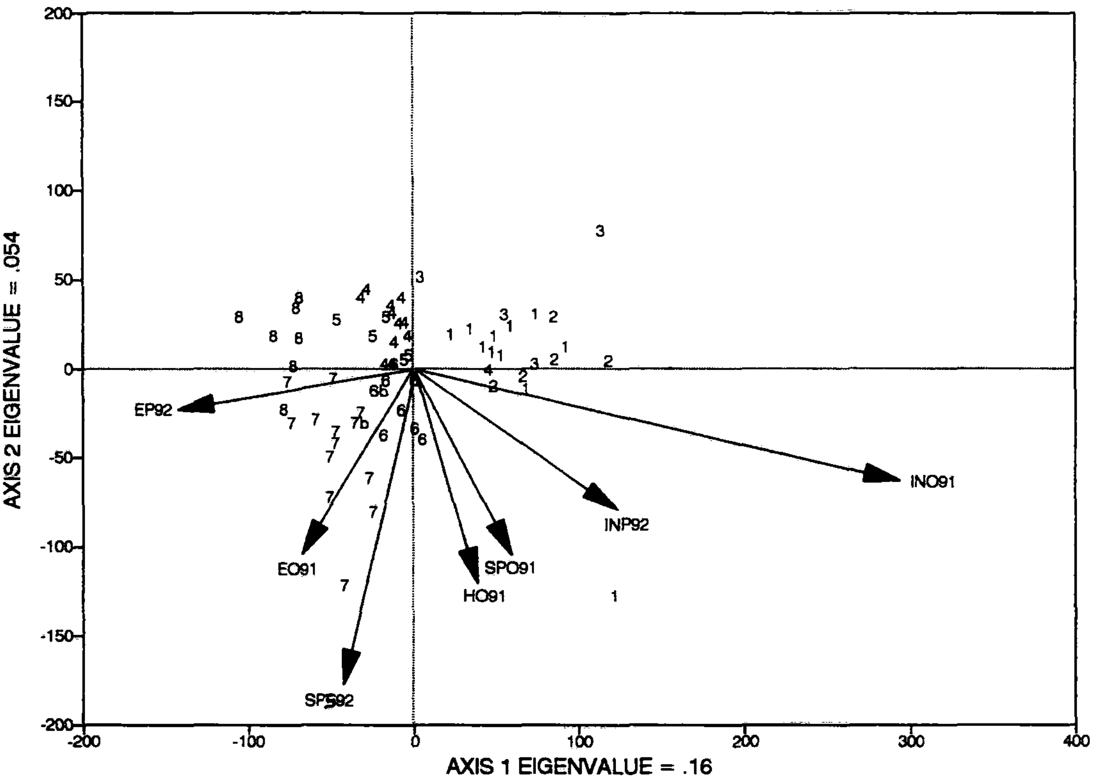


Figure 3.11. Second year canonical correspondence analysis diagram of plant variables with respect to bird diversities (arrows). The diagram displays bird individuals, species richness, diversity and evenness in relation to the vegetation variables used to ordinate the study plots. INO91 = number of individuals in autumn; SPO91 =autumn bird richness; HO91 = autumn diversity; EO91 = autumn evenness; INP92 = number of individuals in spring; SPS92 = spring richness; HS92 spring species diversity; ES92 = spring evenness. Habitat are: 1 = huizachales; 2 = Prosopis huizachales; 3 = mogotes; 4 = mature forests; 5 = coatales; 6 = the vegetation interface; 7 = mixed woodlands; 8 = oak woodlands. Letters beside numbers indicate overlapping in the ordination: a = 1; b = 2; c = 3.

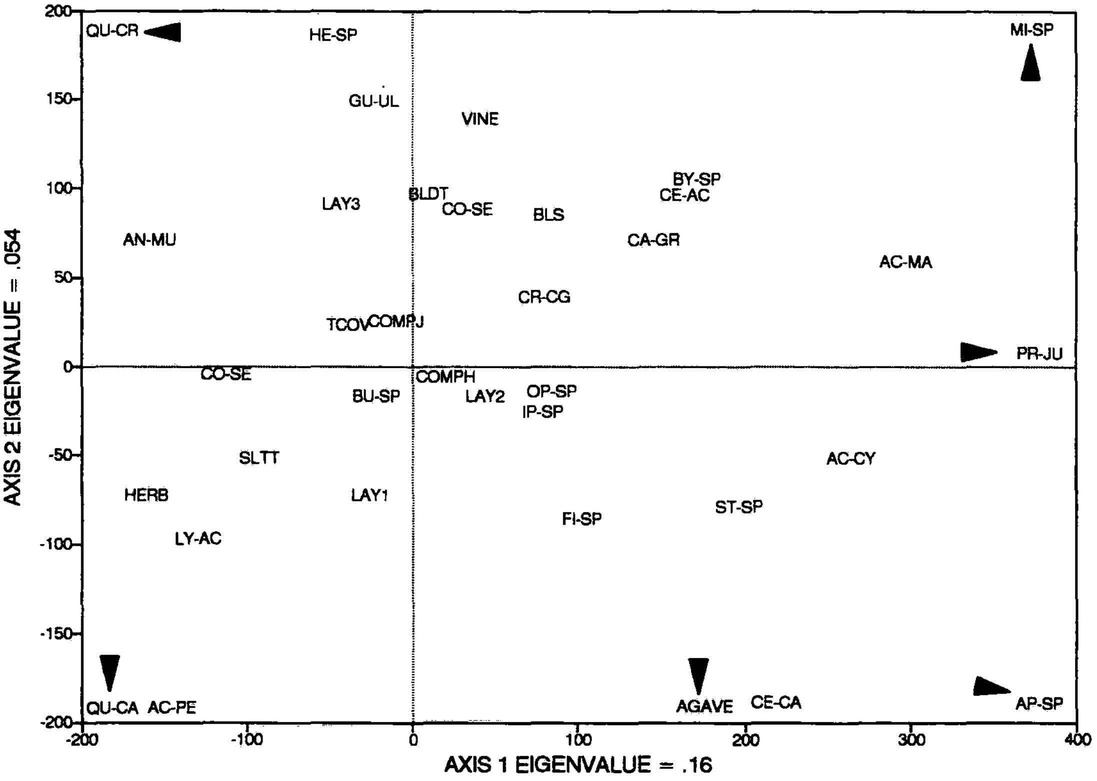


Figure 3.12. Second year ordination of plant variables with respect to bird diversity. The oaks (QU-CR and QU-CA), herbs and A. pennatula (AC-PE) represent the woodlands, while Prosopis juliflora (PR-JU), Mimosa sp. (MI-SP), the Apcynaceae (AP-SP), Acacia cymbispina (AC-CY) and A. macilenta (AC-MA), represent the thorn forests (huizachales) The second axis is exemplified by Quercus crassifolia (QU-CR), Heliocarpus sp. (HE-SP) and Guazuma ulmifolia (GU-UL) which are broad leaved trees with dense foliage, on one extreme, and by Quercus castanea (QU-CA), agaves and Acacia pennatula (AC-PE) on the other. Other symbols are: AN-SP = Annona muricata; MI-GA = Mimosa galeotti; CR-CG = Croton sp. AN-SP Annona muricata; OP-SP = Opuntia sp.; ST-SP = Stenocereus sp.; VINES; LY-AC = Lysiloma acapulcensis; CO-SE = Conzattia sericea; CE-CA = Celtis caudata; TCOV = total cover; BLS = broad leaved shrub; SLTT = small leaved thorny tree; BLDT = broad leaved deciduous tree; LAY1 = 0-1.0m vegetation layer; LAY2 = 1.0-2.5m layer; LAY3 = >2.5m layer. Foliage height diversity and evenness (not shown) are positioned in the center of the plot.

("1" and "2").

The correlation values between the ordination axes and the bird diversity components are shown in Table 3.1 for the first year and in Table 3.2 for the second. These values are reflected by the arrows in Figures 3.9 and 3.11. The arrows point in the direction of maximum variation of each of the bird diversity parameters. The length of the arrow indicates the magnitude of the relationship, that is, the strength of the covariance between bird diversities and the axes. For example, in the first year, spring bird abundance had a weak but significant correlation coefficient with the second axis (Table 3.1) and therefore is represented by a short arrow parallel to the second axis. Autumn abundances, richness and diversity were more strongly correlated with the second axis and so, the arrows which represent them are longer. The arrows for diversity and richness in spring of the first year are diagonal, illustrating their significant correlation with both the first and the second axes (Table 3.1 and Figure 3.9).

The TWINSPAN habitat classification coincide with the first ordination axis. Therefore, the position of the arrows for those diversity components which were correlated with this axis, agree with the diversity values for the habitats in Figures 3.1-3.8. For example, the number of species and diversity in spring 1991 was particularly high in open forests ("6") and the vegetation interface ("7), and lower in oak woodlands ("8"), mogotes ("3") and forests ("4"), as both the histograms in Figures 3.5 and the direction of the arrows for spring bird

Table 3.1. Correlation coefficients and significance levels between the first three CANOCO ordination axes and the bird diversity components for autumn 1990 and spring 1991.

	Axis 1	Axis 2	Axis 3
Autumn abundance	0.246 *	-0.490 **	0.020
Autumn richness	0.089	-0.510 **	0.030
Autumn diversity	0.128	-0.480 **	-0.020
Autumn evenness	-0.252 *	0.200 *	-0.310 *
Spring abundance	-0.030	-0.280 *	0.170
Spring richness	-0.394 **	-0.529 **	0.150
Spring diversity	-0.447 **	-0.500 **	0.040
Spring evenness	-0.335 **	0.100	0.140

* < 0.05, ** < 0.001

Table 3.2. Correlation coefficients and significance levels between the first three CANOCO ordination axes and the bird diversity components for autumn 1991 and spring 1992.

	Axis 1	Axis 2	Axis 3
Autumn abundance	0.717 **	-0.172	-0.164
Autumn richness	0.131	-0.300 *	-0.453 **
Autumn diversity	0.091	-0.341 *	-0.263 *
Autumn evenness	-0.168	-0.301 *	0.214
Spring abundance	0.292 *	-0.234	0.085
Spring richenss	-0.120	-0.499 **	0.131
Spring evenness	-0.369 *	-0.061	-0.051

* < 0.05, ** < 0.001

diversity and richness in Figure 3.9 show.

In the first year bird species diversity, abundance and richness were even more strongly correlated with the second axis, which was related with the type of foliage. These diversity components were depicted in the ordination according to this vegetation gradient. They had higher values in huizachales ("1" and "2"), the vegetation interface ("6") and the mixed woodlands ("7"), were small leaved plants were more abundant.

Spring richness and diversity in 1991 were correlated with both, the first and the second axes. The correlation with the first axis imply that spring richness and diversity were high in woodlands and low in huizachales. On the other hand, the correlation with the second axis, indicate that their values were higher in small leaved dominated sites. This suggests that the higher number of species and diversity indices should be in those woodlands where small leaved plants dominate. The vegetation interface ("6") and particularly the mixed woodlands ("7") share these characteristics and that is where the corresponding arrows in Figure 3.9 are strongly directed.

Evenness was correlated with the first axis in spring 1991 and with the three ordination axes in autumn 1990. The third axis divided woodlands ("8") and mogotes ("3") from mixed woodlands ("7"), the vegetation interface ("6") and huizachales ("1" and "2"). Figure 3.9 shows that evenness was higher in coatales ("5") in autumn, while in spring 1991 it was higher in the interface, mogotes and oak woodlands. It is also apparent that evenness had an inverse relationship with abundance and richness, particularly in autumn.

In the second year, spring and autumn total bird abundances were positively correlated with the first ordination axis (Table 3.1). The arrows representing them (Figure 3.11) show that autumn they had higher values in huizachales ("1" and "2"). Autumn and spring richness, together with autumn diversity and evenness were significantly correlated with the second axis. The arrow for these components are parallel to this axis and show that the values were higher in the vegetation interface ("6") and mixed woodlands ("7").

Autumn richness and diversity were also correlated with the third axis. This axis separated forests, coatales and the interface from woodlands and huizachales. The correlation with both the second and the third axis indicates that autumn diversity and richness were low in huizachales, mogotes and woodlands and high in coatales and, particulalry in the interface, in which small leaved plants dominate (Figure 3.13).

3.3.2.5. Determination of individual factors

Multiple regressions between the vegetation variables and the diversity components were performed in an attempt to identify the individual variables

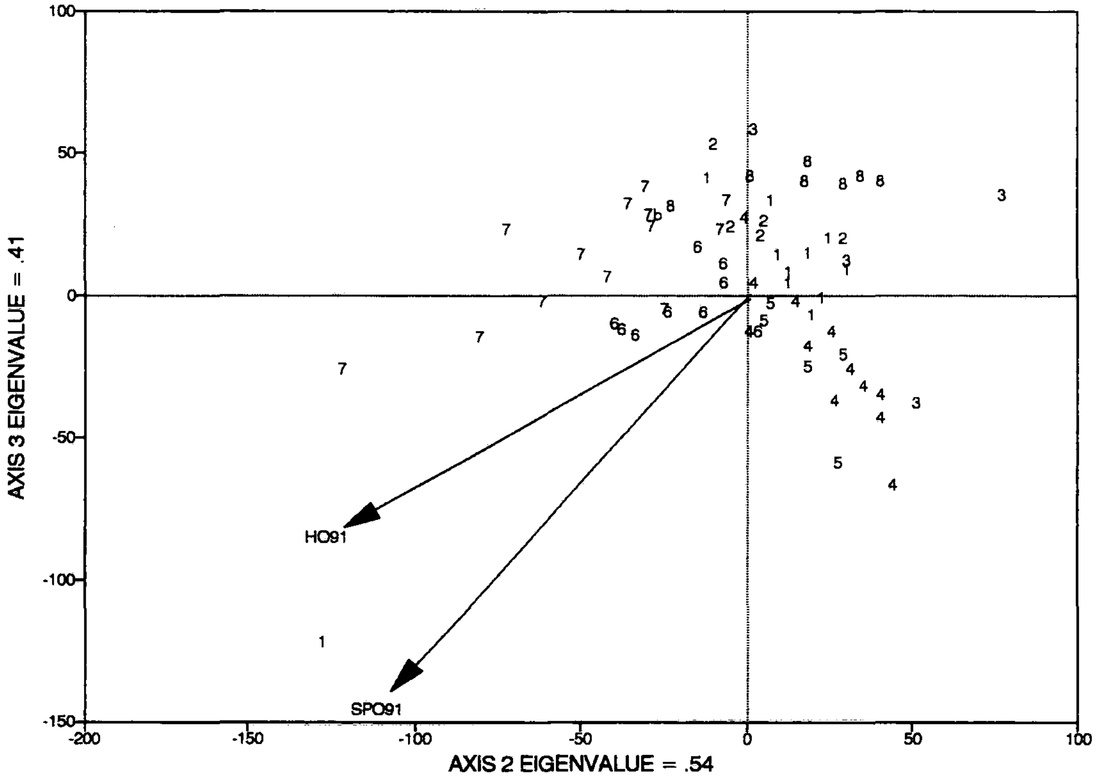


Figure 3.13. Second year canonical correspondence analysis diagram of plant variables with respect to bird diversities (arrows). The diagram displays the bird species diversity and richness in autumn 1991 in relation to the second and third ordination axes of the study plots. SPO91 = autumn 1991 bird richness; HO91 = autumn 1991 bird species diversity. Habitats are 1 = huizachales (thorn forests); 2 = Prosopis huizachales; 3 = mogotes; 4 = mature forests; 5 = coatales; 6 = vegetation interface; 7 = mixed woodlands; 8 = oak woodlands.

affecting the bird species diversity parameters. Since the direction of the arrows in the ordination biplots (representing the diversity components) in relation to the vegetation variables should agree with the regressions, these were inspected as well.

The results of the regressions between the plant variables and the bird diversity parameters are shown in Table 3.3 for the first year and in Table 3.4 for the second. For each variable, the Tables include the step in which it was entered in the regression, its slope and standard error and the t-test together with its significance value.

In the autumn of the first year, *Quercus crassifolia* and either *Guazuma ulmifolia* or *Heliocarpus* sp. (*G. ulmifolia* and *Heliocarpus* sp. are broad leaved forest trees and their cover is significantly correlated: $r=0.47$, d.f. 116, $P<0.001$) were the first two variables entered in the multiple regressions between bird abundance, richness and diversity and the plant variables (Table 3.3). They both had negative correlation values, suggesting that the plots in which these plants had high covers were those with lower number of bird richness, abundance and diversity. *Senecio* sp., the herbs and the foliage height diversity were also included in the regressions for species richness and diversity.

Because of intercorrelations, the importance of some variables may be concealed in multiple regressions analyzes. In particular, in the first year of the present

Table 3.3. First year multiple regressions between bird diversity components and plant variables. Regressions for autumn are shown with all variables and with Q. crassifolia ommited.

	Autumn 1990					Autumn 1990					Spring 1991				
Variable	EO	Slope	SE	T	P	EO	Slope	SE	T	P	EO	Slope	SE	T	P
Total bird abundance															
Quercus crassifolia	1	-2.16	0.35	-6.24	0.00										
Ipomoea sp.						1	1.14	0.36	3.20	0.00					
Guazuma ulmifolia	2	-1.50	0.39	-3.81	0.00										
Bursera sp.											1	0.84	0.20	4.23	0.00
Prosopis juliflora											2	0.67	0.22	3.00	0.00
>2.5m vegetation cover						2	-1.85	0.38	-4.80	0.00	3	-0.57	0.21	-2.71	0.01
Plant composition diversity						3	1.57	0.37	4.20	0.00					
Acacia pennatula											4	0.42	0.20	2.09	0.04
Bird species richness															
Quercus crassifolia	1	-2.38	0.30	-7.91	0.00						6	-1.08	0.25	-4.35	0.00
Ipomoea sp.						1	0.81	0.28	2.89	0.00					
Guazuma ulmifolia	2	-1.13	0.33	-3.48	0.00										
Senecio sp.	3	1.14	0.28	4.01	0.00	4	0.83	0.28	2.96	0.00					
Herbs	4	1.03	0.33	3.17	0.00						8	0.73	0.25	2.97	0.00
Heliocarpus sp.	5	-0.95	0.29	-3.22	0.00										
>2.5m vegetation cover						2	-1.68	0.31	-5.41	0.00					
Foliage height diversity	6	0.69	0.29	2.36	0.02						9	0.52	0.24	2.15	0.03
Plant composition diversity						3	1.51	0.40	3.79	0.00					
Plant composition evenness						5	-0.96	0.36	-2.64	0.01					
Conzattia sericea	7	-0.68	0.33	-2.02	0.05										
Acacia pennatula											1	0.85	0.22	3.80	0.00
Ipomoea sp.											2	0.72	0.21	3.38	0.00
Bursera sp.						6	0.72	0.28	2.55	0.01	3	0.56	0.21	2.67	0.01
Mora											4	-0.79	0.24	-3.31	0.00
Prosopis juliflora											5	0.57	0.25	2.30	0.02
BLDT											7	-0.97	0.26	-3.78	0.00
Bird species diversity															
Quercus crassifolia	1	-0.38	0.05	-7.89	0.00										
Ipomoea sp.						1	0.22	0.05	4.46	0.00					
Heliocarpus sp.	2	-0.18	0.05	-3.57	0.00										
Senecio sp.	3	0.15	0.04	3.56	0.00										
Herbs	4	0.12	0.05	2.55	0.01										
Guazuma ulmifolia	5	-0.16	0.05	-2.89	0.00										
1.0-2.5m vegetation cover						2	0.17	0.05	3.40	0.00					
Broad leaved trees						3	-0.29	0.06	-5.07	0.00					
Plant composition diversity						4	0.34	0.07	5.05	0.00					
Foliage height diversity	6	0.10	0.05	2.08	0.04										
Plant composition evenness						6	-0.13	0.06	-2.21	0.03					
Acacia pennatula											1	0.18	0.04	4.27	0.00
Mimosa galeotti						5	-0.11	0.05	-2.38	0.02					
Ipomoea sp.											2	0.18	0.04	4.16	0.00
Mora											3	-0.15	0.05	-3.07	0.00
Bursera sp.											4	0.11	0.04	2.58	0.01
Bird species evenness															
Quercus crassifolia	1	0.03	0.01	3.54	0.00										
Conzattia sericea	2	0.03	0.01	3.28	0.00										
0-1.0m vegetation cover	3	-0.02	0.01	-2.43	0.02	1	-0.03	0.01	-3.38	0.00					
Herbs						2	0.02	0.01	2.17	0.03	1	0.02	0.01	3.47	0.00
Vines											2	-0.02	0.01	-2.96	0.00
Byrsonima sp.											3	0.03	0.01	3.63	0.00
Prosopis juliflora						3	-0.02	0.01	-2.00	0.05	4	-0.02	0.01	-2.76	0.01
Randia sp.											5	-0.02	0.01	-2.33	0.02
Apocynaceae shrub											6	0.01	0.01	2.45	0.02
Stenocereus sp.											7	-0.01	0.01	-2.27	0.03

EO = step at which variable was entered, SE = slope standard error; T = slope t-test, P = t-test significance value.

study, the regression for the second ordination axis excluded *Ipomoea* sp., which had the highest positive correlation coefficient in simple correlations. In fact, the cover of *Quercus crassifolia* is negatively correlated with that of *Ipomoea* sp. ($r=0.23$, 116 d.f., $P<0.05$). When *Q. crassifolia* was removed from the regressions, the first three variables entered were *Ipomoea* sp., the >2.5m plant cover and plant species diversity in the regressions between the plant variables and bird species abundance, richness and diversity (Table 3.3). This suggests that in the autumn 1990, there were more bird species as well as more individuals in those plots with higher *Ipomoea* sp. cover and higher plant composition diversity indices. Plots with high covers of *Quercus crassifolia*, broad leaved forest trees, and >2.5 plant cover (the latter two were highly correlated; $r=0.59$, 116 d.f. $P<0.001$) on the other hand, had fewer bird species, richness and diversity.

Autumn evenness was positively correlated with *Quercus crassifolia* and *Conzattia sericea*, and negatively with the 0-0.1m vegetation layer (Table 3.3). When *Q. crassifolia* was removed, autumn evenness was still negatively correlated with the first vegetation layer but now it was also negatively correlated with *Prosopis juliflora* and positively with the herb cover (Table 3.3).

It is encouraging that the variables included in the first steps of the multiple regressions are also those towards which the arrows representing the diversity components are directed. For example, the arrows for bird species diversity and richness in autumn points towards *Ipomoea* sp. (the variable with the highest positive significant correlation) and are opposite *Quercus crassifolia* and the broad leaved trees (*Heliocarpus* sp., *Guazuma ulmifolia*, BLDT and L-3) as can be seen when the arrows in Figure 3.9 are overlaid on Figure 3.10.

In spring 1991, the variables in the first steps of the regression analyses for bird abundance, richness and diversity, were *Acacia pennatula* and *Bursera* sp., both with positive slopes. *Ipomoea* sp. was also included for richness and diversity, and *Prosopis juliflora*, for the total number of birds and species richness (Table 3.4). *Celtis caudata*, a tall tree that grows in thorn forests, was included for species richness and diversity with a negative slope and the >2.5, also with a negative slope, was included in the total bird abundance regression. Additionally, bird species richness was positively associated with the herbs and the foliage height diversity, and negatively associated with *Quercus crassifolia* and the broad leaved deciduous trees (Table 3.4).

The position of *Acacia pennatula, Bursera* sp. and *Ipomoea* sp. with respect to the arrows corresponding to bird species diversity, abundance and number of bird species indicates that these diversity components and plant variables were associated in the ordination as well (Figure 3.10).

The results from both, the multiple regressions and the ordinations, indicate that there was a higher number of bird species, abundance and species diversity in

Table 3.4. Second year multiple regression results between bird diversity components and plant variables.

	Autumn 1991					Spring 1992				
Variables	EO	Slope	SE	T	P	EO	Slope	SE	T	P
Total bird abundance										
Acacia cymbispina	1	1.82	0.39	4.69	0.00					
Quercus crassifolia	2	-0.87	0.27	3.21	0.00	1	-0.96	0.24	4.03	0.00
Agave sp.	3	0.89	0.25	3.58	0.00					
Mimosa sp.	4	0.64	0.25	2.54	0.01					
Stenocereus sp.	5	0.65	0.27	2.37	0.02					
Plant composition evenness						2	-0.85	0.34	2.49	0.02
Birds species richness										
Quercus crassifolia	1	-1.73	0.31	5.61	0.00					
Agave sp.	2	0.83	0.23	3.57	0.00					
Herbs	3	1.63	0.38	4.23	0.00					
Bursera sp.	4	-0.70	0.30	2.34	0.02					
0-1.0m plant cover	5	-0.92	0.40	2.32	0.02	1	0.87	0.37	2.36	0.02
>2.5m plant cover						2	-1.49	0.40	3.74	0.00
Lysolima acapulcensis						3	1.10	0.45	2.46	0.02
Bird species diversity										
Quercus crassifolia	1	-0.21	0.04	4.81	0.00					
Herbs	2	0.17	0.05	3.34	0.00	1	0.14	0.04	3.29	0.00
Bird species evenness										
Acacia pennatula	1	0.02	0.01	2.24	0.03					
Foliage height diversity	2	0.03	0.01	2.86	0.01					
Heliocarpus sp.	3	-0.02	0.01	2.34	0.02					
Quercus crassifolia						1	0.02	0.01	2.36	0.02
Acacia cymbispina						2	-0.02	0.01	2.12	0.04

EO = step at which variable was entered, SE = slope standard error; T = slope t-test, P = t-test significance value.

those plots with high *Bursera* sp., *Ipomoea* sp. and *A. pennatula* covers and lower in those plots in which the third vegetation layer and *Celtis caudata* were abundant.

Bird species evenness in spring 1991 was higher were herbs, *Byrsonima* sp. and *Apocynacea* sp. were more abundant, and lower in the plots with high vines, *Prosopis juliflora*, *Randia* sp. and *Stenocereus* sp.

In the second year, the regression for autumn bird abundance included *Acacia cymbispina*, *Quercus crassifolia, Agave* sp., *Mimosa* sp. and *Stenocereus* sp. Only *Q. crassifolia* was negatively correlated (Table 3.4). The ordination biplot, shows that the arrow representing the number of individuals, points in the direction of the positively correlated variables and is opposite *Q. crassifolia* (Figures 3.11 and 3.12).

Autumn bird richness and diversity were positively associated with the herbs and negatively with *Q. crassifolia*. Additionally, species richness was positively associated with *Agave* sp. and negatively with *Bursera* sp. and the 0-1.0m vegetation layer. Both components were correlated with the second and third ordination axes. A biplot of the first and second ordination axes shows that the arrows for richness and diversity point to *Agave* sp. and are opposite *Q. crassifolia*. *Bursera* sp. and the 0-1.0m vegetation cover are also opposite the species richness arrow. Autumn evenness was positively correlated with *A.*

pennatula and foliage height diversity, and negatively with *Heliocarpus* sp. The arrow representing it, point to *A. pennatula* and is opposite *Heliocarpus* sp.

In spring, bird abundance was negatively correlated with *Q. crassifolia* and the plant composition evenness and the biplot positioned the arrow in the correct position (Figures 3.11 and 3.12).

The regression for bird richness in spring of the second year included the 0-1.0m plant layer, the >2.5m plant layer and *Lysolima acapulcensis*. The first and last had positive correlation values. Bird richness was negatively correlated with the second axis and the arrow for bird richness in spring is associated with both the first plant layer and *L. acapulcensis* (Figures 3.11 and 3.12). The spring evenness regression included *Q. crassifolia* (with a positive value) and *A. cymbispina* (with a negative value) (Table 3.4).

The two techniques used in this section are complementary. The canonical correspondence analysis correctly located the bird parameters with respect to the vegetation associations, it also showed that there is an even stronger relationship with a vegetation gradient of dense foliage broad leaved trees to small leaved species. The regression analyses identified those variables which appear to have the most important effect on the bird community structure. In particular, *Quercus crassifolia* and those variables associated with high covers of broad leaved deciduous trees had a negative effect on densities and richness.

In general, small leaved plants had a positive influence on bird richness and abundances, but this variables were not the same in the four seasons. *Bursera* sp. and *Acacia pennatula* were particularly important in spring 1991, while *Acacia cymbispina* and *Lisolyma acapulcensis* were important in the autumn 1991 abundances and spring 1992 richness respectively. In autumn 1990, *Ipomoea* sp., which is mainly present in thorn forests and the vegetation interface, appeared to have a large influence on bird species richness, diversity and abundance. The importance of these variables will be examined in the discussion.

3.3.3. Discussion

Diversity indices can play an important starting point to understand how communities are organized (Wiens 1989). MacArthur and MacArthur (1962) suggested that an increase in foliage height diversity resulted in an increase in bird species diversity in some North American temperate woodlands. Recher (1969) found that the same pattern occurred in Australia, despite the differences in bird composition. Other studies, including one central American tropical rain forests in which MacArthur was also involved (MacArthur, *et al.* 1966), concluded that the relationship was not the same in different vegetation types.

Nocedal (1983) found that birds species diversity did not increase linearly with foliage height diversity in temperate woodlands in Mexico. This was mainly because birds of different guilds had strong preference for different vegetation layers, where their corresponding food resources were more abundant. Holmes and Robinson (1981) and Peck (1989) showed that certain bird species had a strong preference for certain tree species, while Tommoff (1974) concluded that in North American deserts, bird species diversity was correlated with certain plant life forms. This study found that individual plants were more important than structural factors to predict bird species diversity (Tables 3.3 and 3.4).

Since some patterns may be obscured when species diversity is analyzed using a single index (Wiens 1989), the different diversity components (richness, evenness, diversity and abundance) were separated for this study.

The ordinations helped to identify a vegetation gradient (exemplified by the second axis in both years), explained by plant physiognomy (leaf type of the plants), that was more closely related to bird diversity than to the main vegetation types obtained either by the first axis of a plant classification (chapter 3.1). In particular, bird species richness and diversity were higher in those plots dominated by small leaved plants , particularly the interface and mixed woodlands in both springs, but also in the thorn forests in the autumns (Figures 3.9-3.12).

The higher number of species in the interface is not surprising since these communities usually contain species from the "parent communities" (Pianka 1988, Urban and Smith 1989). The high number of both species and individuals in those habitats in which small leaved plants also predominate, may be the result of higher food availability. Arthropod samples in both autumns (chapter 3.2), for example, indicate that small leaved plants support higher number of lepidopteran larvae and homopterans.

The individual variables obtained by straight multiple regressions (between the bird species components and the vegetation variables) coincided with those obtained with the ordination techniques. The differences in the importance of some plant species between years may reflect local changes in resource availability in time and will be discussed next.

Ipomoea sp. in particular, attracted bird species and individuals in autumn 1990. On the other hand, the plots in which *Quercus crassifolia*, broad leaved plants (*Guazuma ulmilolia* and *Heliocarpus* sp.), and the >2.5m vegetation cover dominated had low numbers of bird species and individuals. *Q. crassifolia* was one of the species with fewer arthropods (chapter 3.2), and this may partially explain its negative correlation with bird species richness, diversity and abundance. *Guazuma ulmifolia* and *Heliocarpus* sp., were rarely used by birds (chapter 3.5) and had few homopterans and lepidopteran larvae, both of which appear to be the preferred insect food for the insectivores (chapter 3.6). *Ipomoea* sp., which was significantly correlated with bird species richness diversity and density in autumn 1990 (Table 3.4, Figure 3.10), has large white conspicuous flowers which attract hummingbirds and many passerine birds which seem to search for insects associated with the flowers. In fact *Ipomoea* was the most important tree for the foraging activities of hummingbird and the insectivorous guilds in both autumn 1990 and 1991 (chapter 3.4).

In spring 1991, those plots with high covers of *Acacia pennatula, Bursera* sp. and *Prosopis juliflora* attracted bird individuals (Figure 3.9 and 3.10). As in autumn, those plots with high covers in the >2.5 plant layer had low abundances. Arthropods had very low densities in spring and it was not possible to estimate their relative abundances. Nevertheless, *P. juliflora* is particularly conspicuous in spring because of its abundant foliage at a time when most other plants have shed their leaves. Bird species were seen using these trees for different activities. This may partially explain the positive correlation with bird abundances.

Species richness and diversity, were somewhat related to *A. pennatula*, *Bursera* sp., and *Ipomoea* sp. in spring 1991 (Figures 3.9 and 3.10). On the other hand, *Celtis caudata*, which is a broad leaved deciduous tree present mainly in thorn forests was negatively correlated with bird species diversity and richness. *Bursera* sp. produces small fruits during spring and attracted the hawking flycatchers and some of the generalist insectivorous common in this season. Although bird species and individuals were high those plots where *Acacia* *pennatula* have high covers, birds only seldom looked for food in this tree. Since *A. pennatula* had particularly high covers in mixed woodlands and the vegetation interface, where other small leaved trees (e.g. *Lysolima acapulcensis*) are abundant and where higher number of birds were seen foraging, its importance in the ordination may only be because it represents mixed woodlands and the interface better than any other plant species. *Ipomoea* sp. still had a few flowers in spring and birds were seen looking for food in them during this season (chapter 3.5).

As in the first year, bird abundances, richness and diversity were negatively related to *Q. crassifolia* in autumn. On the other hand, *Ipomoea* was not included either in the regressions and was not very important in the ordinations (Tables 3.5 and 3.6). The fact that diversity was correlated with this plant only in 1990 indicates that, regardless of its importance as a food source in both years (chapter 3.5), it does not always have an impact on bird diversities. *Acacia cymbispina* was the most important variable associated with bird abundances in the second year, while bird species richness was higher in the vegetation interface, where *Agave* sp. is frequent (Figures 3.12 and 3.13, Table 3.4).

A. cymbispina which had high numbers of lepidopteran larvae and homopterans, was particularly used by forest insectivores, the most abundant guild of birds in autumn (chapter 3.5). This may explain the positive correlation with bird abundance. *Agave* sp. on the other hand, is only widely used by birds when it is flowering, which was not the case in this particular season (personal observation). It may have been included in the analysis, because it is particularly abundant in the vegetation interface and the mixed woodlands and, as *Acacia pennatula* in 1990, represents well these habitats.

In spring 1992, *Quercus crassifolia* was again negatively correlated with bird abundance (together with plant composition evenness), while the 0-1.0m plant cover and *Lysolima acapulcensis* were positively correlated with bird species richness (Figures 3.11 and 3.12 and Table 3.4). The >2.5m vegetation cover was negatively associated with bird species richness. *L. acapulcensis* is a big tree whose foliage begins to grow in spring (just before the rainy season). It is widely use by birds of different guilds-(frugivore-insectivores, woodpeckers and woodland insectivores and flycatchers, besides foliage insectivores) which may explain the positive correlation with bird richness.

Bird evenness, particularly in the two autumns, was negatively correlated with bird abundances and with the plant variables with which abundance was positively correlated. This suggest that some of the species attracted by plants such as *Ipomoea* sp. in the first year or *Acacia cymbispina* in the second have high densities. *Ipomoea* sp. for example is used by many species, but it mainly attracts hummingbirds and two warblers (*Dendroica coronata* and *Vermivora ruficapilla*), which represent 35% of the total bird densities in autumn 1990.

Acacia cymbispina, which was the first variable in the multiple regressions for autumn bird abundance (with a positive slope) as well as bird species evenness (with a negative slope) in the second year, was used mainly by the forest insectivores in autumn 1991. This guild includes only two bird species (*Polioptila caerulea* and *Vermivora virginiana*), out of 50, and represents 11% of the total bird abundance.

The similarities between seasons in bird species abundance, richness, diversity and evenness suggest that those habitats which include either more food resources (i.e. higher number of homopterans and lepidopteran larvae in those plots where small leaved plants have high covers or key plants like *Ipomoea* sp., which produces nectar for the hummingbirds), or which includes plants in which food is more easily accesible (the flowers of *Ipomoea* sp. are conspicuous and might advertise the presence of flying invertebrates for insectivores) also support higher bird abundances.

The relationship between food and the bird community organization will be explained in further chapters. The next section will analyze the relationship between the bird species distribution and the vegetation.

3.4. Bird species distribution

3.4.1. Introduction

Multivariate techniques are extensively used to describe the distribution of species and to look for the environmental variables determining it (Gauch 1982, Ludwig and Reynolds 1988). This approach is based on gradient analyses (Gauch 1982), which was first used regularly in biology by Curtis and the Wisconsin school of vegetation analysis (Curtis 1955, Curtis and McIntosh 1951) and was further developed by Whittaker (1956, 1967). Gradient analysis shed more light to the controversy about the nature of ecological communities. In general, it endorsed the individualistic theories developed by Gleason (1926), which opposed the organismic concept of Clements (1916).

Bond (1957) was among the first ecologists to apply this approach to bird communities. His conclusions supported those of the individualistic school. Later on, when big data matrices could be processed with the aid of computers, more quantitative approaches began to be used. These approaches basically follow the same strategy, which consists of arranging the plots in which the organisms under study were counted according to their distribution similarities. The plots are then given certain values according to this arrangement and these scores are then correlated with environmental variables in order to see which of them help explain the distribution of the species. This technique has been successfully used for plants (Austin 1968, Whittaker 1978, Huntley and Birks 1979). Although animals are more difficult to study because of their vagility, these methods have also been successful for spiders (Aart and Smeenk-Enserink 1975, Uetz 1976), carabid beetles (Buterfield and Malvido 1992) and oligochaetes (Standen 1982).

Perhaps because their abundances can be estimated with relative ease, multivariate ordinations used to study animal communities have been mainly applied to birds as summarized by Wiens (1989, chap. 9). Other multivariate methods used in bird communities include discriminant function analysis (DFA), principal components analysis (PCA) and reciprocal averaging (RA) and its derived techniques; detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA).

Discriminant function analysis (DFA) has been used by Anderson and Shugart (1974), Whitmore (1975, 1977), Smith (1977), Rice *et al.* (1983), and Morrison *et al.* (1986). This technique emphasizes on the distance between *a priori* defined groups (i.e. the clusters obtained by the species classification). In this case, a matrix of the variables characteristic of each group are subjected to the DFA to see which of this factors better separate them. Significance between groups can be established by indirect statistics such as Mahalanovich distance (Morrison *et al.* 1986) and Wilkis lambda, which can be then transformed to a chi-squared distribution (Norusis 1988).

DFA can also be based on two more or less subjective groups (based on plant physiognomy for example) and then the organisms on each of these groups can be subjected to the analysis. The percentage of correctly classified sample units belonging to each groups is then obtained (Rice *et al.* 1983).

Principal component analysis usually ordinates the sample units in a multivariate space according to the species distribution similarity (or dissimilarity) matrix. The resulting axes are then correlated with the variables and those which come out as significant will be those which, at least partially, determine the species distribution.

The main problem with PCA and DFA is their dependance of linearity (Meents *et al.* 1983). Sabo and Whittaker (1979) found that the distribution of most species did not follow a multinormal distribution and preferred reciprocal averaging (RA) to analyze their data. Reciprocal averaging based methods are an alternative to linear dependent ordinations techniques. The mechanisms of these have been described by Gauch (1982) and Hill (1973) and the main principles have been described in the methodology section. One of the RA-based algorithms is detrended corresponded analysis (Hill 1979) which has been used by Sabo (1980) to study bird foraging behaviour and more recently, by Fuller and Henderson (1992) to study the bird distribution on British plantations.

A relatively new technique developed from DCA, is canonical correspondence analysis (CANOCO) (Ter Braak, 1986) which, besides being independent of linearity, includes a regression model which restrains the species axes to be correlated with the variables.

This approach was used as an aid to help relate bird species diversity with the main plant associations (chapter 3.3). The distribution of the bird species in this study was also analyzed using canonical correspondence analysis. The significance of the relationship between the variables and the ordination axes can be tested with Monte Carlo permutations.

3.4.1.1. A note on sample size

A total of 107 plots in eleven sites were used to count the birds in the first year and a subset of 67 plots in the second. The vegetation structure and composition were measured in each of those plots (see methods). The vegetation variables were used to obtain the main vegetation types by means of a classification.

The bird community analyses can therefore be performed on the basis of their mean density per site, vegetation sub-type or sample unit. Since the sites do not have a uniform vegetation (i.e. the classification of the 107 sample units results in eight vegetation sub-types each of which includes sample units from different sites) a significant loss of information (regarding habitat preferences) could result if the abundances were averaged by site.

If the plant associations (obtained by the TWINSPAN classification) are used, some noise could be included in the sense that birds observed in one plot could be there by chance, if their favoured habitat is located near the area being sampled (which could in itself be a sub-optimal habitat). The problem could be even worse if birds do not recognize their preferred habitats at the vegetation type level. In this case, the birds found in a patch from one site resembling the vegetation of a faraway site having a different general plant physiognomy would be mixed with the later, potentially making some very confusing results.

Bibby *et al.* (1989) used the individual plots for an ordination of the birds in British plantations. Individual plots are not completely independent and pseudoreplication difficulties arise because the sample units on each site are likely to share more species between them than with those located in other site (Hurlbert 1984). This problem can be partially avoided by keeping a reasonable distance between plots (Reynolds *et al.* 1980) and therefore it was the approach used in this study.

3.4.2. Results

3.4.2.1. Bird species ordination

Figures 4.1, 4.2, 4.4 and 4.5 show the bird ordinations for the four seasons studied. The bi-plot (Ter Braak 1988) shows the mean position of each species with respect to the principal axes and their relationship with the significant variables. These are conventionally depicted by arrows showing the direction of their influence as well as their relative importance. The later is represented by the size of the arrow.

The meaning of each axis can be interpreted by examining the ordination score of each variable and those which are statistically significant were plotted together with the distribution of the bird species in the multivariate space.

Since there was a tendency in which the most common species, and particularly those which were present with high relative densities in only one or two sample units (outliers), to dominate and sometimes eclipse the results, the bird species data set was downweighted (Ter Braak 1988).

Before describing the ordination results, an account follows about the decisions taken to include the most meaningful variables.

Based on the correlation matrix, those variables which were highly intercorrelated were examined. It was found that most of the composite variables (those derived by adding the values of similar life forms) were highly correlated with one of the variables comprising them (the correlations among the individual variables were always lower or non significant) and therefore only the broad leaved shrubs (BLS), the small leaved thorny trees (SLTT) and the broad leaved deciduous trees (BLDT) were retained.

Some plant variables had similar values in all the samples and when they were plotted in an ordination using DCA, their scores indicated that they were not contributing much to the results. These included the composition diversity and the composition and vegetation stratification equitability indices.

CANOCO includes a column with the inflation factors for each variable. Inflation factors are related to the multiple correlations between environmental variables and a large value for a particular variable means that it is almost perfectly correlated with other variables and has no unique contribution to the results (Ter Braak 1988). In those cases in which a variable which had a high inflation factor and yet was significantly correlated with any of the ordination axes, trials were performed without those variables which were not-significantly correlated with any of the axes. Often, the new inflation factor for the variable was lower. Before performing the final run and the Monte Carlo permutations, those variables having no significant correlation coefficient with any of the ordination axes, were removed.

The ordination results for each season will be presented next. A comparison of the distribution of the resident species in the four seasons will follow.

3.4.2.1.1. Autumn 1990

The relationship between the first three bird ordination axes and the vegetation variables were significant when tested by 99 Monte Carlo permutations ($P<0.05$ in all cases) in autumn 1990. The eigenvalues were 0.24, 0.141 and 0.083 for the first three axes and together represented 50.3% of the variance explained by the ordination.

The plant variables with positive correlation coefficients with the first axis were *Prosopis juliflora*, *Croton ciliato-glandulosae*, *Guazuma ulmifolia*, *Acacia cymbispina* (huizache), a *Byrsonima* shrub and the vines. Negatively, the first axis was correlated with *Mimosa galeotti*, *Bursera* sp., both *Quercus crassifolia* and *Q. castanea*, the herbs, *Acacia pennatula*, *Lysiloma acapulcensis*, small leaved thorny trees (SLTT) and the foliage high diversity. The first set of variables represent thorn forests (huizachales) and mature dry forests, while the second is associated with the vegetation interface between forests and oak woodlands (Table 4.1 and Figure 4.1b)

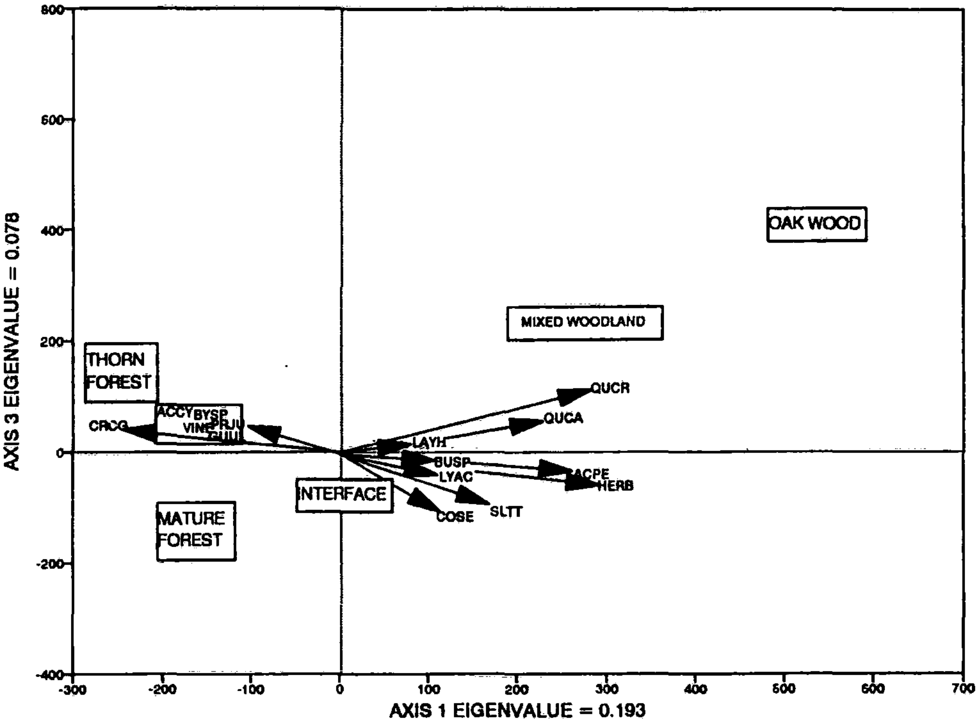
Figures 4.1a and b show the position of the birds in relation to the vegetation variables. The Mexican Jay (*Aphelocoma ultramarina*), together with *Regulus calendula*, *Catharus aurantiirostris*, *Myoborus pictus*, *Dendroica nigrescens*, *Piranga flava*, and *Vireo solitarius* are woodland species and they are shown

Table 4.1. Correlation coefficients between first and second bird ordination axes and significant variables.

	First ordination axis				Second ordination axis				
	Autumn		Spring		Autumn			Spring	
PLANT VARIABLES	1990	1991	1991	1992	1990	1990	1991	1991	1992
Prosopis juliflora	-0.254		-0.263					0.350	
Randia sp.				-0.264					
Annona muricata					-0.238				
Conzattia sericea	0.264					-0.394	-0.333	-0.255	
Bursera sp.	0.258							-0.323	
Croton sp.	-0.529	-0.341	-0.455	-0.503	0.211	0.194			-0.280
Quercus castanea	0.505	0.382	0.249	0.477			-0.373		0.288
Guazuma ulmifolia	-0.265		-0.285	-0.330					
Herbs	0.628	0.383	0.374	0.349		-0.228	-0.537	-0.315	0.509
Acacia macilenta							0.251		
Acacia cymbispina	-0.377	-0.365	-0.397	-0.330		0.293	0.292	0.262	-0.261
Apocynacea sp.									
Agave sp.									
Byrsonima sp	-0.287	-0.275	-0.243	-0.292			0.271		-0.364
Opuntia sp.				-0.351					
Ipomoea sp.		-0.271		-0.299	-0.251	-0.183		-0.332	
Stenocereus sp.					-0.207				
Ceiba acuminata									
Quercus crassifolia	0.614	0.670	0.787	0.765		0.290			
Vines	-0.312		-0.361	-0.333	0.229			0.382	
Heliocarpus sp.				-0.378					
Acacia pennatula	0.575	0.514	0.341	0.416	0.265		-0.371	-0.363	0.530
Ficus sp.									
Lysiloma acapulcensis	0.267				-0.204	-0.201	-0.290	-0.194	0.302
Mimosa sp.				-0.564			0.353		
Broad leaved trees				-0.359					-0.249
Small leaved thorny trees	0.380	0.251	0.245			-0.297	-0.381	-0.412	0.391
0-1.0m vegetation layer					0.258		-0.506		0.383
1.0-2.5m vegetation layer				-0.638					
>2.5 vegetation layer					-0.240				
Foliage height diversity	0.205								

*Second axis without D. coronata.

**C. grammacus was ommited in the Spring 1992 analysis.



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AXIS 3 EIGENVALUE = 0.078
-300
-200
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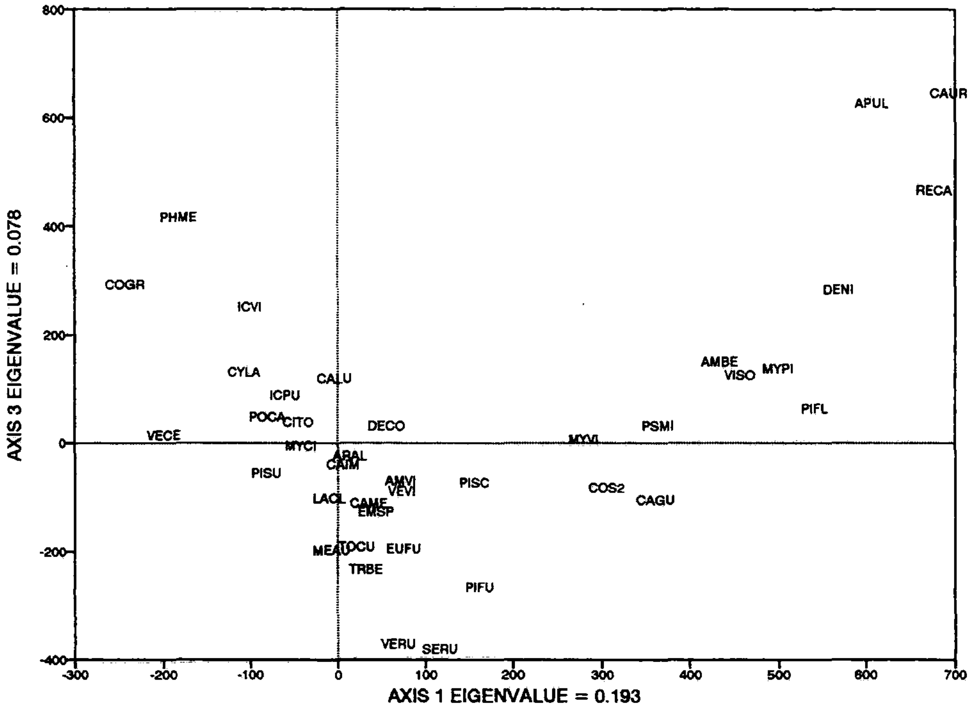
700
AXIS 1 EIGENVALUE = 0.193
OAK WOOD
MIXED WOODLAND
THORN FOREST
MATURE FOREST
INTERFACE
CRCG
ACCY
BYSP
VINE
PRJU
QUCR
QUCA
LAYH
BUSP
LYAC
ACPE
HERB
COSE
SLTT



Figures 4.1a and 4.1b. Autumn 1990 bird species densities ordination in relation to vegetation. Canonical correspondence anaylisis was used. The arrows on Figure 4.1b (acetate) show those variables which were correlated with the axes. The length of the arrows indicates importance of correlation. The position of the main habitats is also shown. Figure 4.1.a shows position of bird species in the ordination space. The first two letters for genus and species were used for abreviations for bird and plant species. SLTT=small leaved thorny trees, LAYH=foliage height diversity.

on the positive extreme of the plot. *Chondestes grammacus*, *Pheucticus melanocephalus* (as will be seen below, the distribution of this species changes notably between the seasons), *Vermivora celata* and *Cynanthus latirostris* were only present in the forests and therefore positioned on the negative side of the first axis.

The second axis of the bird ordination was negatively correlated with a broad leaved shrub (*Annona muricata*), a broad leaved deciduous tree (*Ipomoea* sp.), a columnar cactus (*Stenocereus* sp.), a large small leaved tree (*L. acapulcensis*), and the >2.5m vegetation layer. Positively, it was correlated with a small shrub (*Croton ciliato-glandulosae*), the vines and the 0-1.0m vegetation layer. This axis reflects mainly the distribution of the warbler *Dendroica coronata*. This species had a very high density in autumn 1990, which together with its unique distribution -being very abundant on certain patches plots of the main vegetation types but absent from the rest of the plots of similar vegetation- may explain its influence on the ordination.

The third axis was positively correlated with one of the oak species (*Quercus crassifolia*) and *Acacia cymbispina* and negatively with *Mimosa galeotti*, and the small leaved thorny trees (Table 4.1). When the sample units are plotted, the separation between the oak woodlands from the interface and the mature forests from the thorn forests becomes evident (Figure 4.1b). When *Dendroica coronata* was removed from the analysis, the second axis became very similar to this one (confirming the influence of this bird in the autumn of

1990).

Figure 4.1a shows the plot between axes 1 and 3. *Myiarchus cinerascens,* a flycatcher which is positioned in the centre of the intersect was ubiquitous and not likely to have much effect on the results. The forest birds (those on the left side of the abscissa), are now segregated into those present in the thorn forest (positive side of the ordinate) and those mainly present in the mature forest (negative section of the ordinate). The first group is represented by *Chondestes grammacus*, *Pheucticus melanocephalus*, *Icteria virens*, *Cynanthus latirostris*, *Icterus pustulatus* and *Poliptila caerulea*. The second, by *Centurus aurifrons* and *Toxstoma curvirostrae*, although these were also common in the interface (Figure 4.1a).

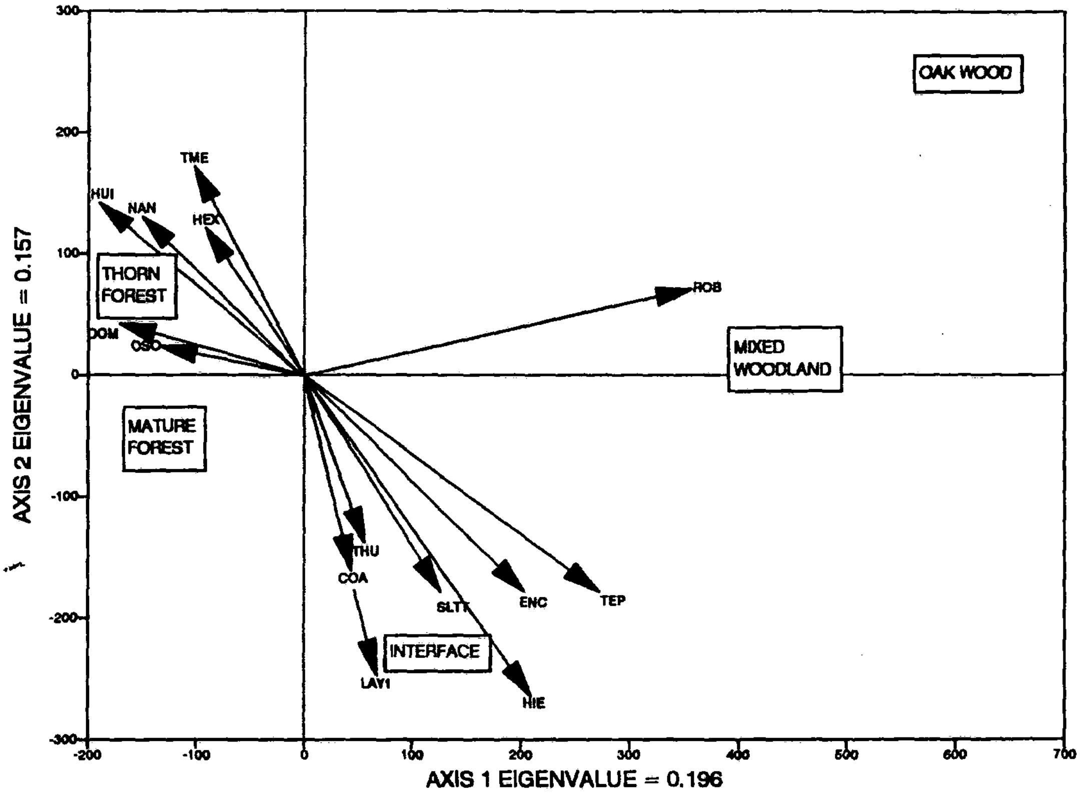
As expected, both woodland and forest bird species were also found in the vegetation interface. *Catherpes mexicanus*, *Empidonax* sp., *Centurus aurifrons* and *Tryomanes bewickii* are mainly forest birds, which were common in the interface. *Calothorax lucifer*, common in huizachales, was also present in the vegetation interface. *Amazilia violiceps*, *Vermivora virginianae, Eugenes fulgens*, *Vermivora ruficapilla*, *Selasphorus rufus* and *Pipilo fuscus*, on the other hand, had higher densities in the vegetation interface. Finally, *Contopus sordidulus* and *Catharus guttatus*, which are common in woodlands, were also found in the transition.

3.4.2.1.2. Autumn 1991

The bird composition in autumn 1991 was similar to the bird composition in autumn of the first year. There were 48 species in the second year and 40 in the first. Thirty six of these where present in both years, representing 97.7% in the total bird density in autumn 1990 and 94.3% of the second year.

Monte Carlo permutations were significant for the first three axes (99 permutations, $P<0.05$ in each case). These axes explained 50.7% of the variance and their eigenvalues were 0.348, 0.233 and 0.141 respectively. In autumn 1990, the first axis was correlated with plants related to the forest-woodland gradient. Both oak species, the herbs, *Acacia pennatula* and the small leaved thorny trees were positively correlated with this axis and are related to the woodlands and the vegetation interface. *Acacia cymbispina, Croton ciliato-glandulosae*, the *Byrsonima* shrub and *Impomoea* sp. are typical of dry forests and are negatively correlated with the same axis (Table 4.1).

The second axis separated the vegetation interface and the mixed woodlands form the oak woodlands and the thorn forests from the mature forests, in the same way that the third axis did in autumn 1990 (or the second, when the warbler *Dendroica coronata* was removed) (Figure 4.2b). It was negatively correlated with the small leaved trees *Mimosa galeotti, Lysolima acapulcensis* and *Acacia pennatula*, the small leaved oak *Quercus castanea*, the small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AXIS 2 EIGENVALUE = 0.157
AXIS 1 EIGENVALUE = 0.196
OAK WOOD
TME
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NAN
HEX
THORN FOREST
ROB
DOM
OSO
MIXED WOODLAND
MATURE FOREST
THU
COA
SLTT
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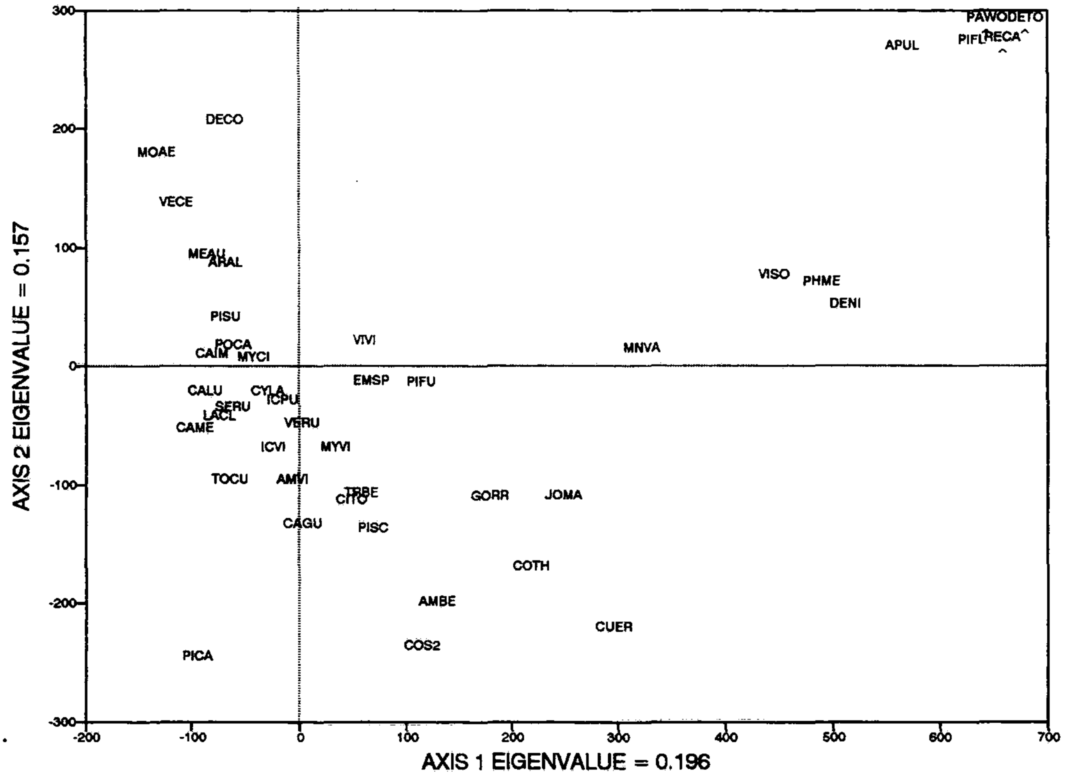
TEP
INTERFACE
LAY1
HIE



Figures 4.2a and 4.2b (acetate). Autumn 1991 bird species ordination in relation to the vegetation. the interpretation is the same as for Figure 4.1. LAY1=0-1.0m plant layer.

leaved thorny trees and more significantly with the herbs. Positively, this axis was correlated with *Acacia macilenta*, *Acacia cymbispina*, the *Apocynaceae* and *Byrsonima* shrubs and the small leaved semi-deciduous *Mimosa* tree. The main difference between both years was that in the later, the first axis did not segregate very clearly the forests form the interface. The third axis was difficult to interpret and will not be discussed here.

3.4.2.1.3. Year to year variation in autumn

As in autumn 1990, there was a group of birds associated with the woodlands: *Aphelocoma ultramarina*, *Regulus calendula*, *Piranga flava*, *Dendroica nigrescens* and *Vireo solitarius*. *Vermivora celata*, *Pitangus sulphuratus*, *Polioptila caerulea* and *Cynanthus latirostris* (*Centurus aurifrons*, *Myiarchus cinerascens*, and *Archilochus alexandrii* were more ubiquitous) on the other hand, were found on forests. A third group of bird species, including *Empidonax* sp., *Thryomanes bewickii*, *Pipilo fuscus*, and *Picoides scalaris,* had higher densities in the vegetation interface in 1991 and also common there in 1990.

The similarities in the bird species distribution was examined more closely by using the data sets for each year in the same ordination.

The correlation between the first two axes and the plant variables were similar to the individual analyses. Again the vegetation gradient from forests to woodlands was represented by the first axis and the segregation between thorn forests and mature forests and between oak woodlands and the interface was evident. Figure 4.3 illustrates the ordination bi-plot and shows the birds present in both years.

More particularly, *Dendroica coronata*, *Vermivora virginianae*, *Archilocus alexandrii*, *Poliptila caerulea*, *Cynanthus latirostris* and *Vermivora celata* were positioned in the thorn forest section of the plot in both years. *Camptostoma imberbe*, *Myiarchus cinerascens* and, to a lesser extent *Icterus pustulatus,* remained near the centre of the plot in both years indicating that both species were widely spread through the sample units.

Pitangus sulphuratus, *Toxostoma curvirostrae* and *Icteria virens* were more frequent in mature forests, while *Amazilia violiceps*, *Selasphorus rufus*, *Myopagis viridicata* and *Picoides scalaris* were also found in the interface. *Amazilia beryllina* and *Contopus* sp. were more abundant in mixed woodland.

Among the species which showed more pronounced changes in their distribution were *Centurus aurifrons*, *Calothorax lucifer* and *Vermivora ruficapilla*. The abundances of these birds was very low in the second year (Appendix 3.2) and therefore, there was only a poor indication of their actual distribution.

Other species that showed changes in their distribution between both years

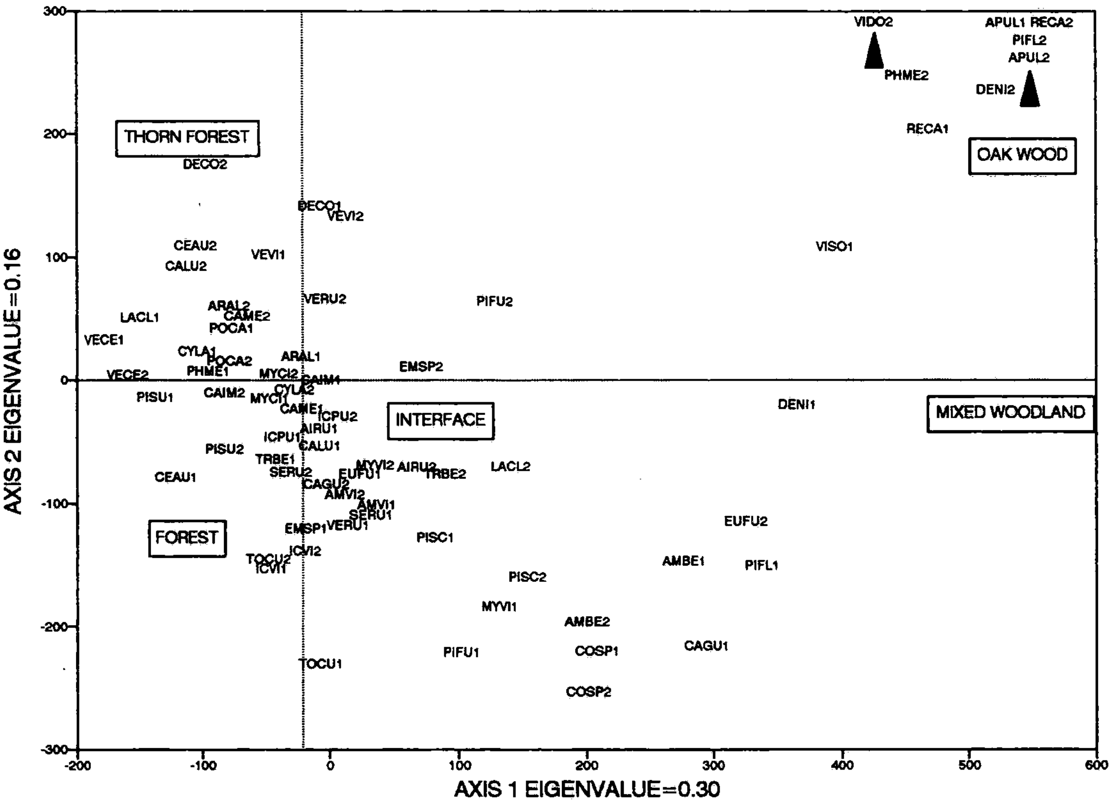


Figure 4.3. Bird species ordination for autumn 1990 and 1991. Only species present in both years are shown to compare distributions.
The number after the bird species name indicates the corresponding year: 1 is for 1990, 2 for 1991.

were *Catharus guttatus*, *Thryomanes bewickii*, *Pipilo fuscus* and *Eugenes fulgens*. These were birds which were most frequently seen at the interface, and their position in the ordination is chiefly indicating partially higher abundances in forests in one year and in woodlands in the other (Figure 4.3).

The woodland birds were *Vireo solitarius*, *Piranga flava*, *Dendroica nigrescens*, *Regulus calendula* and *Aphelocoma ultramarina*.

Pheucticus melanocephalus is a special case. It is commonly seen in a large number of habitats in autumn but its distribution becomes restricted to woodlands during the breeding season. It was seen in forests in the first season but was restricted to woodlands in the second.

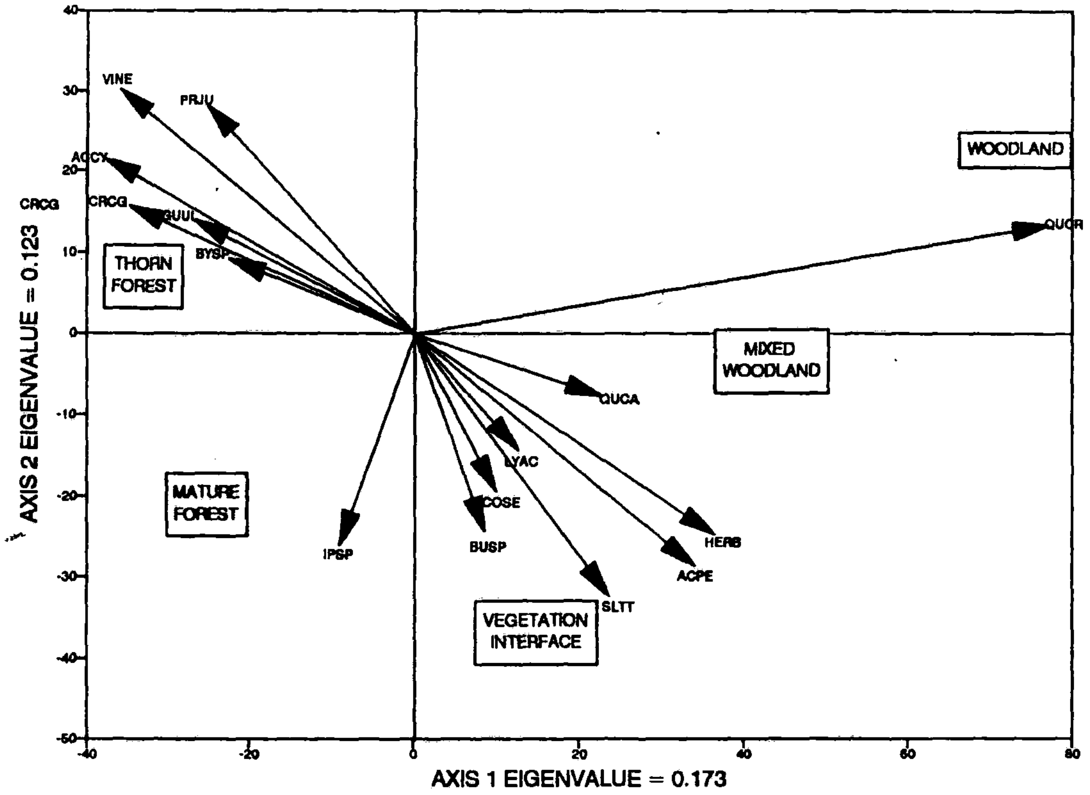
3.4.2.1.4. Spring 1991

The relationship between the bird ordination first three axes and the vegetation was significant in spring 1991 (99 Monte Carlo permutations, $P<0.05$). The first three axes accounted for 48.3 of the variance and the eigenvalues were 0.326, 0.127 and 0.097 respectively. Axis 1 was positively correlated with the small leaved oak *Quercus castanea*, the small leaved thorny trees (*Acacia pennatula* in particular), the herbs and more significantly, with the large leaved oak *Quercus crassifolia* (Table 4.1). The scores of the variables suggests that the first axis represents the gradient from dry forests to oak woodlands.

Axis 2 was positively correlated with the small leaved shrub *Acacia cymbispina*, the vines, and *Prosopis juliflora*, and negatively correlated with *Lysolima acapulcensis*, *Bursera* sp., *Acacia pennatula*, *Impomoea* sp. and the small leaved thorny trees. Again, this axis segregated the oak woodlands from the interface and the thorn forests from the mature forests.

Figures 4.4a and b show the position of the bird species in relation to the variables. The species on the positive side of the abscissa are woodland birds: *Picoides stricklandi*, *Campylorhynchus gularis*, *Trogon elegans*, *Contopus sordidulus*, *Parus wollweberi*, *Piranga flava*, *Psaltriparus minimus* and *Vireo solitarius*. *Regulus calendula*, was also present in the mixed woodland and that is why it was positioned on the negative side of the ordinate (the second axis).

Catharus aurantiirostris, *Dendroica coronata*, *Peucedramus taeniatus*, *Parus wollweberi*, *Aphelocoma ultramarina*, *Contopus pertinax* and *Myoborus pictus* are woodland species more commonly found in the mixed woodland in spring 1991. *Myopagis viridicata*, *Myiarchus cinerascens*, *Tryomanes bewickii*, *Melanotis caerulescens*, *Euphonia elegantissima*, *Icteria virens* and *Catharus guttatus* were found mainly in the vegetation interface between forests and woodlands but also in the dry forests. The rest of the birds are basically forest birds. Those on the positive side of the ordinate (*Denroica petechia*, *Pipilo ocai*, *Catherpes mexicanus*, *Icterus pustulatus*, *Picoides scalaris*, and *Cynanthus latirostris*) were found mainly in the thorn forest, while those on



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80
AXIS 2 EIGENVALUE = 0.123
AXIS 1 EIGENVALUE = 0.173
VINE
PRJU
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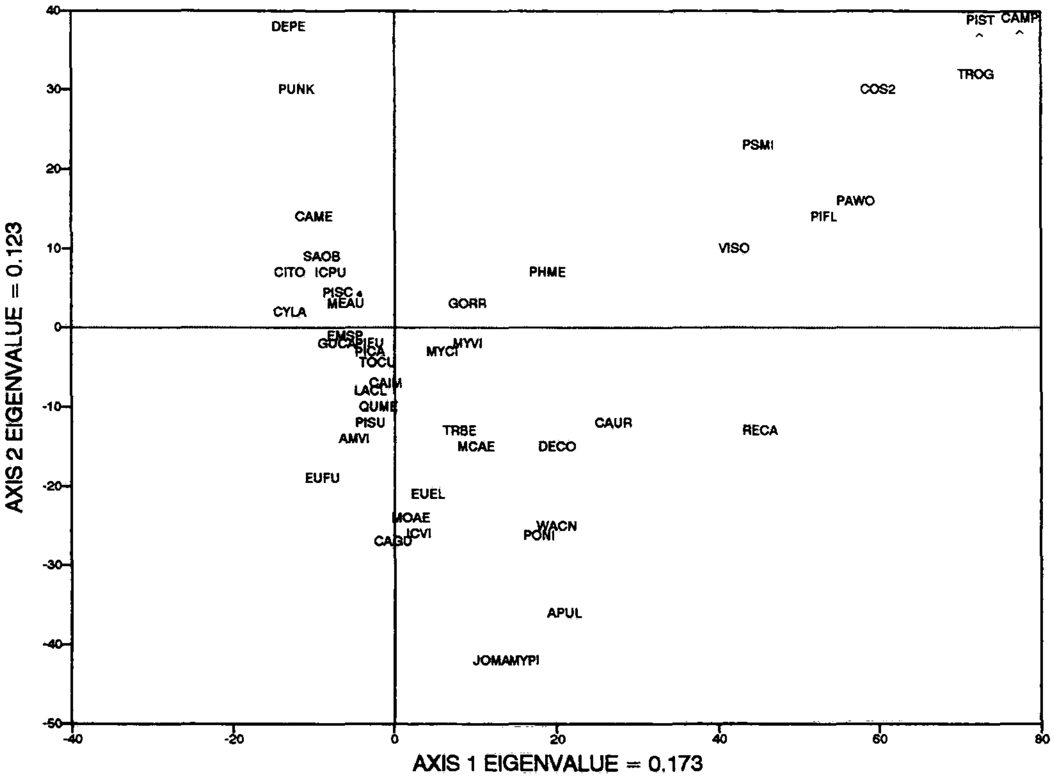
CRCG
GUUL
BYSP
THORN FOREST
WOODLAND
QUCR
MIXED WOODLAND
QUCA
LYAC
COSE
BUSP
IPSP
MATURE FOREST
HERB
ACPE
SLTT
VEGETATION INTERFACE



Figures 4.4a and 4.4b (acetate). Spring 1991 bird species ordination in relation to the vegetation. The interpretation is the same as for Figure 4.1.

the negative side were more frequent in the mature forest (*Eugenes fulgens*, *Amazilia violiceps*, *Pitangus sulphuratus*, *Quiscalus mexicanus* and *Lampornis clemenciae*).

Centurus aurifrons, *Guiraca caerulea*, *Empidonax* sp. *Pipilo fuscus*, *Piaya cayana* and *Toxostoma curvirostrae* were widespread throughout the forests and the vegetation interface.

3.4.2.1.5. Spring 1992

There were 46 bird species recorded in spring 1991 and 57 in spring 1992. Forty one of these were found in both years, representing 98.3% of the first year total abundance and 88.4% of the second.

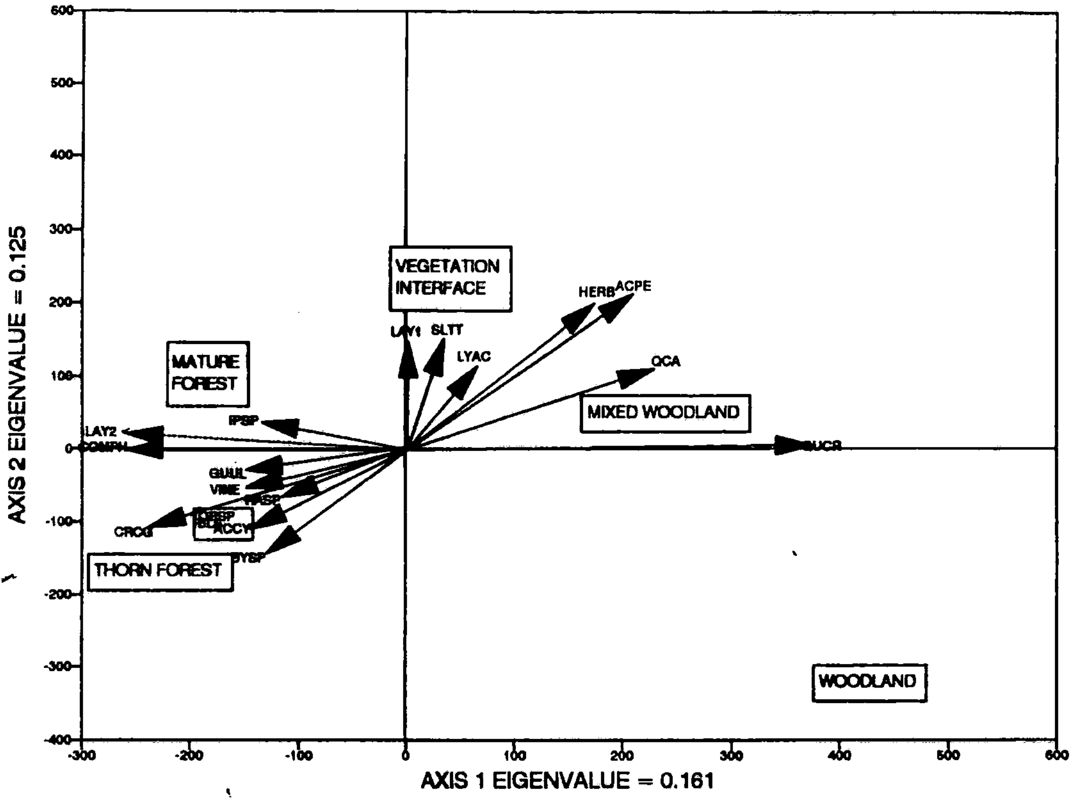
The CANOCO ordination was significant for the first and third axes according to Monte Carlo permutations (99 permutations, $P<0.05$) but not for the second. *Chondestes grammacus* had very high densities in a single plot and therefore was an outlier and was excluded. When it was removed from the analysis, the permutations became significant for the second axis ($P<0.05$). The first three axes accounted for 44.4% of the variance and their eigenvalues were 0.321, 0.171 and 0.154 respectively.

Again, the first Axis depicted the vegetation gradient from forests to woodlands. The first axis was positively correlated with both oak species

(*Quercus crassifolia* and *Q. castanea*), the herbs and *Acacia pennatula*. The *Byrsonima* shrub, *Randia* sp., *Croton-ciliato-glandulosae*, *Guazuma ulmifolia*, *Acacia cymbispina*, the vines, *Opuntia* sp., *Ipomoea* sp., *Heliocarpus* sp., the *Mimosa* tree, the broad leaves shrubs and the 1.0-2.5m vegetation layer were also significant but negatively correlated (Table 4.1).

When *Chondestes grammacus* was removed, the second axis could be interpreted in much the same way as in the first year (although this times the relations are inverted in the plot). It separated the thorn forests from mature forests and the pure oak wood from the mixed woodland and was positively correlated with one of the oak species (*Quercus castanea*), the herbs, *Acacia pennatula*, *Lysolima acapulcensis*, the small leaved thorny trees and the 1.0-2.5m vegetation layer. Negatively, the same axis was significantly correlated with *Croton ciliato-glandulosae*, *Acacia cymbispina*, the *Byrsonima* shrub and the broad leaved shrubs.

Figure 4.5a shows the ordination of the bird species. *Parus wollweberi*, *Trogon elegans*, *Vireo solitarius*, *Piranga flava*, and *Picoides stricklandi* were associated with the oak woodlands, while *Contopus pertinax*, *Euphonia elegantissima*, *Contopus sordidulus*, *Regulus calendula* and *Catharus aurantiirostris*, also woodland birds, were most frequent in the mixed wood. *Molothrus ater*, *Catharus guttatus*, *Icteria virens*, *Pipilo fuscus*, and *Thryomanes bewickii* were common in the interface and *Pitangus sulphuratus*, *Salpinctes obsoletus*, *Guiraca caerulea*, *Cynanthus latirostris*,


AXIS 2 EIGENVALUE = 0.125
AXIS 1 EIGENVALUE = 0.161
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VEGETATION INTERFACE
MATURE FOREST
MIXED WOODLAND
THORN FOREST
WOODLAND
LAY1
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GUUL
VINE
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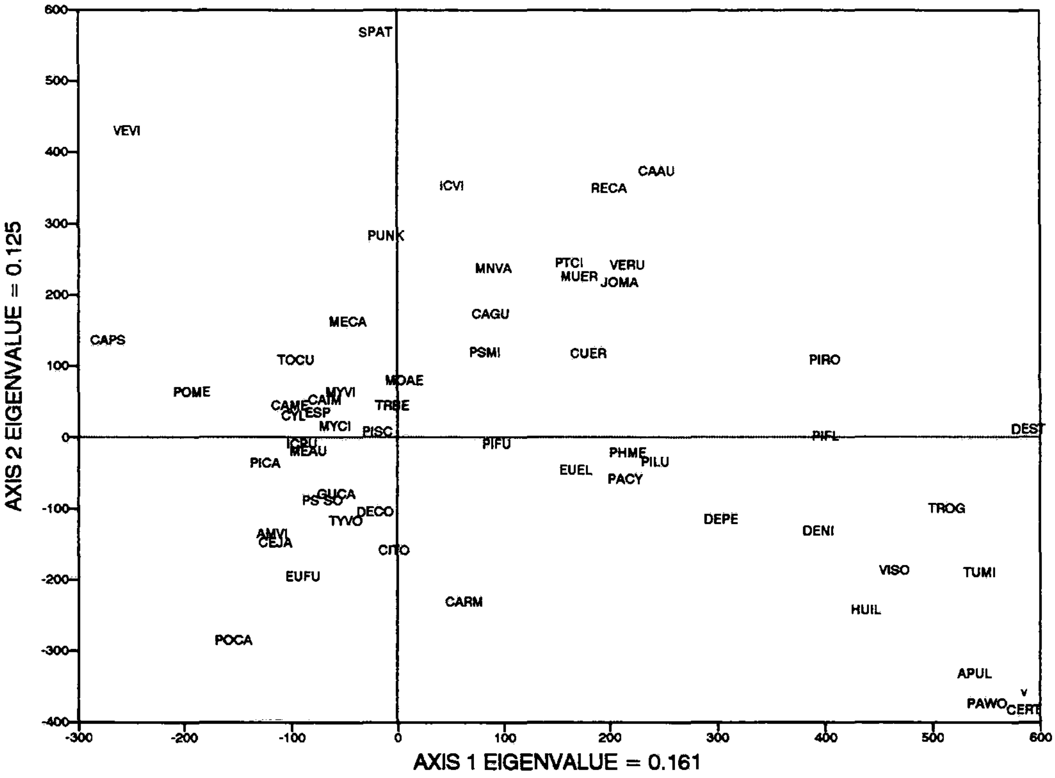


Figures 4.5a and 4.5b (acetate). Spring 1992 bird species ordination in relation to the vegetation. The interpretation is the same as for Figure 4.1. LAY2=1.0-2.5m plant layer; BLS=broad leaved shrubs.

Empidonax, sp., *Centurus aurifrons*, and *Piaya cayana* were found mainly in forests (Figures 4.5a and b).

3.4.2.1.6. Year to year variation in spring

The distribution of the birds in spring of both years was similar. Again, the tendency of the birds to look for the same habitat type was inspected by using both species data sets in the same ordination. The ordination in this case was more subtle. The first axis depicted the vegetation gradient but the second only discriminated the edge from the forests (no distinction was made between the two forest types). The third axis, on the other hand, separated the thorn forests from the mature forests. The ordination therefore, is better explained when the three axes are considered together.

Axes 1 and 2 separated mainly the woodlands from the edges and Figure 4.6 show the ordination of the birds found most frequently in these habitats. *Picoides stricklandi*, *Piranga flava*, *Vireo solitarius* and *Parus wollweberi* were found in the pure woodland. *Aphelocoma ultramarina Trogon elegans*, *Contopus pertinax*, and more obviously *Euphonia elegantissima* and *Psaltriparus minimus*, were more abundant in the mixed woodlands in one of the seasons and in the oak woodlands in the other.

Camptostoma imberbe, *Thryomanes bewickii* and *Icteria virens* had higher abundances in the interface, while *Toxostoma curvirostrae Polioptila melanura* and *Empidonax* sp. were most common in the edge in one year and in the dry forests in the other (Figure 4.6). *Melanotis caerulescens* was more abundant in the edge in the second year and in the mixed wood in 1991. The importance of considering the three main axes is clear when looking at the distribution of *Toxostoma curvirostrae*, *Thryomanes bewickii* and *Empidonax* sp. Each pair of these species (corresponding to the first and second years), appears close together when plotting axis 1 against axis 3 because, in this case, the edges are not clearly segregated from the other vegetation types.

Figure 4.7 shows the ordination with respect to axes 1 and 3. *Salpinctes obsoletus*, *Pipilo ocai*, *Pitangus sulphuratus*, *Molothrus aenus*, *Guiraca caerulea* and *Cynanthus latirostris* where more abundant in huizachales while *Myapigis viridicata*, *Centurus aurifrons* and *Piaya cayana* (less so) were more common in mature forests. *Icterus pustulatus* and *Myiarchus cinerascens* were ubiquitous, showing a slight change in abundances between these habitats. *Picoides scalaris*, *Lampornis clemenciae*, *Amazilia violiceps*, *Aimophila ruficeps* and *Carpodacus mexicanus* on the other hand changed their distribution between thorn and mature forests in the two years. These changes are not obvious in the first two ordination axes, in which both forest types appear grouped together.

Although some of the species described above showed some changes in their distribution, they remained in the same general vegetation type. *Dendroica coronata*, and *Dendroica petechia* on the other hand showed more drastic

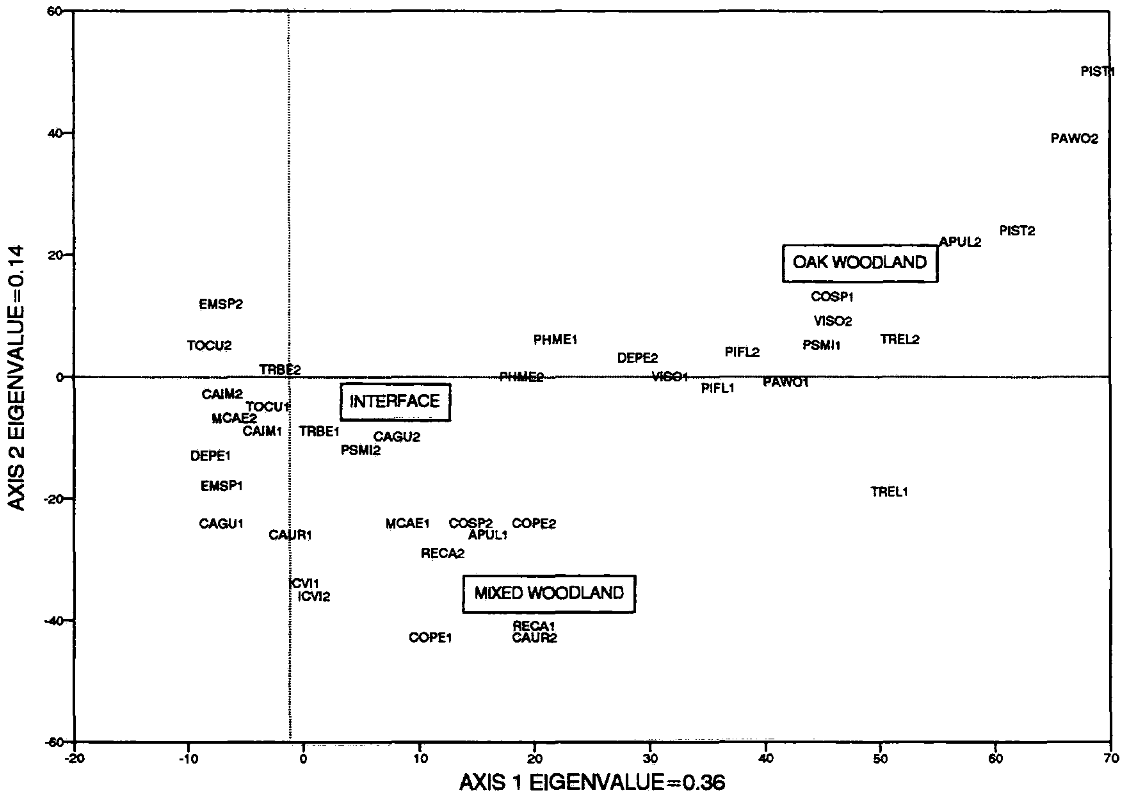


Figure 4.6. Bird species ordination for spring 1991 and 1992. Mature and thorn forest (huizachal) bird species positions are shown in relation to axes 1 and 2.

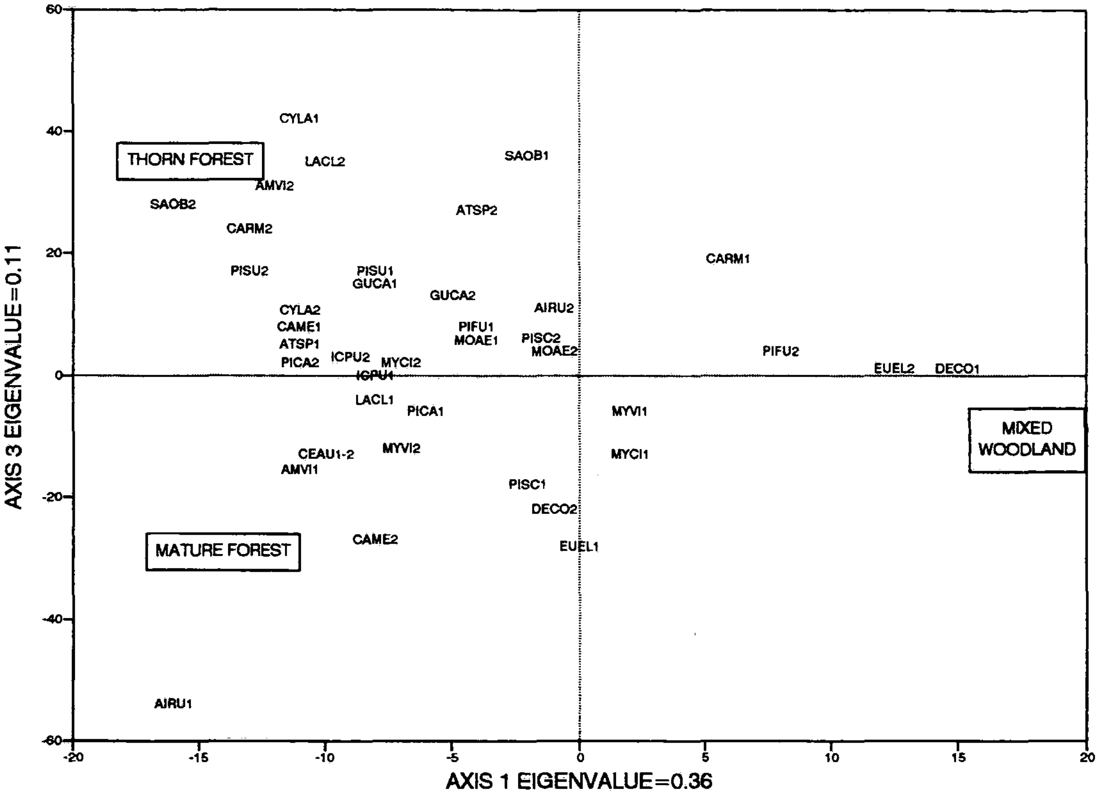


Figure 4.7. Bird species ordination for spring 1991 and 1992. Mature and thorn forest (huizachal) bird species positions are shown in relation to axes 1 and 3.

changes. The first one was common in forests in the second year but was seen mainly in woodlands in the second. *D. petechia* was seen mainly in the forest edge in the first year and in the oak woods in the second (Figure 4.7).

3.4.2.1.7. Statistical significance of the bird species distribution in dry forests

A difference between dry forests and woodlands was expected in the bird species ordination. The distinction between thorn forests and mature forests was more difficult to anticipate. While the overall relative abundances and physiognomy are different between the two forests, floristically they are very similar (with the exception of three plants, all species are found in both of them). Furthermore, both forests had patches which were structurally similar (i.e. mogotes have a similar structure to the mature forests, while open patches in mature forest resemble thorn forests, as was seen in the vegetation section). Since in all the ordinations the mature forests were segregated from the thorn forests, it is clear that the birds recognized the differences (at least to a certain extent).

In order to test the significance of these differences, ordinations were performed for the forests alone (removing the woodlands and the interface plots) and Monte Carlo permutations were performed. In autumn 1991 and both springs, the first axis separated the vegetation types and 99 permutations gave a significant result ($P<0.05$ for autumn 1991 and spring 1992, and $P<0.05$ for spring 1992). The permutations were also significant for autumn 1990 but in this case, the first axis ($P<0.05$) reflected the distribution of *Dendroica coronata*. The test was repeated again for the second axis (which did segregate the vegetation types) and the results were also significant ($P<0.05$). Table 4.2 shows the correlation coefficients between the forest ordination axes and the vegetation variables.

In the final part of this chapter, a brief description of the distribution of the resident species is given.

3.4.2.2. Seasonal variation in the two years

Bird species turnover between spring and autumn was considerable (54% of the total number of species were shared between autumn 1990 and spring 1991, while 66% were shared between autumn 1991 and spring 1992) and therefore it was surprising that the ordinations, which were based on bird densities, segregated the main vegetation associations in both spring and autumn of the two years. In order to study the seasonal changes in the species distribution, ordinations were made in which only the resident species were included.

The results were similar to the ordinations in which all species were included (Figures 4.8-4.11). The first axis represented the vegetation gradient in the four seasons. One extreme of this axis represented the woodlands and, in all cases, the variables which were significantly correlated included the both

Table 4.2. Coeficients for correlations between forest bird ordination axes and significant variables.

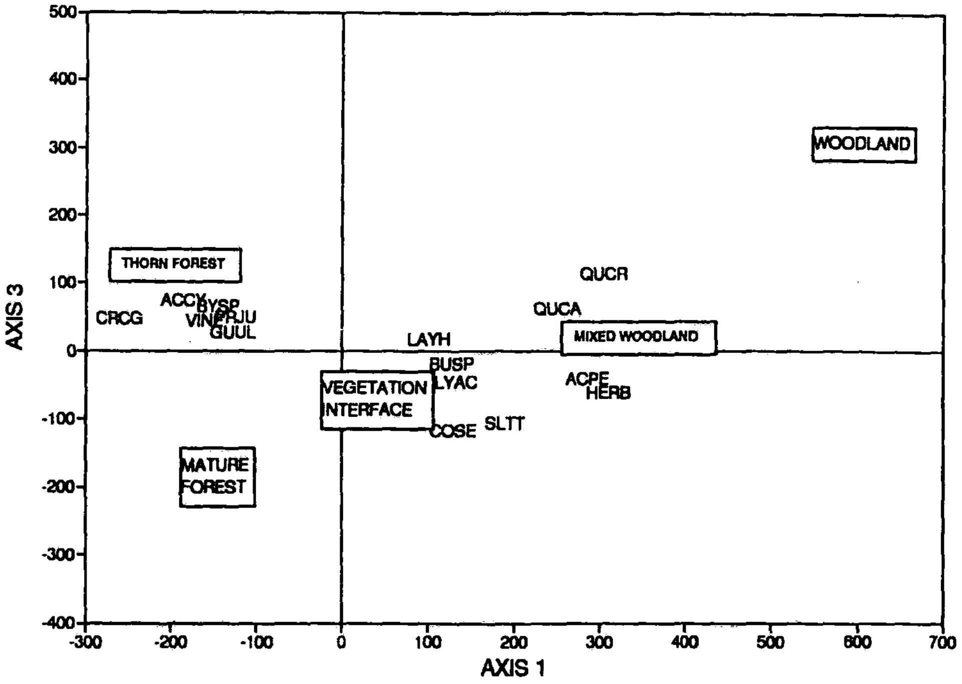
PLANT VARIABLE	Autumn 90 Axis 1	Autumn 91 Axis 2	Spring 91 Axis 1	Spring 92 Axis 1
Prosopis juliflora	-0.245	-0.387	0.352	
Annona muricata			-0.238	
Mimosa galeotti	0.335	0.378	-0.422	-0.420
Bursera sp.	0.252		-0.260	
C. ciliato-glandulosae	-0.239		0.303	
Guazuma ulmifolia				-0.525
Herbs	0.439	0.475	-0.330	-0.371
Acacia macilenta		-0.351		
Acacia cymbispina	-0.231	-0.282	0.425	0.465
Apocynaceae shrub	-0.236			
Byrsonima sp.	-0.217			0.408
Opuntia sp.	0.273		-0.347	
Ipomoea sp.			-0.390	
Ceiba acuminata	0.254			
Vines			0.433	-0.349
Heliocarpus sp.				-0.554
Acacia pennatula	0.429	0.496	-0.419	
Lysiloma acapulcensis	0.241	0.260		-0.547
Mimosa sp. tree		-0.354		
Conzattia sericea		0.387		
Celtis caudata		-0.351	0.341	
Total Cover				-0.483
Composition diversity	0.270		-0.534	
Composition equitability			-0.296	
Small leaved thorny trees	0.373		-0.506	
0-1.0m vegetation layer			0.243	
1.0-2.5m vegetation layer			0.320	
> 2.5m vegetation layer			-0.302	-0.512
Foliage height diversity			-0.283	

oak species, the herbs, *Acacia pennatula*, and in all except spring 1992, the small leaved thorny trees. Negatively, the axis was correlated with *Croton ciliato-glandulosae*, *Acacia cymbispina*, *Guazuma ulmifolia* and the *Byrsonima* shrub. Both, the vines and *Prosopis juliflora* were correlated with the first axis in autumn 1990 and spring 1991, while *Ipomoea* sp. was significant in autumn 1991 and spring 1992.

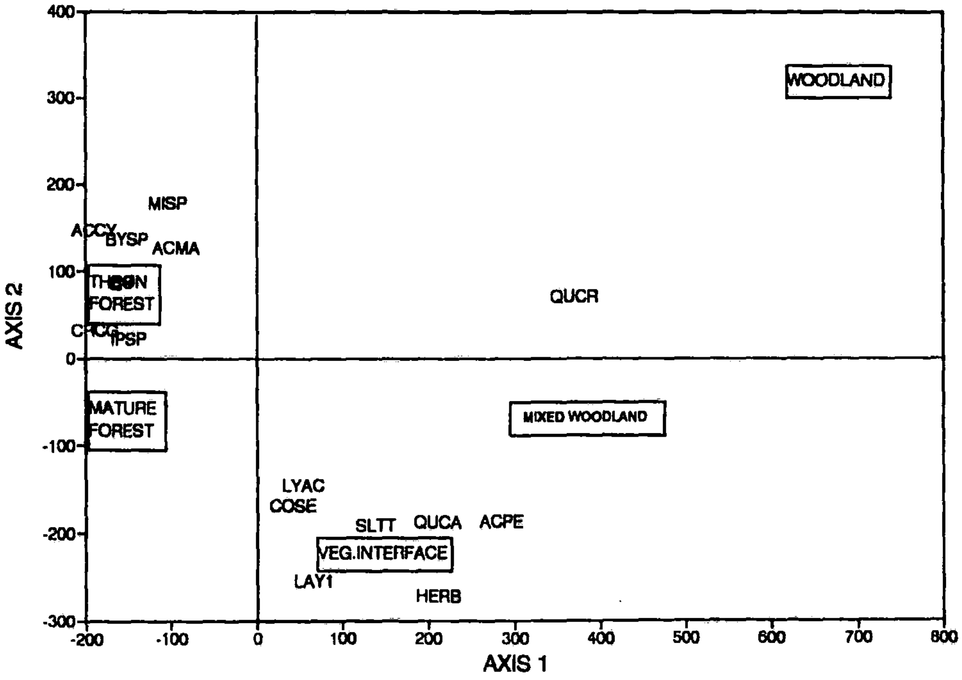
The second axis separated the thorn forests from the mature forests and the mixed woodlands the from oak forests. The interface was also segregated by either the first (in autumn 1990 and spring 1991) or the second axis (autumn 1991 and spring 1992).

Acacia cymbispina, the dominant plant species in thorn forests (huizachales) was significantly correlated with the second axis in all cases (and linked with the thorn forests). Additionally, *Croton ciliato-glandulosae* was also correlated in autumn 1990 and spring 1992, and *Byrsonima* sp. in autumn 1991 and spring 1992.

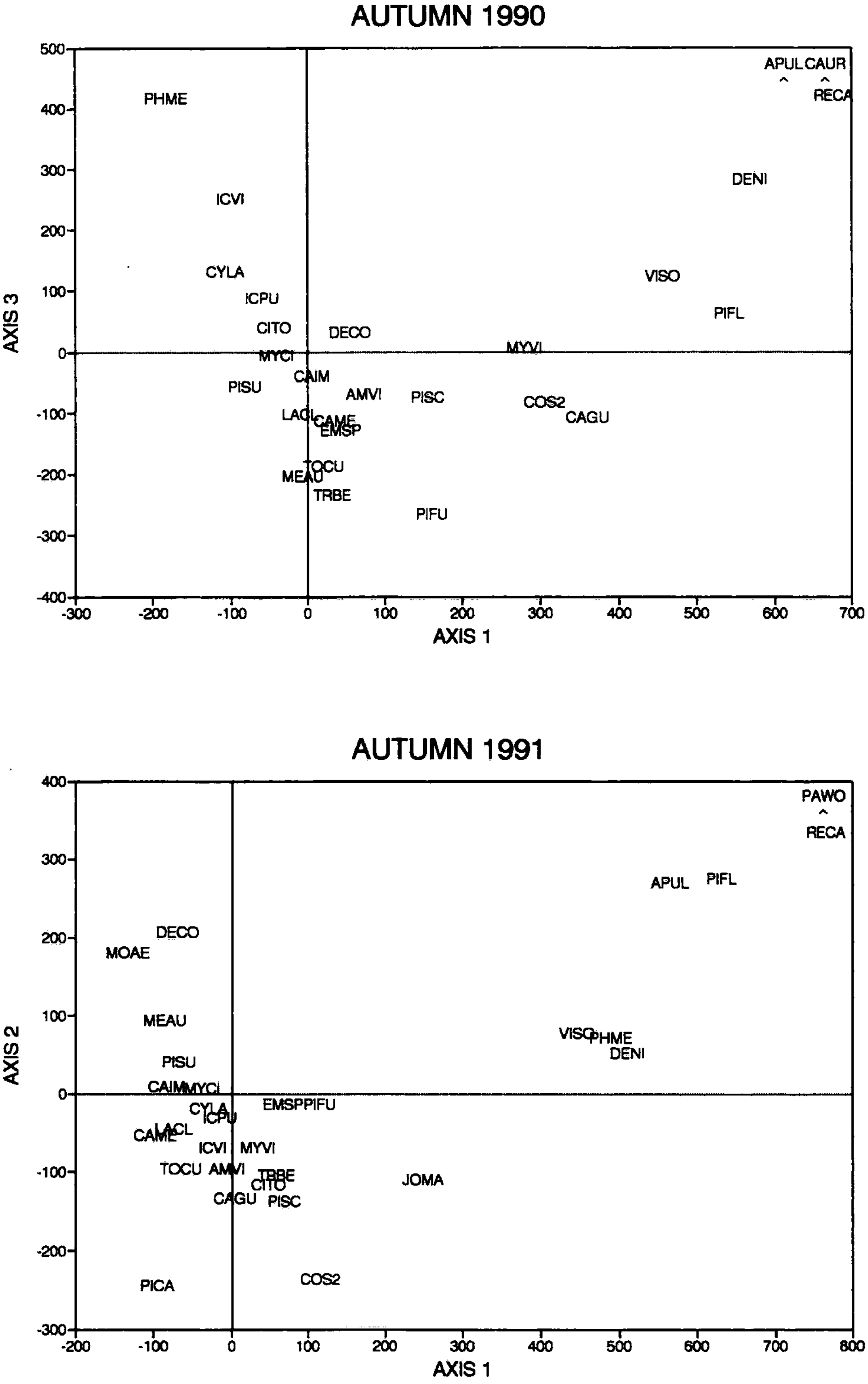
The second axis was also correlated with small leaved thorny trees, herbs and *Lysolima acapulcensis*. These plants, together with *Mimosa galeotti* (which was significant except for in spring 1992) and *Acacia pennatula* (not significant in autumn 1990) represented the interface and the mixed woodlands. Figures 4.8-4.11 show the position of the resident bird species in relation to the vegetation. A brief description of the individual species



AUTUMN 1990

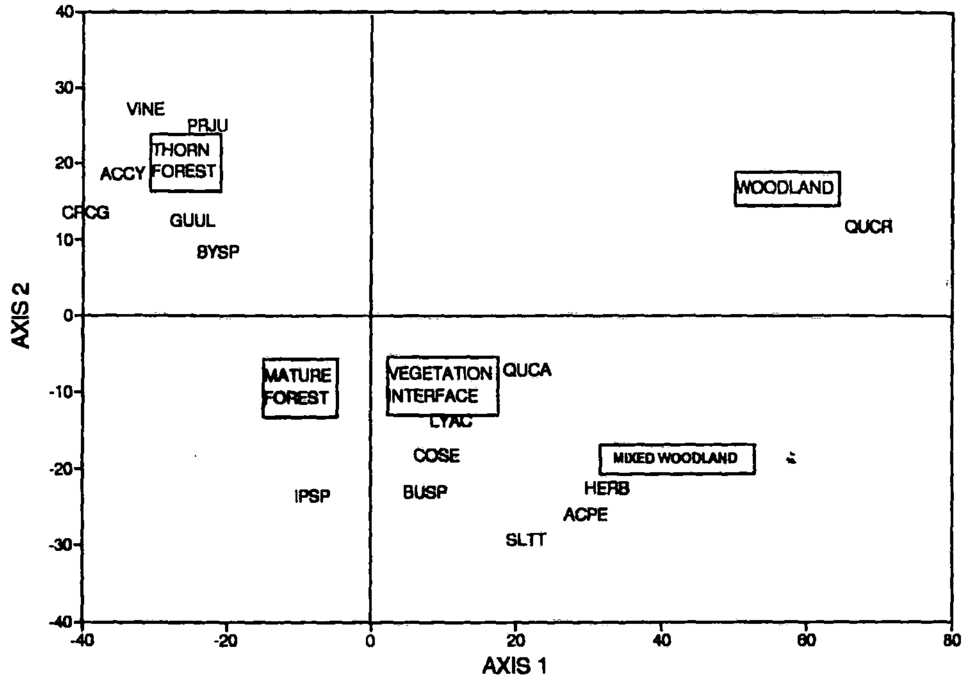


AUTUMN 1991

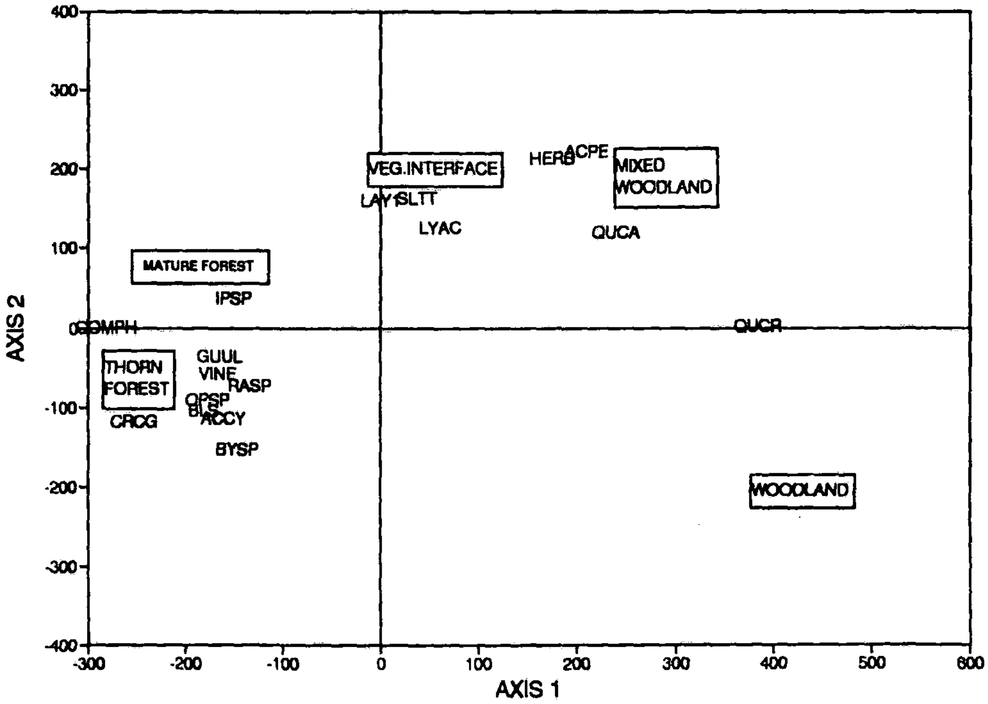


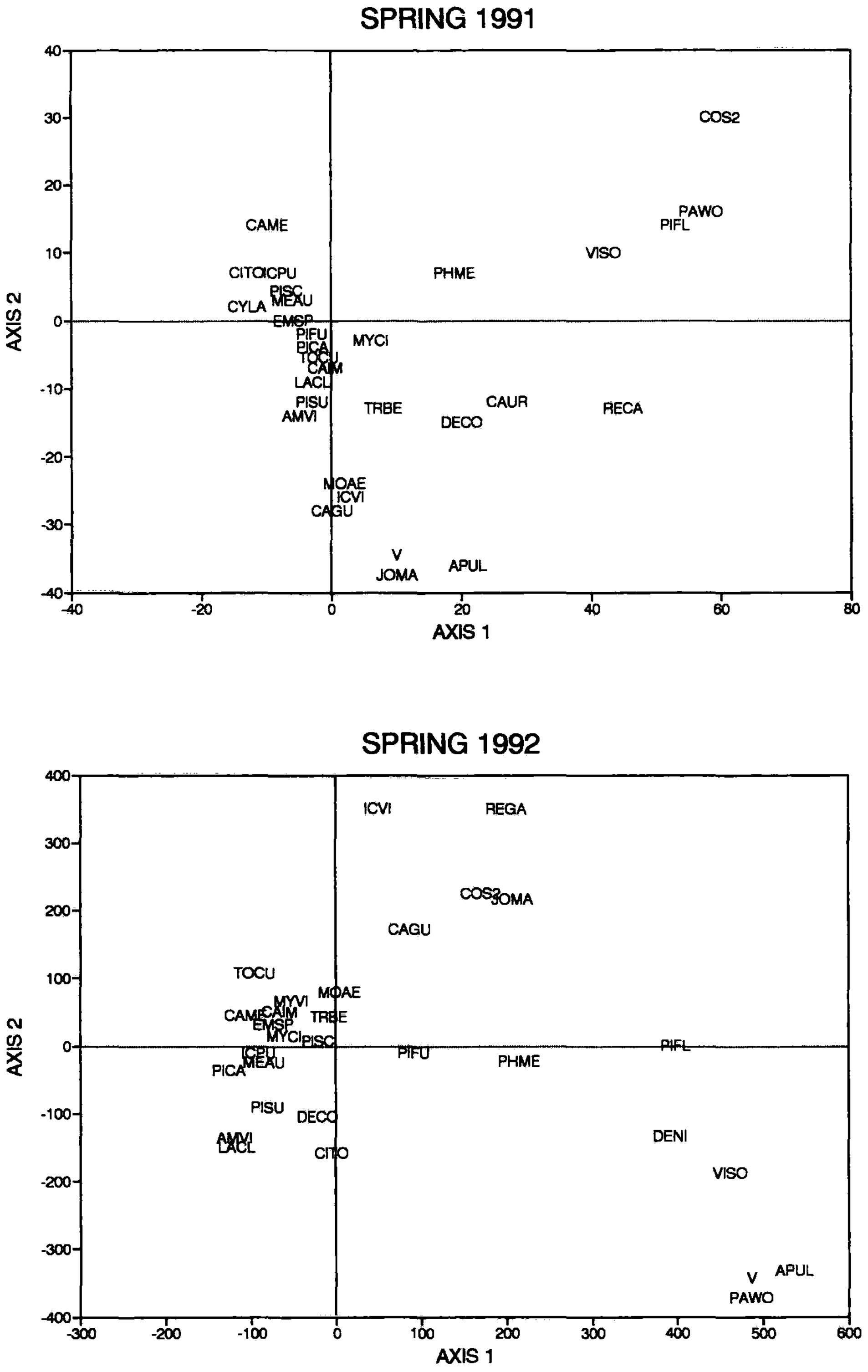
Figures 4.8a-b and 4.9a-b. Autumn bird ordination of resident birds in relation to the vegetation.

SPRING 1991



SPRING 1992





Figures 4.10a-b and 4.11a-b. Spring bird ordination of resident birds in relation to the vegetation.

distribution follows.

Pheucticus melanocephalus. This species distribution is more restricted to the woodlands during Spring, when courtship begins. The rest of the time it is common in other vegetation types.

Cynanthus latirostris. Although ubiquitous, it was commoner in thorn forests as can be seen in its position in the ordination plots in three of the four season (Figures 4.8a,10a and 11a). *C. latirostris* was more randomly distributed within the forests in Autumn 1991 (Figure 4.9a).

Icterus pustulatus is an ubiquitous bird in forests and open sites. As the last species, it was most frequent in thorn forests (with the exception of Autumn 1991 were was common at the vegetation interface).

Aimophila ruficeps is another generalist which was commoner in thorn forests. Its density was so low in autumn 1991 that its position in the ordination for this season is questionable.

Mototthrus aenus is found in altered sites, scrub and edges. It was more frequent in the interface in Spring, and in thorn forests in Autumn 1991.

Myiarchus cinerascens is a flycatcher commonly found in forest edges, open sites, forests and arid regions. It was widely distributed in the forests and the interface and its therefore located near the origin in the four plots (Figs 4.6-9a).

Pitangus sulphuratus is a neotropical flycatcher which changed its distribution between mature (autumn 1990, spring 1991) and thorn forests (autumn 1991, spring 1992).

Dendrocia coronata is a widely distributed warbler which was among the most common species in both autumn 1990 and spring 1992. Its importance in the first season was already mentioned (it had a major effect in the ordination second axis). Its distribution in the two seasons was similar (Figures 4.8a and 4.11a).

Camptostoma imberbe is a small flycatcher common of dry forests. Its distribution seemed more or less random within both forest types and the interface.

Lampornis clemenciae was more frequent in mature forest in the first three seasons but was more abundant in thorn forest in spring 1992.

Centurus aurifrons was another ubiquitous species within forests (found also in the interface).

Catherpes mexicanus is a wren commonly found near cliffs and walls of old building and was more frequently seen in one of the forests which was near a large gully. It was also common in one of the huizachales situated near a reservoir (presumably attracted by the reservoir wall). Its density in spring 1991 was so low that its position in the corresponding plot (Figure 4.10a), might have little to do with its true habitat preferences.

Empidonax sp. The *Empidonax* flycatchers are known for their similarity and are difficulty to identify in the field. Although not completely certain, *Empidonax oberholseri* (a neartical winter visitor) was the species present in spring, while *E. difficilis* was the species seen in autumn. The last species is more typical of woodlands but outside its breeding season, its distribution is more extensive. *E. difficilis* had a similar distribution in both seasons where it was present, showing larger densities in one of the mature forests vegetation subtypes. It was also present in thorn forests in the second year. *E. oberholseri* was very rare in spring 1991 and was found mainly in mature forests in spring 1992.

Myopagis viridicata is a neotropical flycatcher which, although present in woodlands, was only found in the mixed woodland of the study sites in one season (autumn 1990). It was rare but widespread in the following autumn and in spring was most common in mature forests.

Toxostoma curvirostra. This thrasher is a forest species found most frequently in the vegetation interface and mature forests, particularly in plots with sparse vegetation.

Tryomanes bewickii (a wren) is another forest species which was seen mainly in the interface between forests and woodlands.

Amazilia violiceps is a ubiquitous species. Together with the other hummingbirds, its densities were much higher in Autumn. Its low densities in Spring do not allow a reliable description of its main habitat in the study site.

Picoides scalaris is a common woodpecker in North America and is frequent in deserts. It was found in all forest and interface sites. The main difference between the two seasons was that it was more abundant in mature forests and the interface in Autumn, and in mature forests in Spring.

Pipilo fuscus is a widely distributed sparrow in Mexico. It was most abundant in the interface in this study.

Contopus sordidulus. This flycatcher was present mainly in the mixed woodlands. Although it was found in the oak woodlands in spring 1991 it was particularly rare in this season and therefore its distribution is not very reliable.

Contopus pertinax is common in woodland edges. It was more abundant in the mixed woodland of the study site.

Catharus guttatus is a thrasher which was common in the interface and the mixed woodlands.

Vireo solitarius was found in the mixed and pure oak woodlands in all seasons.

Dendroica nigrens is a warbler which was also found in both, mixed and pure woodlands.

Finally, *Regulus calendula*, *Aphelocoma ultramarina*, *Catharus aurantiirostris*, *Parus wollweberi* and *Piranga flava* were all mainly present in the oak woodlands, although *C. aurantiirostris* and *R. calendula* are also found in forests and edges in other parts of the country.

The present account of the bird distribution in the study sites suggests a general pattern through time. Although no species were found exclusively in either of the main vegetation types, and most species (particularly the forest birds) were also found in the vegetation interface (some even were more common here), the distribution of the birds was very similar in both years.

3.4.2.3. A recapitulation of the bird species distribution

As a recapitulation of the species distribution, Tables 4.3 and 4.4 show the relative bird abundances on the habitats defined by the ordination. Four levels of abundance were used in these Tables: 0-1.0, 1.0-3.0, 3.0-9.0 and >9.0 birds per 10 sample units. The birds species arrangement in the tables was based on their scores in the ordination axis.

Since the ordination plots combined the plots for both huizachales on one extreme of the second axis (third axis in autumn 1990), and the plots for coatales and forests (mature forests) on the other, the average densities for both huizachales and the two forests were used in the Tables.

The distribution of most bird species was similar between years. Furthermore, with a few exceptions, the resident species had similar distributions between seasons. The exceptions include four spring forest species which were more frequently found in the vegetation interface and mixed woodlands in autumn (*Amazilia violiceps, Eugenes fulgens, Picoides scalaris* and *Empidonax* sp.), and three autumn forest birds which became more ubiquitous in spring (*Myiarchus cynerascens, Aimophila ruficeps* and *Camptostoma imberbe*). *Pheucticus melanocephalus*, although uncommon in autumn was seen in forests in 1990 but spring it more common in woodlands. *Dendroica coronata* was very uncommon in spring 1991, but as in autumn, it was present in forests and woodlands in spring 1992.

Table 4.3. Autumn relative bird densities according to the CANOCO ordination. Horizontal lines divide groups of birds with similar distributions.

	HUIZACHAL		MOGOTE		FOREST		INTERFACE		MIXED WOODLAND		OAK WOODLAND	
Bird species	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991	1990	1991
C. grammacus	o											
M. aenus		o				+						
V. celata	o	o				+	+					
C. latirostris	ooo	oo	oo	oo	oo	oo	oo	o	+	o		+
P. sulphuratus	oo	+	o		o	+	o	+				
P. caerulea	ooo	ooo	ooo	ooo	oo	oo	ooo	ooo	oo	oo		+
A. alexandri	oo	ooo	oo	oo	oo	oo	ooo	o	oo	o	o	+
A. ruficeps	o	ooo	+	ooo	+	oo	o	+	+	ooo		+
M. cynerascens	ooo	ooo	ooo	oo	ooo	oo	ooo	oo	oo	oo		+
D. coronata	oo	ooo	oo	ooo	ooo	oo	o	o	oo	+	oo	oo
C. lucifer	o	o	oo	o	o	o	o	+	o			
I. pustulatus	o	oo	oo	oo	oo	o	o	oo	o	o		+
L. clemenciae	+	+	o	o	o	o		o	+			
C. imberbe	oo	oo	oo	o	oo	o	o	oo	o	+		
V. virginianae	+			+	o	o			+			
C. aurifrons	+	+	+	+	+	+	o	+	+			
T. curvirostrae	+	+	+	+	+	+	o	o	+			
T. bewickii	o	o	+		o	o	oo	o	+	oo		+
C. mexicanus	o	+	+		o	+	o	+	o			
Empidonax sp.	o	oo	o	o	oo	oo	oo	oo	oo	oo		o
Carpodacus sp.		+		+		+		+		o		
V. ruficapilla	o	o		+	o	o	oo	o	o	+		+
A. violiceps	oo	oo	o	o	oo	oo	oo	oo	oo	oo		
E. fulgens	+				+	+	o	+	o	oo		
S. rufus		oo		oo	+	+	+	ooo	+	o		
P. scalarix	+	+	+		+	+	o	+	o	o		+
P. cayana						+				+		
P. fuscus		o	+				o	o	o	o		
M. viridicata		+		o	+	+	+	+	+	+		
Contopus sp.					+	+	+	o	o	o		
C. guttatus						+		+	+			
P. minimus					+				+		o	
T. migratorius										+		+
A. beryllina		+			+	o	o	oo	oo	oo	o	o
V. solitarius				+		+	+		o	+	o	+
M. picta							+		+		+	
P. flava									oo	+	+	o
D. nigrescens					+				oo	o	o	o
A. ultramarina											o	+
R. calendula									o	o	o	o
C. aurantirostris									+			
P. melanocephalus	+				+					+		+
I. virens			+		+			+				
D. townsendi										+		o
C. pertinax								+		+		+
P. wollweberi						+						oo
M. varia										+		

+=0-1.0; o=1.0-3.0; oo=3.0-9.0; ooo=>9.0 numbers per 10 sample plots.

Table 4.4. Spring relative bird densities arranged according to CANOCO ordination.

Bird species	HUIZACHAL		MOGOTE		FOREST		INTERFACE		MIXED WOODLAND		OAK WOODLAND	
	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
C. latirostris	o	o		+		+		o		+		
G. caerulea	oo	oo	oo	oo	o	oo	o	oo	o	o		o
T. vociferans		o		o		+		+		+		
A. violiceps	+	o		+	+	+		+				
L. clemenciae	+	o			+				+			
P. sulphuratus	+	+	+		+		+	+	+			
Car. mexicanus	+	+			+		+		+		+	
A. ruficeps		oo		ooo	+	oo		oo		oo		o
D. petechia	o		oo	+			+		o	+		+
Q. mexicanus			o				o					
C. aurifrons	+	o	o	o	o	o	o	+	+	+		
P. cayana	o	+	o	+	o	+	+	+			+	
M. kieneri	o				+		+	+	o			
C. mexicanus	+	+	+	+	+	o		+	+	+		
E. fulgens	+	o		o	+	+		+				
I. pustulatus	ooo	ooo	ooo	ooo	ooo	oo	ooo	oo	oo	oo	+	+
P. scalaris	oo	o	o	o	o	o	o	o	o	o		+
D. coronata		oo		+		oo	+		+	+		o
Empidonax sp.		o	o	oo	+	oo		o	+	o		
P. fuscus	oo	oo	oo	o	oo	o	ooo	oo	oo	oo		oo
T. curvirostrae	oo	o	oo	oo	oo	oo	oo	oo	oo	o	+	
C. imberbe	oo	oo	oo	o	oo	oo	oo	oo	oo	oo		
M. cynerascens	o	oo	o	oo	oo	oo	oo	oo	oo	oo	o	+
T. bewicki	o	o	+	+	oo	oo	oo	oo	oo	oo	+	+
M. viridicata	+	o	+	o	o	oo	o	o	o	o	o	
M. caerulescens	+	+			+	+	o	+	+	+	+	
C. guttatus					+	+		+	+	+		+
M. aenus	+	+	o	+	+	+	o	+	o	o		+
P. nigrescens				+	o	+	+		o			
I. virens	+				o		o	o	oo	+		
S. atrogularis								o		oo		
P. cinereus						+		+		o		
E. elegantissima				+		+			o	+		+
C. pertinax								+	+	o		o
M. picta									o			
P. melanocephalus	+	o	o	o	+	+	o	o	o	oo	oo	oo
P. minimus	+	o			+	+		o	+	oo	oo	+
P. cyanea		o								o		+
P. ludoviciana				+		+				+		+
V. solitarius					+				o	+	o	o
C. aurantirostris							o		o	+	o	
Contopus sp.						+		o	o	o	oo	o
T. migratorius		+						+		+		oo
A. ultramarina									+	+		o
R. calendula								+	+	o		+
P. flava								+	oo	o	oo	oo
P. wollweberi									o		oo	oo
T. elegans									+	+	o	o
D. nigrescens										+		o

+=>0-1.0; o=1-3; oo=3-5; ooo=5-10 birds per 10 sample plots

It is interesting that the ordination of the sample units using the bird densities coincide with the main vegetation types in the study area in both years. There is clearly one group of birds which is found in woodlands (*Turdus migratorius, Amazilia berillyna, Vireo solitarius, Myoborus picta, Piranga flava, Dendroica nigrescens, D. townsendi, Parus wollweberi, Aphelocoma ultramarina, Regulus calendula* and *Trogon elegans*) and other which includes dry forest birds from both huizachales and mature forests (*Cynanthus latirostris, Pitangus sulphuratus, Icterus pustulatus* and *Lampornis clemenciae* in both years, *Chondestes grammacus, Vermivora cellata, Polioptila caerulea, Archilochus alexandri, Calothorax lucifer* and *Vermivora virginianae* in autumn, and *Guiraca caerulea, Tyranus vociferans, Carpodacus mexicanus* and *Piaya cayana* in spring) (Tables 4.3 and 4.4).

The bird composition in huizachales and mature forests was similar in all seasons. Nevertheless, the bird species ordination separated the sample units belonging to each vegetation type. This division was in part due to differences in bird densities (some bird species having relatively higher abundances in huizachales while others had higher densities in forests) but mainly to the combination of habitats which loose groups of bird species shared. In autumn, for example, one group of species represented by *Polioptila caerulea, Archilochus alexandri* and *Aimophila ruficeps* had relatively lower densities in forests, but was abundant in both huizachales and the vegetation interface in both years. *Dendroica coronata, Calotorax lucifer, Icterus pustulatus, Lampornis clemenciae* and *Camptostoma imberbe* represent another group which had high abundances in huizachales, mogotes and mature forests and low in the interface and mixed woodlands. A third group can be recognized by being commoner in mature forests, the vegetation interface and mixed woodlands (*Toxostoma curvirostrae, Tryomanes bewickii, Catherpes mexicanus, Empidonax* sp., *Vermivora ruficapilla, Eugenes fulgens, Selasphorus rufus, Picoides scalaris, Pipilo fuscus, Myiopagis viridicata, Contopus* sp. and *Catharus guttatus*) (Table 3.3).

In spring, three forest groups can be distinguished. The first one is a loose group of birds with low densities represented by *Cynanthus larirostis, Guiraca caerulea, Tyranus vociferans, Amazilia violiceps, Lampornis clemenciae, Pitangus sulphuratus, Carpodacus mexicanus, Aimophila ruficeps, Dendroica petechia, Quiscalus mexicanus, Centurus aurifrons, Piaya cayana, Melozone kieneri, Catherpes mexicanus* and *Eugenes fulgens*. These are birds with relatively higher densities in huizachales although the last five species were present in dry forests (huizachales and mature forests) and the vegetation interface (Table 3.4).

The second group included seven species with an ubiquitous distribution in dry forests but which also were common in the mixed woodlands. These species are: *Icterus pustulatus, Picoides scalaris, Dendroica coronata, Empidonax* sp., *Pipilo fuscus, Toxostoma curvirostrae* and *Camptostoma imberbe*. *Myarchus cynerascens, Thryomanes bewickii, Myiopagis viridicata* and *Melanotis caerulescens* conform another group which was present in all dry forests, but had higher densities in mature forests, the vegetation interface and mixed woodlands. *Catharus guttatus, Molothrus aenus, Polioptila melanura, Icteria virens, Spizella atrogularis, Ptilogonis cinereus* and *Euphonia elegantissima* were seen mainly in mature forests, the vegetation interface and the mixed woodlands (Table 3.4). As in autumn, the first species of this group had some individuals present in huizachales, while the last ones were mainly present in the mature forests, the interface and the mixed woodlands.

3.4.3. Discussion

The debate on the nature of communities (i.e. self- sufficient "super-organisms" or collections of individualistically distributed organisms) has ceased to be a controversial topic in this days. Nevertheless, the issue is still discussed in general ecology texts (Whittaker 1975, Krebs 1985). It is certain that different communities tend to be more autonomous than others. Sabo (1980), for example, found that species tended to be found in discrete groups in his study sites. On the other hand, Bond (1957), Whitmore (1977) and Smith (1977), working in North American forests, found an individualistic distribution in the ordination plots of the bird species they studied.

Even though communities are seldom discreet, there is a tendency for groups of species to have similar distributions corresponding with the vegetation physiognomy (Hutto 1985). From an ornithological point of view, it might well be true that biomes or vegetation types correspond to habitat types (Hutto 1985).

The effect that the general appearance of vegetation can have on bird species distribution, has been well illustrated in the altitudinal studies in Peru and Mexico by Terborgh (1977) and Navarro (1992). Navarro (1992) found that species turnover was as high as 30% between some of the habitats in his altitudinal study in the Sierra Madre del Sur. In contrast to the results of Terborgh (1977) and Noon (1981), he also found competition to have only a slight effect and suggests that the vegetation "physiognomical classes" are more important for the distribution of the birds.

In this study, the discontinuity between woodland and forests was obvious in both the plant physiognomy and the bird community. Only 16%, 28%, 32% and 34% of the bird species were shared between dry forest and oak woodlands in the four seasons studied. On the other hand, although the segregation between the two forest vegetation types was evident in the ordinations, the bird species distribution was less clearly divided. In fact a uniform distribution similar to those shown by Whitmore (1977) and Smith (1977) was found in the ordination plots. In contrast to the differences between woodlands and forests, 77%, 75%, 66% and 64% of the bird species were shared between thorn and mature forests in autumn 1990, spring 1991, autumn 1991 and spring 1992. The more abundant species were found in both vegetation types, the differences consisted on higher of lower relative abundances in either habitat.

The two types of distribution are shown in Figures 4.1-4.4. Woodland birds appear clustered together, and separated from the forest birds along the first axis. The ordination across the ordinate, representing the division between thorn and mature forests, shows no such abrupt separation.

The combination of species in the vegetation interface between forests and woodlands was anticipated. This is a common phenomenon well documented by Ornelas (1992) and Terborgh (1977). Perhaps more interesting was the fact that species such as *Icteria virens*, *Toxostoma curvirostrae*, *Thryomanes bewickii* and *Pipilo fuscus* had higher densities in the interface plots. The mixed woodland which shares 44% of the plant species with the forests, but only 23% with pure oak forests (and therefore could be seen as and interface as well) also contained four species with peak densities: *Contopus sordidulus*, *Contopus pertinax*, *Catharus guttatus* and *Vireo solitarius*. All of these birds, are common in edges and open vegetation which may explain their higher numbers in transitions.

3.4.3.1. Habitat changes in time and space

Quite independently from the type of distribution found in any given season, habitat shifts are expected to occur throughout a year. These changes have been the subject of studies in North American deserts (Raitt and Pimm 1976), Fennoscandian woodlands (Jarvinen and Vaisanen 1976) and in a succession from heathland to pine plantations in Belgium (Bilke 1984).

Raitt and Pimm (1976) compared changes between years, seasons and habitats. They found that a number of bird community properties kept changing in time: overall abundance, composition, relative abundance, and "impact on other components of the ecosystem". These variations did not occur only between seasons, but in the same season in different years as well. Rotenberry and Wiens (1990), in their detailed studies in shrubsteppe vegetation, also found intense changes in the bird community attributes.

Bilke (1984) found that during the breeding season, bird species tend to be more restricted in their distribution, suggesting that availability of good nesting sites might be one of the reasons of this pattern (e.g. hole-nesting species need woodland habitat during their breeding period).

There is also a theoretical reasons to expect changes in habitat use in time. When densities are high, birds may profit by occupying sub-optimal habitats, thus avoiding resource competition in high quality sites (Fretwell 1972, Fretwell and Lucas 1969).

There were seasonal changes in the present study although the bird species distribution in the same season but in different years was remarkably similar (Figures 4.3 and 4.6). Although 31% of the autumn species were present in one year, these only represented 2% and 6% of the densities for autumn 1990 and autumn 1991. In spring 34% of the species were found in one year, but they only represented 2% and 12% of the densities for the first and second year. Because of migration, the changes between seasons were greater and only 53% of the species found between Autumn 1990 and Spring 1991 were present in both years (corresponding to 61% and 83% of the autumn and spring densities). Similarly, only 60% of the species found in the first year were found in both autumn 1991 and spring 1992, respectively corresponding to 79% and 82% of the abundances.

Variations between the bird communities of forests and woodlands were obvious, nevertheless it was difficult to predict the extent of the changes between the main forest habitats. Roth (1979) for example, studied four brush-grasslands in North America and found substantial differences in bird species composition and relative abundance. Morrison *et al.* (1986), studied the resident birds of North American temperate woodlands. Although they found differences "in the overall pattern of habitat use" between winter and summer, "...an unbiased classification procedure separated all species poorly".

Some authors (Wiens 1985, Wiens *et al.* 1986) have not found a direct relationship between vegetation and bird distribution in harsh environments.

If "within habitat" variation in densities and composition were large enough at the present study sites, a combination of thorn and forest plots would appear in the ordinations. As it happened, within habitat variation was smaller than variation between habitats and therefore, the majority of thorn forest plots were segregated from the mature forests (Figures 4.1-4.4).

The relatively less extreme environmental conditions of dry forests, in comparison to those of deserts or shrubstepe, may partially explain the moderate changes in the birds species distribution. This is partly confirmed by the studies of Raitt and Pimm (1976) and Roth (1979). The former, found that bird densities tended to fluctuate more strongly in the driest locations of their desert sites (i.e. differences between years were greater in deserts, where a high variation in productivity is characteristic). Roth (1979) compared the bird communities in different vegetation types in America and found that chronological fluctuations in composition and abundance were stronger in harsher environments, resulting in a more erratic distribution.

3.4.3.2. The relationship between the plant structure and composition and the bird distribution

Due to the enormous influence of the work by MacArthur and MacArthur (1961), during two decades, most bird community ecologists, thought structure was, a decisive influence controlling the bird species community organization (Pearson 1975, Recher 1969). Chapter 3.3 explores the relationship between the vegetation and the bird species diversity in the study area.

Fuller and Henderson (1992) sustain that, since the paradigm was so widely accepted, many ecologists tried to explain bird species distribution (in addition to diversity) in terms of simple measures of the vegetation structure. Bibby *et al.* (1989) and Fuller and Henderson (1992) agree, in the sense that floristic relations might be obscured by loss of information resulting from condensing vegetation structure and composition into one or two indices. In fact, the important role floristics may have on the bird species distribution has been confirmed in many studies (James and Wamer 1982, Rotenbery 1985, Peck 1989, Bibby *et al.* 1989).

Rotenberry (1985) suggests that the inconsistencies in the structure-floristic controversy may have to do with the scale of the study. Physiognomy may play a role at a gross habitat scale but, at more local levels, plant composition may be more important. The reason for this is that when Rotenbery and Wiens (1980) compared different communities of the same basic vegetation type, but on a much larger spatial scale, their results shown that structure was playing an important role in the bird communities.

Rotenberry (1985) also mentioned studies made at local scales in which floristics were found to be more significant than vegetation structure. On the other hand, Bibby *et al.* (1989) and Peck (1989) worked on large areas containing different habitats and still found floristics to play a dominant role.

Some plant species have an important effect on bird species diversity in the present study, as was shown in chapter 3.3. This section shows that particular plant species were more significant than the vegetation structure in the determination of the bird species distribution as well. This can be seen in Tables 4.1 and 4.2 in which the correlations between the variables and the ordination axes are shown. These relationships seem to hold regardless of scale, since the area and vegetation types covered in Table 4.1 were much larger than those of Table 4.2 (in which the interface and the woodlands were excluded), and still, the structural factors did not play a predominant role. In fact, when ordinations were made using only the structural variables, the eigenvalues were much lower than when using plant composition. This was also true regardless of scale.

Fuller and Henderson (1992) and Peck (*pers. comm.*) think that the inconsistencies over the importance of either floristics or physiognomy, might have to do with the statistical methods used. The data for some plant species might be non-linear while traditionally, bird community-vegetation studies are based on regression methods. According to this the use of non-linear dependent methods (such as DCA and CCA) may results in different patterns, generally elucidating the role of composition.

Some ecologists have found direct connections between certain aspects of the vegetation and the bird distribution. Fuller and Henderson (1992) for example, proposed that more than narrow fringes and single trees had a disproportionately effect and were beneficial in British plantations. Similarly, Peck (1989) proposed that adding a few trees of particular species would boost the bird diversity.

Still, the significant variables should be regarded with caution. They may be the results of statistical artifacts, particularly when many intercorrelations between the matrix data set are found (Norusis 1988). Fuller and Henderson (1992) say that without experimentally manipulating the variables, it is difficult to say which components of the vegetation affect the distribution of different bird species. Moreover, abundance studies (which are the basis for distribution and diversity analyses) say nothing about the direct use of the vegetation by birds, which would help explain the importance of the individual plant variables. Few bird distribution reports include results of the vegetation use by the bird species. One exception is the work of by Peck (1989), who complemented her distribution studies with foraging behaviour observations. She found that those sites with higher bird abundances included trees which were particularly rich in invertebrates and birds were frequently seen foraging on them.

This does not mean that bird species distribution is directly linked with food, particularly at regional or larger scales, but at a local scale, food abundance might indeed play an important role. Rotenberry (1985) found it likely that those plants to which the variation in bird densities are likely to respond are those which provide more food. Raitt and Pimm (1976) found a link between the distribution of certain guilds (particularly the seed-eaters) and food availability.

There also seems to be a connection between bird composition and food availability in this study. Insectivores and hummingbirds, for example were more common in autumn, when there are more flowers and more invertebrates. In spring, where more fruit is to be found, frugivores and opportunistic species were more abundant.

The bird species diversity chapter (chapter 3.3) suggested that those plots with high small leaved tree covers as well as high covers of some individual plant species, like *Acacia cymbispina* and other small leaved plants and *Ipomoea* sp. had higher bird species diversity. Small leaved trees had high lepidopteran larvae and homopteran abundances, while *Ipomoea* sp. has large nectar producing flowers which attract hummingbirds as well as other birds (which presumably look for insects attracted by the flowers).

In this section the first axis of the bird species ordination was negatively correlated with *Croton ciliato-glandulosae*, *Acacia cymbispina* and *Byrsonima* sp. in all seasons. *Guazuma ulmifolia* and the vines were correlated with the first axis in autumn 1990 and in both springs. Positively, the first axis was correlated with *Quercus castanea, Quercus crassifolia*, the herbs, *Acacia pennatula* and the small leaved thorny trees (the latter was correlated with both autumns and spring 1991).

The second ordination axis was correlated with the *Conzatia sericea* (with the exception of spring 1992), the herbs, *Acacia pennatula* (with the exception of autumn 1990), *Lysolima acapulcensis* and the small leaved thorny trees on one side, and with *Acacia cymbispina* on the other (Table 4.1).

Although some of the significant variables in this study may simply represent the main vegetation types, others are used by birds directly. As a first step to understand the importance of the individual plant variables in the distribution of the bird species, the use of individual plants by the birds was examined. The results of this survey will be described in the following chapter.

3.5. Guild determination and foraging use of the plant species

3.5.1. Introduction

The previous chapter showed that bird distribution is associated with the plant species represented in the main habitats. Chapter 3.3 also suggested that bird species diversity might be related to food availability. In this section the foraging strategies in the four study seasons will be compared. The importance of the favoured plant species used in foraging in the distribution of the bird community will be examined in chapter 3.6. The analysis will be based mainly on groups of birds with similar foraging strategies. The approach used to quantify bird foraging behaviour is explained in the methods.

Foraging behaviour is an indirect method to study food resource utilization. This strategy has been widely used in bird studies because of the relative ease with which information can be gathered (Wiens 1989). Bird foraging tactics have been used to study competition between members of the same guild (MacArthur 1958, Morse 1980, Feisinger 1976), niche relationships in one vegetation type (Sabo and Whittaker 1979), niche comparisons between vegetation types (Sabo and Holmes 1983), adaptive syndromes (Ekhardt 1979), resource partitioning and seasonality in diferent temperate forests (Rabenold 1978), foraging preferences and conservation (Peck 1989) and habitat structure and foraging behaviour (Robinson and Holmes 1982, 1984).

Guilds are groups of species attaking common resources using simmilar techniques in a given habitat (Root 1967) and foraging behaviour has also been useful to help identify guilds.

Although there is always some degree of subjectivity (Hawking and MacMahon 1989), the guild concept is useful because comparisons of the functional organization between communities can be investigated even when no common species are shared (Terborgh and Robinson 1986). Additionally, guild studies are valuable in identifying the resources determining the structure of animal communities (Terborgh and Robinson 1986). Poulin *et al.* 1994 used this approach to determine the influence of the change in resources in the bird structure throughout the year. Eckhardt (1979) used guilds as a tool in order to study the ways in which insectivores birds capture their prey. He suggested that every species fits into adaptive syndromes, manifested, among other characteristics, as particular foraging tactics. This syndromes may be shared by a number of species which, regardless of their taxonomic affinities, belong to the same guild.

Guilds are frequently identified *a priori*, based on diet, foraging behaviour, foraging location, nest site, body size, taxonomy, singing location, resting location and habitat (Eckhardt 1979, Terborgh 1977, Diamond 1975, Raitt and Pimm 1976). Although preliminary, these surveys can provide a useful account of community structure and organization (Wiens 1989). More quantitatively, other studies have relied on food stomach contents (Poulin *et* *al.* 1994) to classify the bird species into guilds.

A posteriori categorizations rely more commonly on foraging observations (Wiens 1989). The birds are then classified according to their foraging tactics, and grouped in clusters which represent the guilds (Holmes, Bonney and Pacala 1979, Landres and MacMahon 1980 and Recher and Holmes 1985).

In this section, general guild patterns will be discused first. Guilds then will be determined on the basis of foraging observations and then seasonal changes in foraging tactics will be analysed.

3.5.2. Results

3.5.2.1. Guild densities between seasons; a preliminary analysis

As a preliminary analysis, the birds found on the study area were grouped into guilds according to their feeding habits as recorded in the literature (Bent 1963a, 1963b, 1963c, 1964a, 1964b, 1964c, 1964d, 1965a, 1965b, Arizmendi *et al.* 1990, Rappole *et al.* 1993) as well as to their distribution in the study area (species must be sympatric to be included in the same guild). Appendix 5.1 shows the list of these *a priori* identified groups as well as the species belonging to each of them. Although the number of guilds are large, it must be remembered that two quite distinct vegetation areas are included in the study (dry forest and oak woodlands) and some species with similar feeding tactics are not sympatric.

The categories include **hummingbirds** (with ten species), **granivore-insectivores** (four species), **ground insectivores** (two species), **forest omnivores** (seven species), **forest insectivores** (three species), **wood probers** (which look for food mainly on the surface of branches and the trunk of trees and consists of five species), **woodpeckers** (which feed both on the invertebrates on the surface and the inside of tree trunks and branches; three species in the study area), **frugivore-insectivores** (two species), **flycatching hawkers** (these birds feed by giving short sallies or jumps mainly within the canopy of trees and shrubs and consist of four species), **flycatchers** (in contrast to flycatching hawkers, individuals of this group sally form a branch and catch flying insects in the air, four species were found in forests and woodlands, and two more which foraged in woodlands), **ubiquitous insectivores** (11 species), **woodland insectivores** (six species) and **woodland omnivores** (seven species).

Figures 5.1-3 show the densities of each guild in the main vegetation types by season. The vegetation in the study area were grouped into the groups obtained by the plant classification (the thorn forests and the mature forests data were pooled for the general descriptive purposes). These habitats are: thorn forests, mature forests, the vegetation interface between forests and woodlands, the mixed woodlands and the oak woodlands. Figure 5.1 present the densities for hummingbirds, ground insectivores, flycatchers and

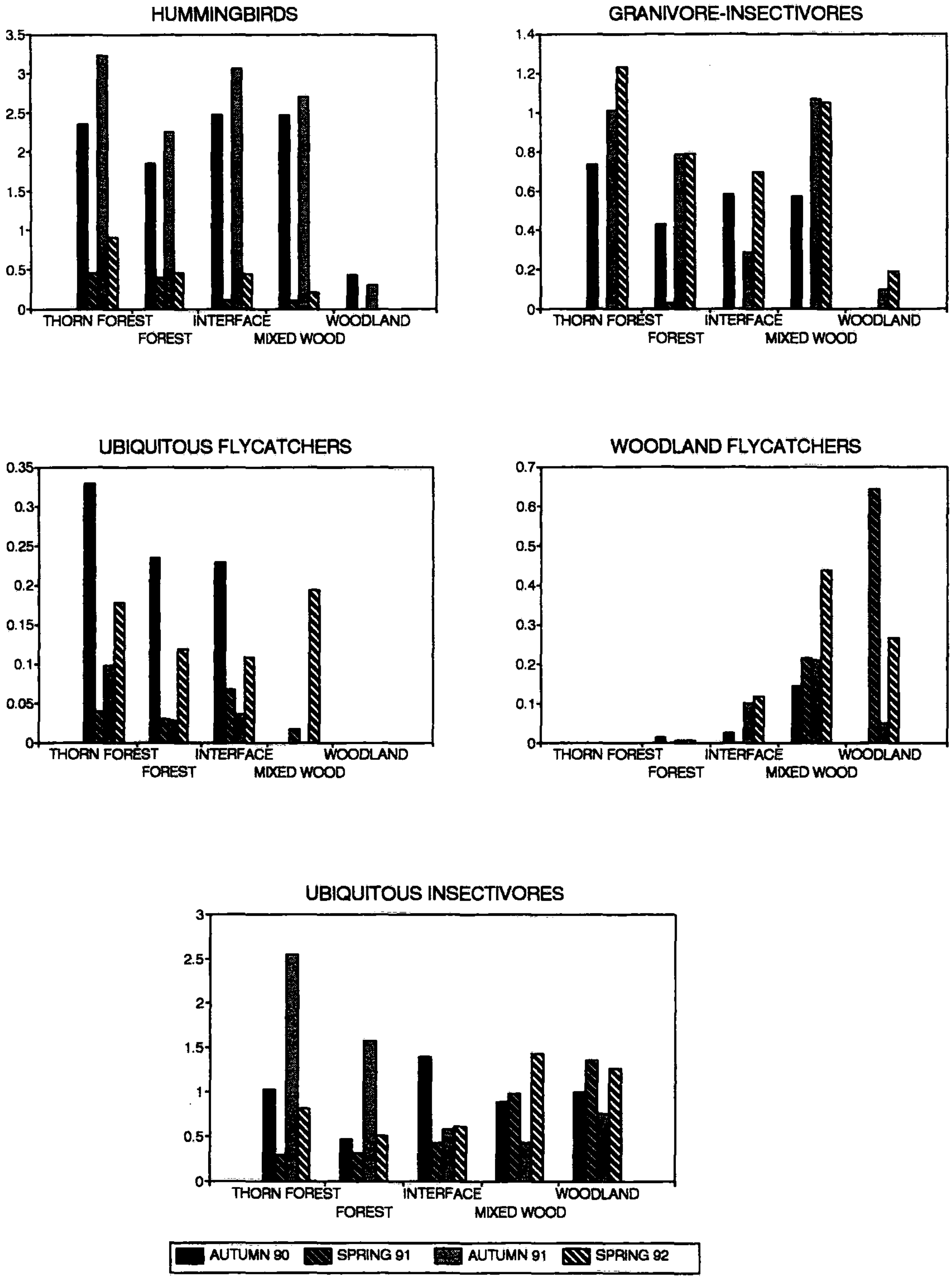


Figure 5.1. Seasonal densities of a priori identified guilds in the main vegetation types (numbers per sample unit).

ubiquitous insectivorous. Hummingbirds were more common during autumn and had higher densities in thorn forests and the interface in both years.

Ground insectivores were more abundant in spring. They were more abundant in forests than in woodlands in the first spring but the reverse prevailed in the second spring (Figure 5.1).

One group of flycatchers was widespread, while another was more abundant in the woodlands (Figure 5.1). The first group was more frequent in autumn 1990 and spring 1992. The second was more abundant in both springs (the first year in woodlands and the second in the interface).

Insectivores were divided according to their distribution. The first group was found almost exclusively in forests (Figure 5.2), the second only in woodlands (Figure 5.3) and the third was ubiquitous (Figure 5.1). The three guilds were more abundant in autumn, just after the rainy season, when the plants have not yet shed their leaves. Woodland insectivores were commonest in the woodland patches of the interface in the first year, and commonest in pure woodlands in the second. Ubiquitous insectivores were commoner in the autumn in forests but this pattern was reversed in spring, in which they were more abundant in the interface and particularly in the woodlands. Forest insectivores were more abundant in thorn forests in both autumns and less so in small leaved forests and the interface.

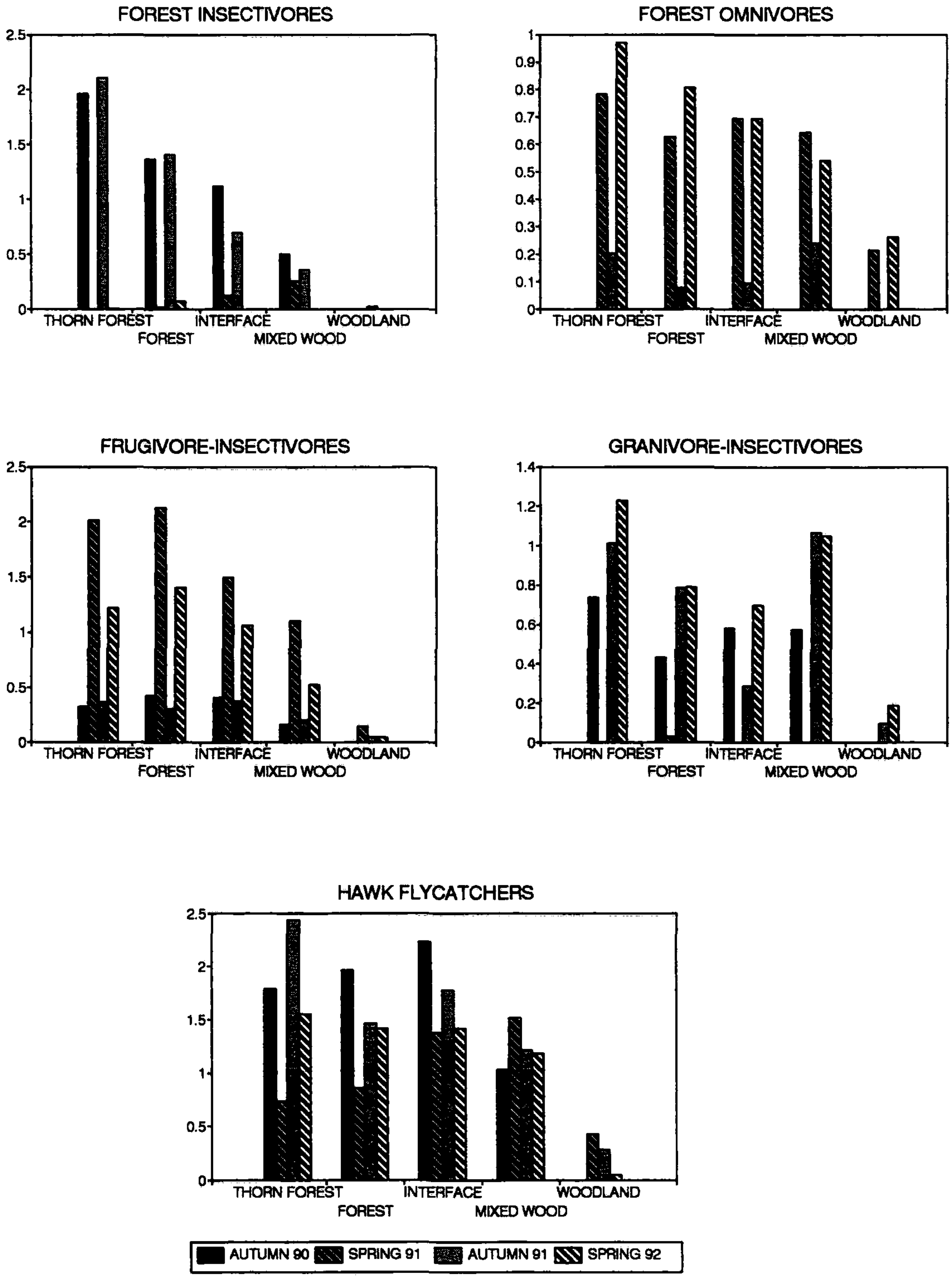


Figure 5.2. Seasonal densities of a priori identified guilds in the main vegetation types (numbers per sample unit).

Omnivorous birds were also divided in two groups, also according to their distribution. Figures 5.2 and 5.3 shows the densities of forest and woodland omnivores respectively. In both cases their abundances were higher in spring.

Frugivore-insectivores were more abundant in spring. Interestingly, in both spring 1991 and 1992, the higher densities were in broad-leaved forests, where more fruit is available (Figure 5.2).

Granivores were almost absent during spring 1991. Their abundances were similar in the other three seasons and were commoner in thorn forests and the interface. They were rare in woodlands (Figure 5.2).

Flycatching hawkers (Figure 5.2) were slightly more abundant in the autumn. They were commoner in thorn forests.

Woodpeckers were more abundant in spring (Figures 5.3), particularly in thorn forests. In the autumn of the first year there were two abundance peaks: one in small leaved forests and another in the interface. Wood gleaners were similarly abundant in all seasons (Figure 5.3). These densities peaked in small leaved forests and the interface.

3.5.2.2. Formal guild determination

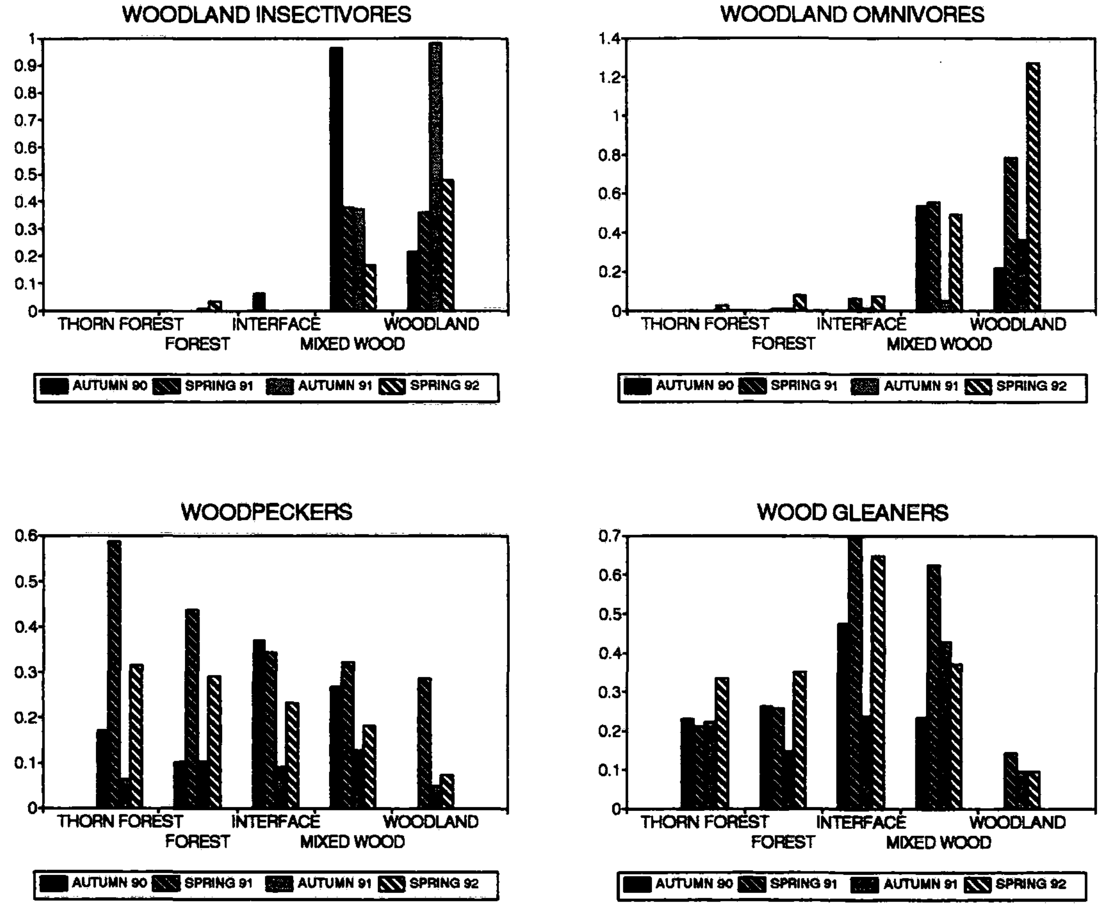


Figure 5.3. Seasonal densities of a priori identified guilds in the main vegetation types (numbers per sample unit).

Section 2.1.2 in the methods explained how the foraging observations for the bird individuals were obtained. Foraging activities were grouped in four categories (maneouvre, height, target and plant species used) and the guilds were obtained based on these categories.

The birds species for which 10 or more foraging observations were obtained were also grouped in guilds using multivariate analyses. Both, ordinations and classifications were used and they were based on a matrix in which the rows represented the bird species and the columns the foraging categories.

Birds were often difficult to observe when they were looking for food. This was mainly because of the density of vegetation in autumn and because of the low densities of bird species in spring. Since the low number of observations made a formal guild determination somehow ambiguous, the analyses were used mainly to help in the guild identification and to corroborate the *a priori* classification.

Because many birds were inconspicuous, only 33 species were included in the classification, 25 were present in each season. These included 49% of the species present in autumn 1990, 53% of those found in autumn 1991 and 40% of those found in both spring 1991 and 1992. With respect to abundance, the birds included represented 61% of the individuals found in autumn 1990, 76% of those in autumn 1991, 74% of the individuals found in spring 1991 and 69% of all of the birds counted in spring 1992.

Table 5.1. Number of foraging observations per bird species. Species with less than nine observations for plant species were omitted. Codes are given in the appendix. Foraging observations include height at which the bird was foraging, type of manouvre used to obtain food, attack sustrate (i.e. flower, bark), and plant species on which a bird was searching for food.

BIRD SP.	H	M	A	P	BIRD SP.	H	M	A	P
AIRUO2	16	8	15	45	ICPUP1	61	38	37	101
AIRUP1	15	20	21	21	ICPUP2	46	25	24	55
AIRUP2	50	79	70	88	JOMAP2	5	11	11	12
AMVIO1	22	18	24	33	MOAEP1	11	10	10	9
AMVIO1	36	60	58	69	MYCIO1	28	13	9	42
APULO1	10	10	10	12	MYCIO2	28	41	21	45
APULO2	7	7	9	17	MYCIP1	53	45	29	65
APULP2	22	4	5	28	MYCIP2	49	30	34	71
ARALO1	14	9	15	24	PAWOO2	15	20	14	20
ARALO2	51	68	71	82	PAWOP2	11	7	7	17
CALUO2	7	10	10	10	PCINP2	13	19	20	40
LACLO1	21	28	31	32	PHMEP1	12	7	15	15
LACLO2	9	18	28	21	PHMEP2	38	29	34	52
LACLP1	33	48	33	50	PIFLO2	9	15	15	17
LACLP2	15	23	23	14	PIFLP1	27	17	10	38
CHGRO1	7	10	10	10	PIFLP2	24	17	18	39
CHGRP2	8	25	16	23	PIFU?O1	5	5	5	3
COSPP1	16	16	10	19	PIFUP1	22	10	32	27
COSPP2	5	6	6	20	PISCO2	13	12	12	13
CYLAO1	18	13	18	27	PISCP1	11	13	9	16
CYLAO2	9	11	10	18	PISCP2	13	16	18	19
DECOO1	74	73	72	100	POCAO1	104	105	64	150
DECOO2	112	66	71	186	POCAO2	113	156	107	208
DECOP1	8	7	6	11	PSMIO2	12	12	6	15
DECOP2	108	30	42	135	PSMIP1	22	23	7	24
DENIO1	22	21	16	38	PSMIP2	24	10	10	30
DENIO2	16	20	20	39	RECAO2	8	10	5	22
DETOO2	14	32	17	18	TRBEO2	9	8	8	11
EMSPO1	19	11	8	17	TRBEP1	17	17	19	18
EMSPO2	22	44	20	39	TRBEP2	20	16	19	25
EMSPP1	14	10	7	22	TYVEP2	6	6	6	34
EMSPP2	24	16	18	45	VECEO2	9	20	10	16
EUELP2	9	6	6	11	VERUO1	40	38	25	59
EUFUO2	24	25	13	19	VERUO2	31	58	39	57
SERUO2	41	68	59	70	VEVIO1	9	14	10	17
GUCAP1	15	11	30	32	VEVIO2	8	10	5	9
ICPUO1	7	7	7	16	VISOO2	5	9	9	12
ICPUO2	7	4	11	13	VISOP1	15	11	6	15

H=height, M=maneouvre, A=target, P=plant sp., O1=autumn 1990, O2=autumn 1991, P1=spring 1991, P2=spring 1992.

Table 5.1 is a list of the species included with the number of observations for each of them.

3.5.2.2.1. Between year species comparisons

A first ordination was made in order to examine the resemblance in foraging behaviour of the paired species (those present in the same season but different years). Therefore, one data set contained the information of all the species included in both autumns, and another included the foraging information for the species in both springs. In subsequent analyses all species with enough foraging observations, including those present in only one year, will be incorporated.

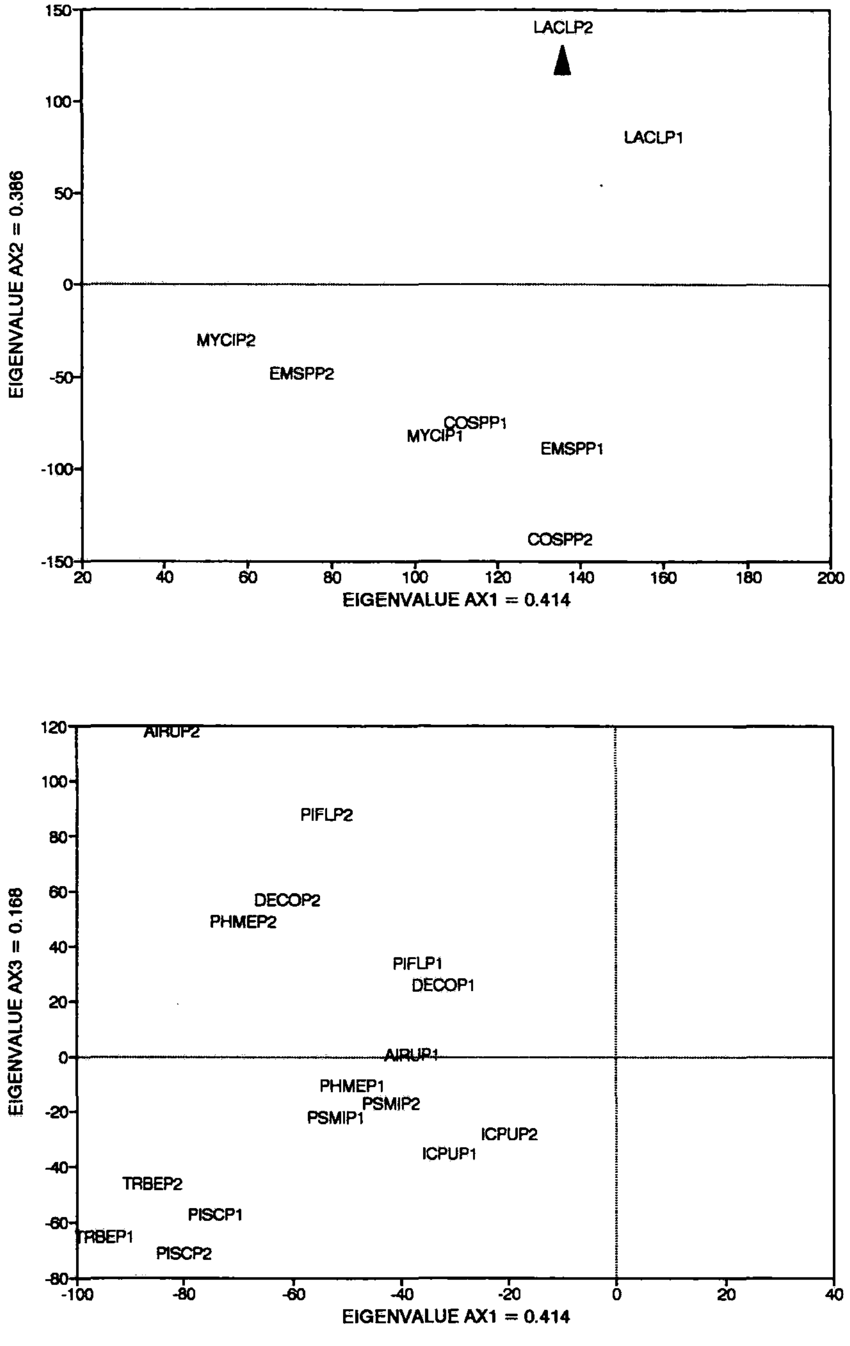
Assuming bird species should respond in a similar way under the same circumstances, the consistency of the results represent one way to test the strength of the information collected during the study period. Although some differences were expected (which will be investigated bellow), major disagreements would mean that the observations were insufficient to detect the foraging strategies statistically. Furthermore, an agreement in the data between years means that inter-season comparisons can be performed with confidence.

3.5.2.2.2. Ordination of paired species in spring

There were 12 species present in both springs that were included in the analysis. The first axis of the ordination separated the hummingbirds, flycatchers and hawkers of both years from the rest of the bird species. The second axis separated mainly the hummingbirds from the flycatchers. The third axis segregated the birds in three main groups (besides the hawkers and flycatchers which were segregated in the first axis): granivores and one group of gleaners (*Aimophila ruficeps, Piranga flava* and *Dendroica coronata*), a second group of gleaners and frugivores (*Psaltriparus minimus* and *Icterus pustulatus*) and woodpeckers and probers (*Thryomanes bewickii* and *Picoides scalaris*). The importance of variables contributing to the main divisions is going to be discussed bellow. The relevance of the ordination at this point is that most species maintained the same positions in the ordination space in both years (Figures 5.4 and 5.5).

3.5.2.2.3. Ordination of paired species in autumn

As with the spring comparisons, the position of the 14 pairs of species included in the autumn ordination space remained remarkably constant in both years (Figure 5.6). The first axis separated the hummingbirds form the rest and the second separated the hawkers form the gleaners. The woodland gleaners (*Aphelocoma ultramarina* and *Dendroica nigrescens*), although to a lesser extent, appear segregated form the frugivorous species (*Icterus pustulatus*) and forest and ubiquitous gleaners (*Dendroica coronata, Vermivora virginianae, Vermivora ruficapilla* and *Poleoptila caerulea*). Again,



Figures 5.4. and 5.5. Spring paired ordination of birds according to foraging tactics. First and second axes are shown in Figure 5.4 and first and third axes are shown in Figure 5.5. Suffix added to bird species names (mnemonics explained in Table 5.2.) correspond to season: P1=spring 1991, P2=spring 1992.

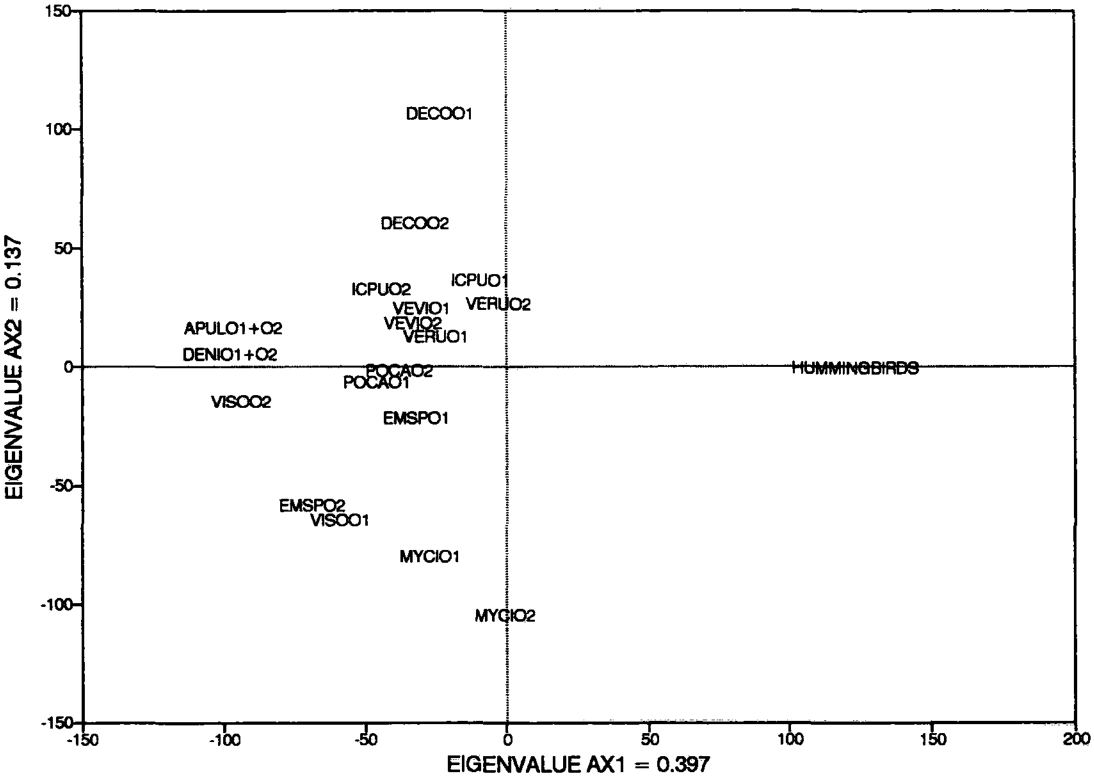


Figure 5.6. Autumn paired species ordination of birds according to foraging tactics. First and second axes are plotted. Suffix added to bird species names (mnemonics explained in Table 5.2) correspond to seasons: O1=autumn 1990, O2=autumn 1991.

these results confirm the consistency of the bird species position in autumn.

3.5.2.3. Analysis of the pooled two year data for each season

The former ordinations show that paired species occupy similar general foraging niches between years. These results also suggest that the data are reliable to continue further with a formal guild determination. Since no major disagreements between the position of species were found, it is also justifiable to pool the data for the next analyses (adding the data for both autumns and for both springs). This procedure was done by Holmes, Sabo and Pacala (1979), although they also pooled the observations from different seasons in order to define the bird guilds in their study areas. Nevertheless, they admitted finding some seasonal differences in the foraging patterns (also between sexes). In this study, the guild determination is based on the pooled data for each season.

3.5.2.3.1. Spring guilds

The results of the spring foraging behaviour ordination are shown in Figure 5.7. Eigenvalues for the first three axes were 0.421, 0.287 and 0.187.

The first axis, divides the flycatchers and hawkers from the woodpeckers and the wren (in particular *Centurus aurifrons*). The variables with the highest positive ordination scores are drilling, large branch and trunk and those with

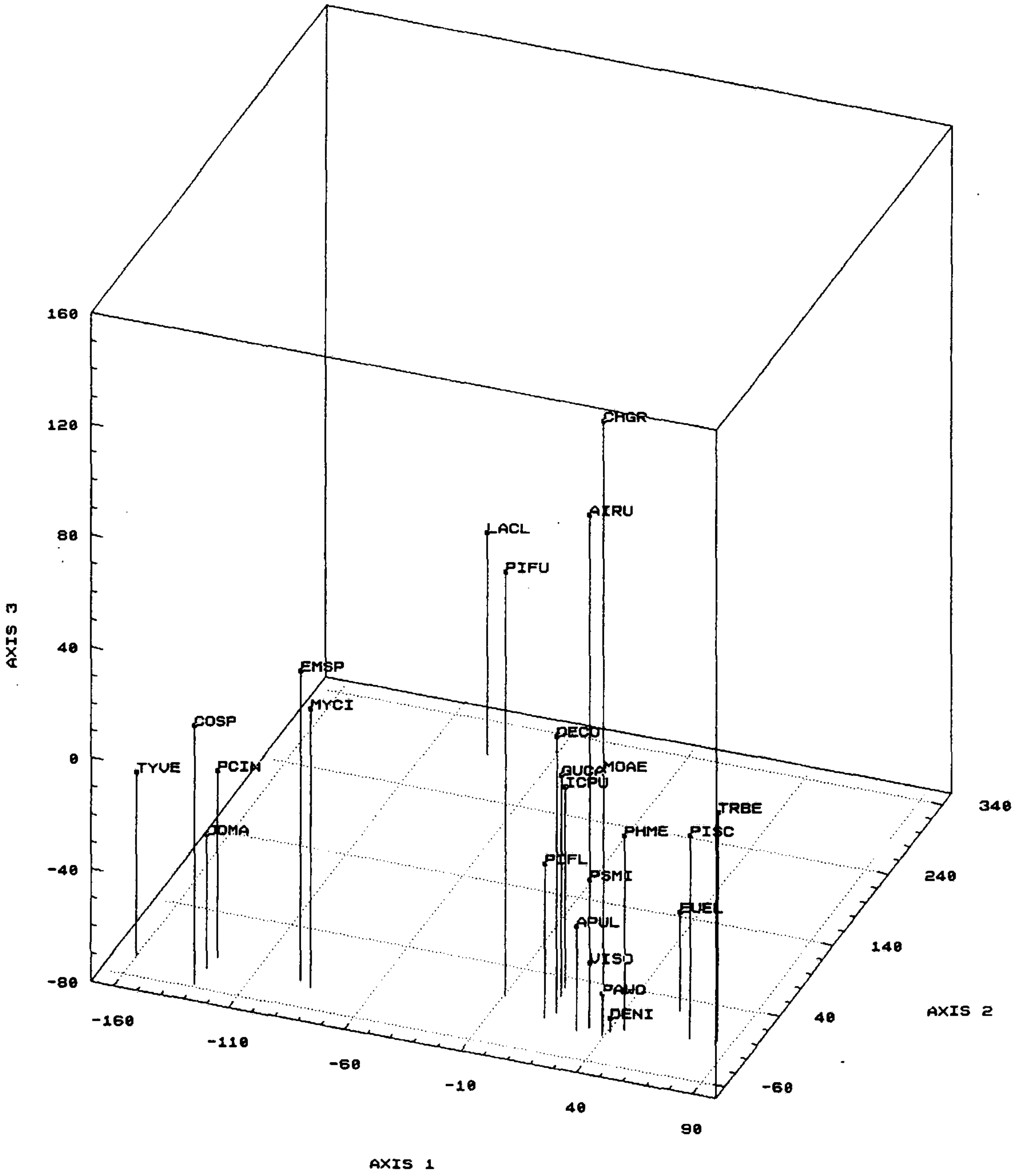


Figure 5.7. Ordination of spring bird species according to their foraging behaviour. Mnemonics are based on first two genus and species words. *Centurus aurifrons* was ommited from the plot in order to make it more intelligible; its coordinates are 232, 22, 13.

the large negative scores are flying insect, flycatching and hawking. The first group is clearly related with the woodpeckers *C. aurifrons* (which was ommited from the plot in order to make it more intelligible; its coordinates were 232, 22,13) and *Picoides scalaris* and the Wren *Thryomanes bewickii*, while the second is linked with the flycatchers (*Tyranus verticalis, Ptilogonis cinereus, Contopus pertinax*, and *Contopus* sp.) and the hawkers (*Empidonax* sp. and *Myarchus cinerascens*). Sparrows and gleaners appear clustered together as another group on the positive side of the first axis. These groups are separated from the hummingbird *Lampornis clemenciae* in the second axis. The variables with positive scores and therefore associated with the hummingbird are: hover, vines and *Opuntia* sp. The variables with high negative scores are flying insect and hawking again, as well as the plants *Ceiba acuminata*, herbs, *Acacia cymbispina*, *Salix* sp. and *Croton ciliato-glandulosae*.

The third axis segregated the granivorous birds and *Pipilo fuscus* (a ground insectivore) from the gleaners. Also, the forest gleaners (*Dendroica coronata*, *Molothrus aenus*, *Guiraca caerulea* and *Icterus pustulatus*) appear in the positive side or this axis, while the woodland gleaners appear on the negative side (*Dendroica nigrescens*, *Aphelocoma ultramarina*, *Piranga flava* and *Psaltriparus minimus*). *Pheucticus melanocephalus*, also a gleaner, was present in both habitats, and appears in the middle.

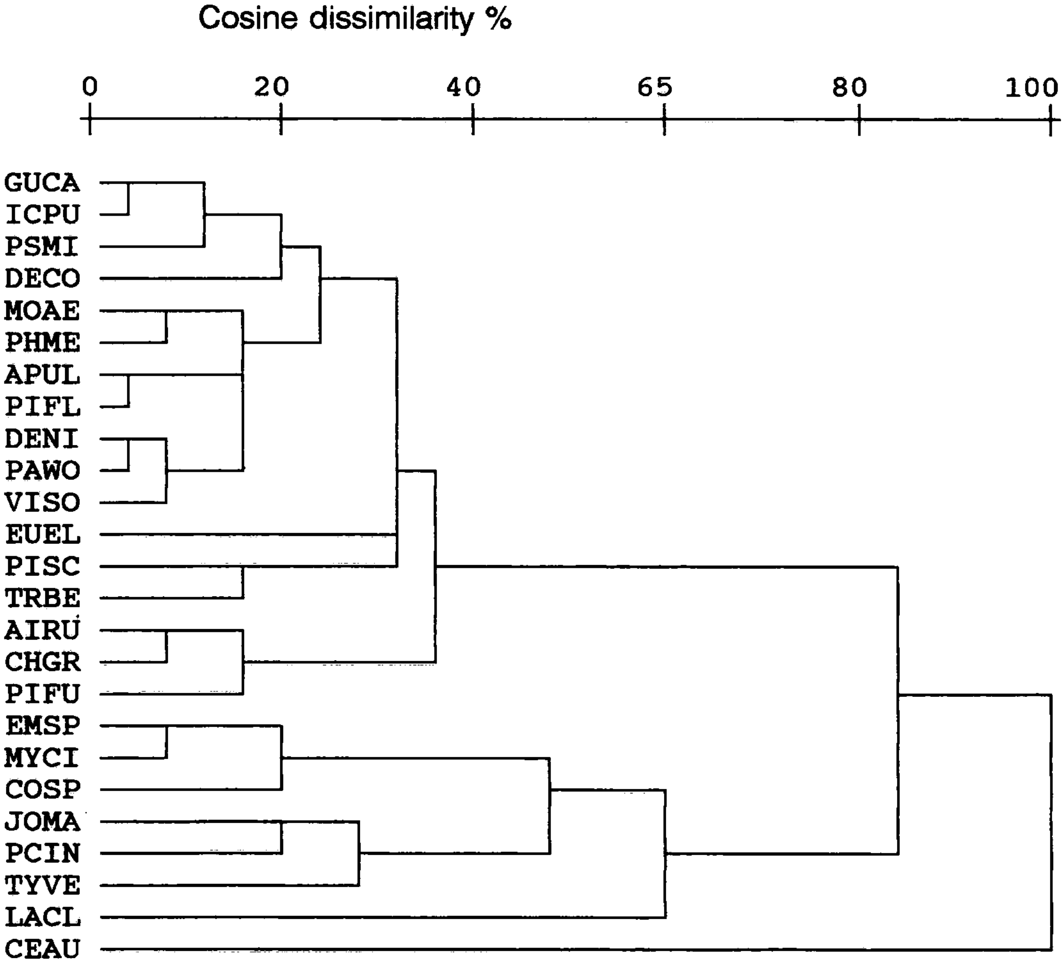
When the three axes are seen simultaneously, more differences may be appreciated; both hawkers (*Empidonax* sp. and *Myarchus cinereus*) are segregated from the flycatchers (*Contopus* sp., *Contopus pertinax*, *Ptilogonis cinereus* and *Tyranus verticalis*) and *Pipilo fuscus* from the granivorous sparrows *Aimophila ruficeps* and *Chondestes grammacus* (Figure 5.7).

In order to facilitate the guild determination, a cluster analysis was performed based on the foraging data matrix. As shown in Figure 5.8, the main clusters agree with the position between the birds in the ordination. At the 20% dissimilarity level, six clusters are formed: the forest omnivores, the ubiquitous insectivores (represented by *Dendroica coronata*); the woodland insectivores; the granivorous sparrows together with *Pipilo fuscus*; the hawkers, and finally, the wood searching insectivores.

Additionally, the hummingbird *Lampornis clemenciae*, forages in a different way from the other birds, while *Centurus aurifrons* forages in different plants and therefore were not associated with any other species. The flycatchers *Ptilogonis cinereus*, *Tyranus verticalis*, *Contopus* sp. and *Contopus pertinax* are joined at a higher level since they have different distributions and therefore were observed in different plant species. These four species, together with the hawkers (*Myarchus cynerascens* and *Empidonax* sp.) were positioned in a loose group. *Euphonia elegantissima*, as in the ordination appears on its own.

The ordination agrees with this classification. In addition, the third axis

Figure 5.8. Spring classification of bird species according to foraging tactics. Values for both years were pooled. The cosine distance between species was used. Symbols are given in Table 5.2.



separates *Pipilo fuscus*, *Lampornis clemenciae* and the two granivorous sparrows (*Chondestes grammacus* and *Aimophila ruficeps*) from the other birds. This same axis, divides the woodland gleaners (*Guiraca caerulea*, *Icterus pustulatus* and *Psaltriparus minimus*) from the woodland gleaners. This last division is also evident at the 15% dissimilarity level of the classification in which the gleaners are clustered in three groups: *Molothrus aenus* and *Pheucticus melanocephalus*; *Aphelocoma ultramarina* and *Piranga flava* (large wood gleaners); and *Dendroica nigrescens*, *Parus wollweberi*, and *Vireo solitarius* (small wood gleaners).

Dendroica coronata is separated from other insectivorous gleaners in the classification. This species is found in both woodlands and forests (mainly thorn forests) and therefore its segregation from both woodland and forest gleaners seems to be appropriate.

At the 15% dissimilarity, *Picoides scalaris* is also separated from *Thryomanes bewickii* and *Pipilo fuscus*, is separated from the granivorous sparrows. Finally, *Contopus* sp. a small flycatcher is separated from the hawking flycatchers.

3.5.2.3.2. Autumn guilds

Figure 5.9 shows the bird species ordination according to the first three axes foraging resource utilization. Eigenvalues were 0.431, 0.196 and 0.148.

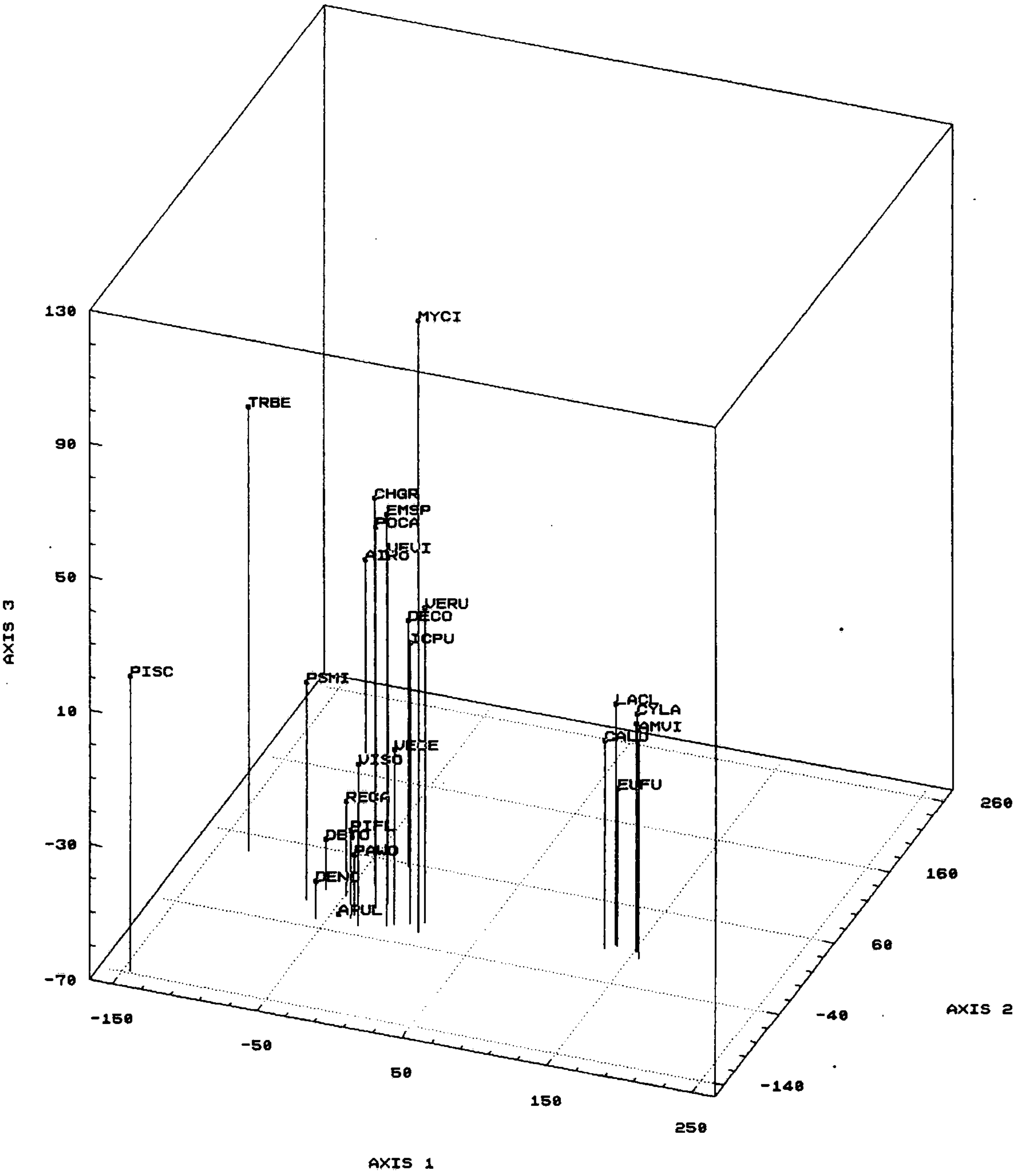


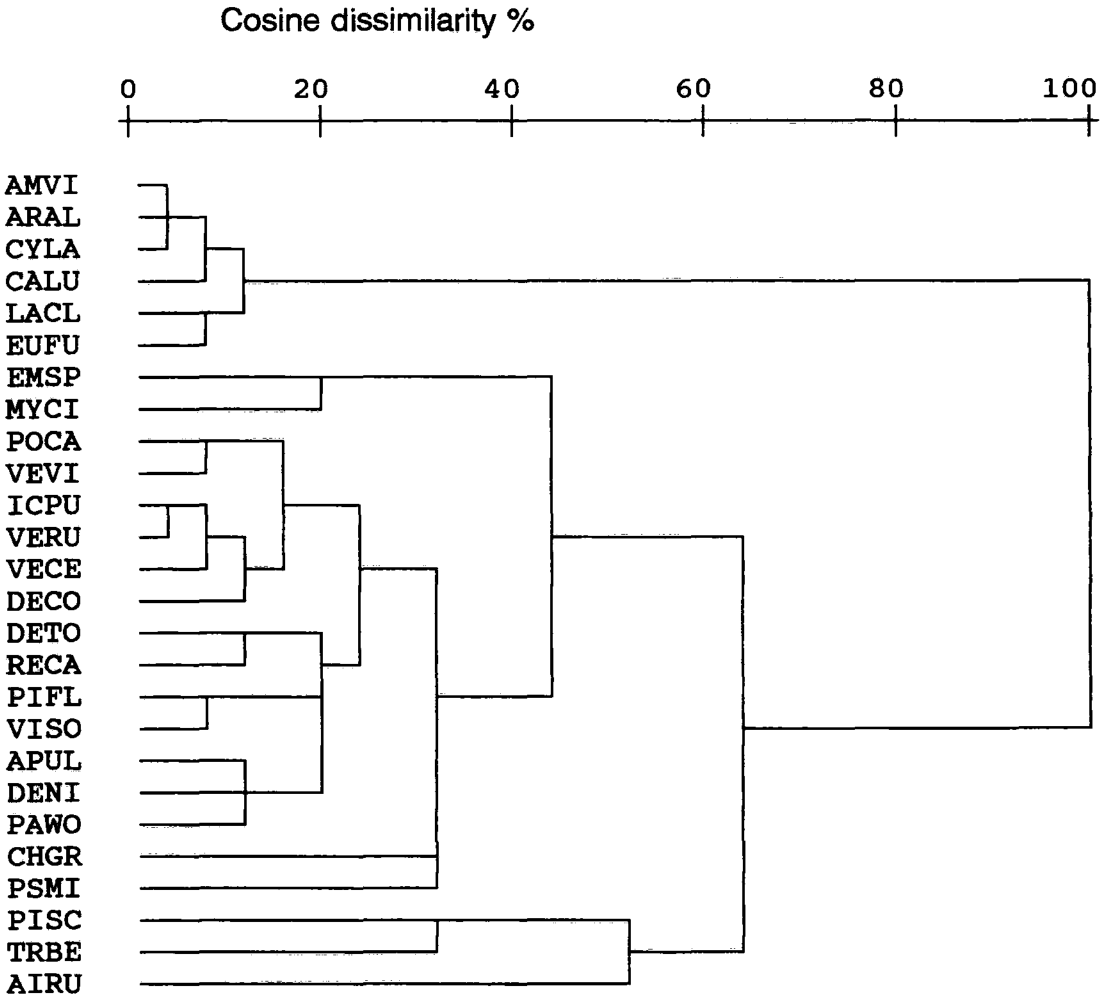
Figure 5.9. Ordination of autumn bird species according to their foraging behaviour. Mnemonics are based on first two genus and species words.

The first axis segregated the woodpecker and the wren (wood prober) from the hummingbirds. The first group is associated with drilling, trunk, drybranch, largebranch and ground while the hummingbirds are associated with hovering, flying insect, flower, *Ipomoea* sp., and the high vegetation layer. The second axis, separated the woodpecker *Picoides scalaris* from *Thryomanes bewickii* (a wood prober). Not surprisingly, the variables associated with the first one are drilling, trunk and drybranch in addition to *Ceiba acuminata*. The variables associated with the second are ground, herbs and the lower vegetation layer.

The third axis separated the hawkers (*Myarchus cinerascens* and *Empidonax* sp.), the sparrows (*Chondestes grammacus* and *Aimophila ruficeps*) and the forest gleaners (*Polioptila caerulea*) from the woodland gleaners. The variables associated with the first group are hawking, *Mimosa* sp., *Acacia macilenta*, *Prosopis juliflora*, *Croton* sp. and with the second, broad leaved oak, lichen, medium branch, *Acacia pennatula*, small leaved oak and *Lysolima acapulcensis*. The plants included in the first group are forest plants, while those of the second are woodland plants.

A classification of the autumn birds according to their foraging techniques and plant preferences resulted in the dendrogram shown in Figure 5.10. Six main groups emerge at the 20% dissimilarity level: hummingbirds, hawkers, forest gleaners, woodland gleaners, a woodpecker, and a woodprober represented by the wren *Thryomanes bewickii*. Both granivorous sparrows

Figure 5.10. Autumn classification of bird species according to foraging tactics. Values for both years were pooled. The cosine distance between species was used. Symbols are given in Table 5.2.



(*Aimophila ruficeps* and *Chondestes grammacus*) were associated with different groups. The second one was loosely clustered with *Psaltriparus minimus* (at the 40% dissimilarity level), a generalist gleaner, while *Aimophila. ruficeps* was weakly grouped with the woodprober-woopecker species (52% dissimilarity).

As in the spring analysis, perhaps a biologically more meaningful classification results if the dissimilarity level is taken at the 15% level. In such case, the following clusters are formed: the hummingbirds represented by *Amazilia violiceps*, *Archilochus alexandri*, *Cynanthus latirostris*, *Calothorax lucifer*, *Lampornis clemenciae* and *Eugenes fulgens*; two groups of forest gleaners (*Polioptila caerulea* and *Vermivora virginianae* and *Icterus pustulatus*, *Vermivora ruficapilla*, *Vermivora celata* and *Dendroica coronata*) and three groups of woodland gleaners: *Dendroica townsendi* and *Regulus calendula*; *Piranga flava* and *Vireo solitarius*; and *Aphelocoma ultramarina*, *Dendroica nigresens* and *Parus wollweberi*. In addition the woodpecker *Picoides scalaris* and the woodprober *Thryomanes bewickii*. Both granivorous species remain independent as well as the generalists gleaner, *Psaltriparus minimus*.

3.5.2.4. Reassessment of the guild determination

Although the classifications are satisfactory, there are some obvious inconsistencies, due partially to the fact that not enough observations were available for some species. Furthermore, the ordinations and the classifications did not entirely agree.

It has to be emphasized that guild characterization cannot be completely objective (Hawking and MacMahor 1989) and it is difficult to decide the relative importance that should be given to each set of variables when some of them have to do with behaviour and others with foraging preferences. Furthermore, in order to depend on the multivariate results for the guild classification, more field observations would be needed. The aim of this section is therefore to help identifying the main guilds but additional information will be taken into account for the final categorization.

In spring, the classification and the ordination (Figures 5.7 and 5.8) segregated the hummingbird (*Lampornis clemenciae*), the wood prober (*Thryomanes bewickii*), the ground insectivore (*Pipilo fuscus*) and the hawking flycatchers (*Empidonax* sp. and *Myarchus cinerascens*) as discreet groups. The woodpeckers were also separated from other guilds, (*Picoides scalaris* and *Centurus aurifrons*). Although *Guiraca caerulea*, *Icterus pustulatus* and *Psaltriparus minimus* were grouped in the classification, in the ordination the first two species appear closer together to *Molothrus aenus*, while *Psaltriparus minimus* appears closer to the woodland insectivores. Since *Molothrus aenus* and *Guiraca caerulea* are both omnivorous and are found in open and secondary vegetation they were placed in the forest omnivorous guild, while *Icterus pustulatus*, being the only species with a high preference for fruits (Arizmendi *et.al.* 1990) was placed in a corresponding guild. *Psaltriparus minimus* appears closer to *Vireo solitarius* in the ordination (Figure 5.7). Both species are ubiquitous (although more common in woodlands) and were grouped in the ubiquitous insectivorous guild.

Dendroica coronata, another ubiquitous insectivore had very high abundances in forests in some months of the year. It joins *Guiraca caerulea, Icterus pustulatus* and *Psaltriparus minimus* at the 20% dissimilarity level in the classification and is close to the first two in the ordination. Since it is an insectivore bird and more common in woodlands than either *Guiraca caerulea* and *Icterus pustulatus* and feeds mainly on insects, it was placed (together with *Vermivora ruficapilla* in autumn) in another insectivorous guild.

Piranga flava and *Aphelocoma ultramarina* are omnivorous woodland birds. They were clustered together in both multivariate analyses. *Contopus pertinax* and *Contopus* sp. appear together in a loose group with the other flycatchers in the classification. In the ordination, they are separated with respect to the third axis (Figure 5.7). This is because *Contopus* sp. was seen more often in the interface and therefore associated with forest plants. In fact, the distribution of both species is similar and were joined in the woodland flycatcher guild. *Tyranus verticalis* and *Ptilogonis cinereus* are much more ubiquitous and therefore were positioned in another guild.

In autumn, the hummingbirds (*Amazilia violiceps, Archilochus alexandri, Cynanthus latirostris, Calothorax lucifer, Lampornis clemenciae* and *Eugenes* *fulgens*), woodpeckers (*Picoides scalaris*) and woodgleaners (*Thryomanes bewickii*) were appropriately categorized. Forest insectivores (*Polioptila caerulea* and *Vermivora virginianae*) were clustered together in the classification, but were joined by *Empidonax* sp. (a hawking flycatcher) and the granivore sparrows *Chondestes grammacus* and *Aimophila ruficeps* in the ordination. This is mainly because the sparrows were often seen looking for food in the foliage. Additional observations outside the study area, made clear that these species forage as frequently in the ground and were separated (as in spring) to form the granivore-insectivorous guild.

As in spring, *Empidonax* sp. appears in the same cluster (at the 20% dissimilarity level) as *Myarchus cineresus* in the classification (Figure 5.10) and were placed in the same guild (hawking flycatchers).

Vermivora celata, Icterus pustulatus, *Vermivora ruficapilla* and *Dendroica coronata* were clustered together in the classification (Figure 5.10) but *Vermivora celata* was grouped with the woodland insectivores in the ordination. The last two species, as was said above, are ubiquitous insectivores and were therefore put together in the corresponding guild. *Icterus pustulatus*, as in spring, was left as the only frugivore.

In the ordination (Figure 5.9), *Vermivora celata*, *Vireo solitarius* and *Regulus calendula* appear close to the woodland insectivores. They are ubiquitous (albeit more abundant in woodlands) and were included in the corresponding guild.

Woodland insectivores are close together in the ordination (in the classification all they are joined at the 20% dissimilarity level) and were perhaps somehow subjectively separated, as in spring, in two groups: the woodland omnivores or large insectivores, represented by *Aphelocoma ultramarina* and *Pipilo fuscus*, and the small woodland insectivores, represented by *Dendroica townsendi*, *Parus wolweberii* and *Dendroica nigrescens*.

The multivariate results, are very similar to the *a priori* guild categorization. These analyses, as was said above, were used as a guide to corroborate the first determination. The final classification, based on both these results and the distribution of the birds is shown in Table 5.2.

3.5.2.5. Resource exploitation of the bird guilds

There are many approaches to study the change in foraging tactics either in time or in different communities. Most directly, goodness-of-fit test can be used to analyze and then compare plant preferences by the guilds in different times or places. A second approach is to relate the guild densities with the resources abundance either in time (Poulin *et al.* 1994) or in space. Finally, a simmilar approach to the ordinations which helped to identify the guilds may be used (Sabo and Whittaker 1979). In this case, the data are subjected

Table 5.2. Bird guilds based on detrended correspondence analysis and cluster analysis. Birds belonging to each guilds are shown. Mnemonics (codes) appear on several Figures. Season were bird species were present is indicated.

GUILD	CODE	BIRD SPECIES	CODE	SPRING	AUTUM
HUMMINGBIRDS	HUMM	*L. clemenciae*	CEJA	X	X
		A. alexandri	ARAL		X
		C. latirostris	CYLA		X
		C. lucifer	CALU		X
		A. violiceps	AMVI		X
		E. fulgens	EUFU		X
WOODPECKER	WPCK	*C. aurifrons*	CEAU	X	
		P. scalaris	PISC	X	X
WOODGLEANER	WPRB	*T. bewickii*	TRBE	X	X
UBIQUITOUS FLYCATCHER	UFLY	*T. verticalis*	TYVE	X	
		P. cinereus	PTCI	X	
WOODLAND FLYCATCHER	WFLY	*C. pertinax*	JOMA	X	
		Contopus sp.	COSP	X	
HAWKING FLYCATCHERS	HAWK	*M. cinerascens*	MYCI	X	X
		Empidonax sp.	EMSP	X	X
GRANIVORES INSECTIVORES	GRAN	*A. ruficeps*	AIRU	X	X
		C. grammacus	CHGR	X	X
GROUND INSECTIVORE	RASC	*P. fuscus*	PIFU	X	
FOREST INSECTIVORES	FGLN	*P. caerulea*	POCA		X
		V. virginianae	VEVI		X
FOREST OMNIVORES	FOMN	*G.caerulea*	GUCA	X	
		M. aenus	MOAE	X	
FRUGIVORE	FRUG	*I. pustulatus*	ICPU	X	X
UBIQUITOUS INSECTIVORES 1	UGLN1	*V. ruficapilla*	VERU		X
		D. coronata	DECO	X	X
PHEUCTICUS	PHME	*P. melanocephalus*	PHME	X	
UBIQUITOUS INSECTIVORES 2	UGLN2	*V. solitaruis*	VISO	X	X
		P. minimus	PSMI	X	
		V. celata	VECE		X
		R. calendula	RECA		X
WOODLAND OMNIVORES	LWGL	*A. ultramarina*	APUL	X	X
		P. flava	PIFL	X	X
WOODLAND INSECTIVORES	SWGL	*P. wolweberii*	PAWO	X	X
		D. nigrescens	DENI	X	X
		D. townsendi	DETO		X

to an ordination and the change in the "niche" or multivariate space position of the different guilds/species is observed. Since it is known which parameters are related to each axes (i.e. by examining their ordination scores) it is easy to relate them with the position or the scores of the birds in the ordination.

The plant preferences of each guild will be first determined by goodnes-of-fit tests, an ordination will then be used in order to understand how these plants were used.

3.5.2.5.1. Plant Preferences

Foraging plant preferences can be determined with dietary preference indexes (Krebs 1989) or goodness-of-fit tests (Peck 1989). In this study, the later approach was used. The null hypothesis was that each plant species was used according to its abundance. For each guild, the expected values were obtained by estimating the utilization frequencies if each plant species was used according to its proportional cover. The observed values were the frequencies with which the individuals of a guild used each plant. Chi-squared tests were used and each season was analyzed separately. The results are shown in Table 5.3.

Hummingbirds had a strong preference for *Ipomoea* sp. in both autumns and for vines in both spring. Additionally, *Opuntia* sp. and *Stenocereus* sp. were

Table 5.3. Plant preferences by bird guilds determined by goodnes-of-fit tests. Only significant results are indicated. Preference is shown by "+", avoidance by "-". One sign is $P < 0.05$, two, $P < 0.001$. A90=autumn 1990, A91=autumn 1991, S91=spring 1991, S92=spring 1992. Codes for plant specie (appearing in various figures) are shown.

PLANT		HUMMINGBIRDS				WGLN	HAWKING FLYCATCHER				GRANIVORES				GRINS	F-INSECT		F-O	FRUGIVORES		
SPECIES	CODE	A90	A91	S91	S92	S92	A90	A91	S91	S92	A90	A91	S92	S92	S91	A90	A91	S91	A91	S91	S92
Randia sp.	RASP		-														++				
Conzatia sericea	COSE					++				+		+									
Bursera sp.	BUSP						++	++	++	++		++		++							
Croton sp.	CRCG	-	--	-			-	-	--	-		-		--		--	--	-		--	-
Quercus castanea	QUCA									++											
Pithecollobium dulce	PIDU	-																		++	
Guazuma ulmifolia	GUUL		-								++	-		-							
Herbs	HERB	-	--	-			-	-						--		-	--	-		--	-
Acacia macilenta	ACMA															++					
Acacia cymbispina	ACCY			-					-		++			++		++	+			-	-
Prosopis juliflora	PRJU							++							++	++	++			++	
Byrsonima sp.	BYSP																				
Opuntia sp.	OPSP		-	++												-					
Ipomoea sp.	IPSP	++	++				++	++	+	+			++			++	++	++	++	++	++
Stenocereus sp.	STSP			++														++		++	
Ceiba acuminata	CEAC																				
Quercus crasifolia	QUCR		-				++		+							-	-			-	
Vines	VINE			++	++																
Salix sp.	SASP																				
Heliocarpus sp.	HESP							++	+								+				
Ficus spp.	FISP									++										++	
Mimosa sp.	MISP						++									+					
Acacia pennatula	ACPE	-										++		-		-					
Lysiloma acapulcensis	LYAC		++			++			++	+			++							++	++
Mimosa galeoti	MIGA																				

WPCK=woodpeckers, WGLN=wood gleaners, F-INSECT=forest insectivores, F-OMN=forest omnivores, GRIN=ground insectivores

Table 5.3. (cont.)

PLANT SPECIES	CODE	U.FLY S92	W-FLYC S91	W-FLYC S92	UBIQ. INSECTIVORES 1 A90	A91	S91	A92	PHEUC. S91	S92	UBIQ. INSECTIVORES 2 A90	A91	S91	S92	WOODLAND OMNIVORES A90	A91	S91	S92	WOOD. INSECTIVORES A90	A91	S91	S92
Randia sp.	RASP					-																
Conzatia sericea	COSE											++	+	++						++		
Bursera sp.	BUSP											++	++			++				++		
Croton sp.	CRCG	-			--	--		--		-		-	-			-	-	-	-	-		
Quercus castanea	QUCA													++					++			++
Pithecollobium dulce	PIDU				-	--		-										-				
Guazuma ulmifolia	GUUL									-		-								-		
Herbs	HERB	--			-	--		--		-		-	-			-		-	-	-		
Acacia macilenta	ACMA				++																	
Acacia cymbispina	ACCY	-								-						-	-	-	-	-		
Prosopis juliflora	PRJU																					
Byrsonima sp.	BYSP				-	-		-														
Opuntia sp.	OPSP				-	-																
Ipomoea sp.	IPSP	++			++	++		++			++									-		
Stenocereus sp.	STSP																					
Ceiba acuminata	CEAC	++				++																
Quercus crasifolia	QUCR			++	+					++	++	++	++		++	++	++	++	++	++		
Vines	VINE					-		-														
Salix sp.	SASP				++																	
Heliocarpus sp.	HESP							-										-		-		
Ficus spp.	FISP					++		++														
Mimosa sp.	MISP					++																
Acacia pennatula	ACPE				-								+						+	-		++
Lysiloma acapulcensis	LYAC	++	++	++	-		++	++	++	++		+	++		++	++	++	++		+		
Mimosa galeoti	MIGA				+																	

U.FLY=ubiquitous flycatchers, W-FLYC=woodland flycatchers, PHEUC=P.melanocephalus favoured in spring 1991.

There were not enough observations for woodpeckers to use chi-squared. For woodprobers, enough data were only available for the spring of 1992. The results show that *Mimosa galeotti* and *Lysolima acapulcensis* were favoured.

Flycatchers preferred tall trees to look for food. For the first group of ubiquitous flycatchers, *Ipomoea* sp., *Lysolima acapulsencis* and *Ceiba acuminata* were predominantly used. Woodland flycatchers used mainly broad leaved oaks and *L. acapulcensis*.

Hawking flycatchers had a strong preference for *Bursera* sp. in all seasons. Both *Empidonax* sp. and *Myarchus cinerascens* were frequently seen eating the fruit of these trees. In fact, besides these birds, only *Guiraca caerulea* was seen eating the *Bursera* fruits (once) even though they can be very common in both autumn and spring. The members of this guild were also seen looking for insects on *Ipomoea* sp. and *Lysolima acapulcensis* foliage in spring.

Granivore-insectivores search mainly on the ground. They also look for food in the foliage of some plants but there are no seasonal patterns associated with this guild. *Acacia farnicosa* was used in autumn 1990 and spring 1992 while *Bursera* sp. were used in autumn 1991 and spring 1992. Additionally

Guazuma ulmifolia was used in autumn 1990, *Acacia pennatula* in autumn 1991, and *Ipomoea* sp. and *Lysolima acapulcensis* in spring 1991.

Foliage insectivores were present only in autumn, which is, in itself, interesting, since there was little foliage and low arthropod densities in spring. This guild used *Acacia cymbispina*, *Prosopis juliflora* and *Ipomoea* sp. for its foraging activities. This pattern was consistent in both years. Additionally, there was a marked preference for *Mimosa galeotti* and *Heliocarpus* sp. (a broad leaved tree) in 1991 and for *Mimosa* sp. in 1990. In both years, there was a rejection to look for food in herbs.

Forest omnivores had a preference for *Ipomoea* sp. and *Stenocereus* sp. Frugivore-insectivores favoured *Ipomoea* sp. in autumn 1991 (there was not enough data in autumn 1990). In spring, they also favoured *Ipomoea* sp. in addition to *Lysolima acapulcensis*. They were also seen looking for fruit in *Pithecollobium dulce*, *Ficus* spp., and *Stenocereus* sp. and searching for arthropods in the foliage of *Prosopis juliflora* in spring 1991.

Ubiquitous insectivorous were divided in two groups; those found more often in woodlands and those who were more frequent in forests. The later had a strong preference for *Ipomoea* sp. in both autumns and spring 1992 and for *Lysolima acapulcensis* in both springs. In addition, they were seen in broad leaved oaks and *Conzatia sericea* in autumn 1990 and in *Ceiba* sp. and Mimosa sp. in autumn 1991. They were also seen foraging in *Ficus* sp. in both autumn 1991 and spring 1992. *Pheucticus melanocephalus*, also had a preference for *L. acapulcensis* in spring.

Woodland omnivores favoured *Quercua crassiflia* and *Lysolima acapulcensis* in all seasons in addition to *Bursera* sp. in autumn 1991. Woodland insectivores had a significant preference for *Q. crassifolia* in both autumns and for *Q. castanea* and *Acacia pennatula* in autumn 1990 and spring 1992. They did not have any significant preference in spring 1991.

3.5.2.5.2. Foraging manoeuvres and plant preferences

The goodnes-of-fit test is a useful mean to test the foraging plant preferences by each guild. Nevertheless, the same plant may be used in different ways and therefore, different guilds may be used diferent resources even when foraging in the same species. Ordinations are useful to help in understanding how food resources are partitioned. The data matrix in this study included the frequencies with which each plant was used, as well as those of the technique used to obtain food.

One advantage of evaluating the foraging information by means of multivariate statistics is that those parameters with no inherent values can be included in the analysis (i.e. it is not possible to use correlations or chi-squared with such parameters as flying insects or nectar if no data are available on their abundances). Since it is known how frequently these resources were used by the bird species, another important dimension can thus be incorporated. Although, the preference for these resources can not be quantified, their inclusion in the analysis can help explain how the favoured plants (whose relative cover was measured) are used.

Sherry *et al.* (1979) used classifications exclusively in order to identify the bird guilds; in a second step, they detected the variables associated with them by using factor analysis. In this study, classifications and ordinations have been used only as a guideline to corroborate the *a priori* defined groups due to small sample sizes for many birds (Table 5.1). The variables on which the guild organization were based were only briefly mentioned because the results were not conclusive.

Since the foraging observation sample sizes are larger for guilds, it is now possible to determine the variables associated with each of them. Detrended correspondence analysis, was used following a similar approach than the one used by Sabo and Whittaker 1979.

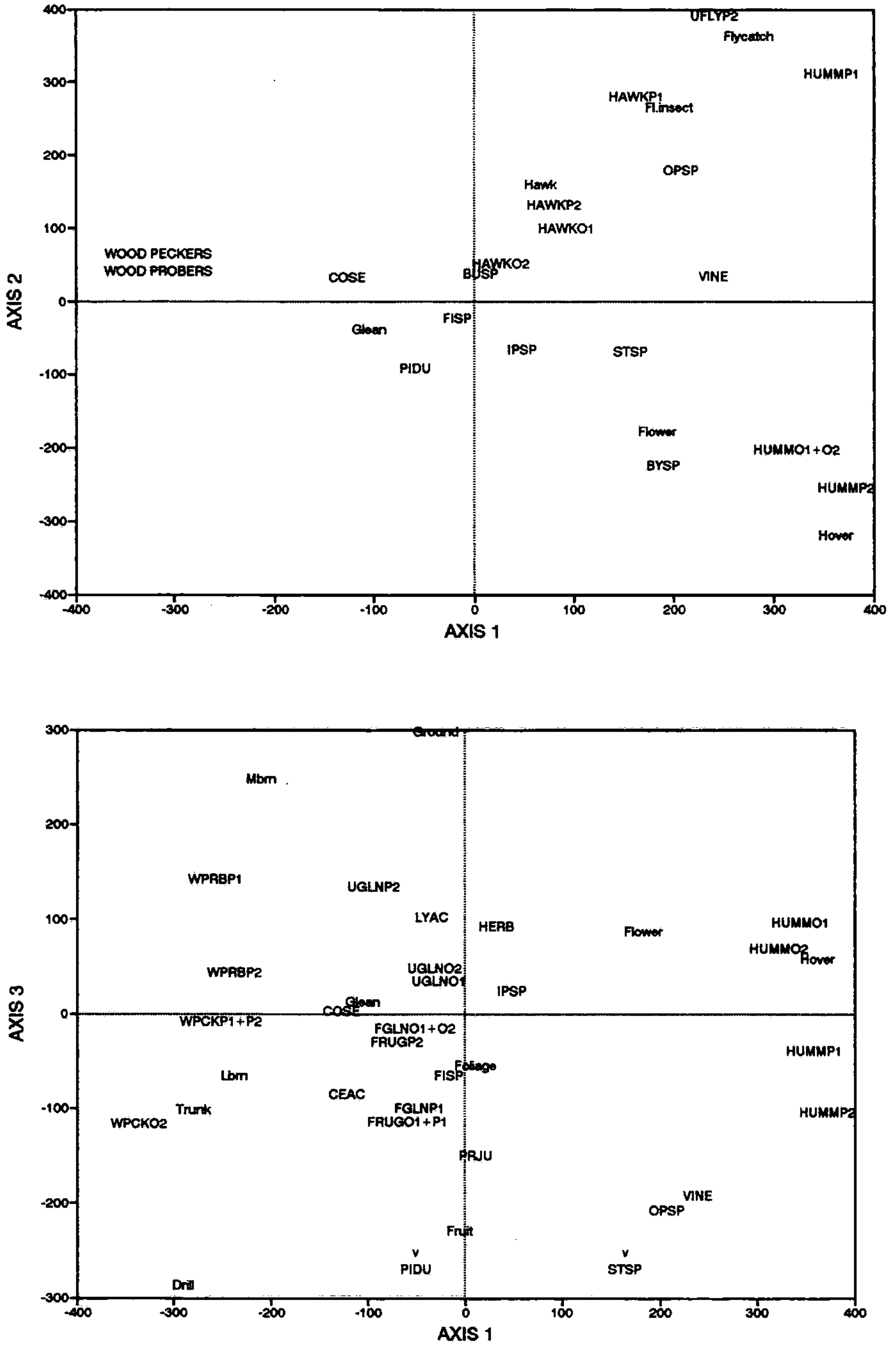
The guilds were separated in two data sets; one containing mostly forest bird and the other including those found mainly in woodlands. The data for the four seasons were analyzed together for comparative purposes.

3.5.2.5.3. Forest Guilds

Figure 5.11 plots the first two axes of the forest guild ordination. It show the ubiquitous flycatchers, the hawking flycatchers (HAWK), the hummingbirds (HUMM), the woodpeckers (WPCK) and the woodgleaners (WPRB). The first two axes are related mainly with the foraging manoeuvres. Thus, hummingbirds are related with hovering, flycatchers with flycatching, flycatcher hawkers with hawking and woodpeckers and woodgleaners with drill and glean. The plot also shows that flycatchers look mainly for flying insects, hummingbirds look for flowers and woodpeckers and wood gleaners for tree trunks and tree branches. Furthermore, and more relevantly, hummingbirds look for flowers mainly in *Ipomoea* sp., *Stenocereus* sp., *Byrsonima* sp., while hawking flycatchers prefer *Bursera* sp. and *Ipomoea* sp. Woodpeckers and woodprobers look for food mainly in the bark of *Conzatia sericea*.

Axis three (Figure 5.12) is more interesting since it shows more subtle differences having to do with seasonal changes and with differences in plant use by similar guilds. Accordingly, autumn hummingbirds are still related to *Ipomoea* sp. but in spring the ordination indicates that they prefer to look in vines, *Stenocereus* and *Opuntia* sp.

Woodgleaners (WPRB) are now segregated from woodpeckers (WPCK). The first guild appear to prefer medium branches, while woodpeckers have a preference for trunks and large branches. Besides, axis three now associated the woodpeckers with bark drilling.



Figures 5.11 (axes 1 and 2) and 5.12 (axes 1 and 3). Forest guilds of birds ordinated according to foraging tactics. Bird guild symbols are on Table 5.2. Suffix added correspond to seasons: O1=autumn 1990; O2=autumn 1991; P1= spring 1991; P2=spring 1992. Symbols for plant species are shown in Table 5.3.

Flycatchers (UFLY) are not divided any further, but insectivores (FGLN) and frugivores (FRUG) are separated by the third axis (this guilds were located near the intersect of the first two axes and therefore did not show any response to their associated variables). Forest gleaners in autumn show only a weak relationship with *Guazuma ulmifolia*, *Ficus* sp. and *Prosopis juliflora*, but in spring 1991 (the only season for which enough data was available to be included in the analysis), forest omnivores together with frugivores looked mainly for fruit (but also in the foliage) on *Ficus* sp., *Ceiba* sp., *P. juliflora* and *Pithecollobium dulce* (a very infrequent legume tree with large fleshy fruits) (Figure 5.12). The third axis also suggests that woodpeckers search for food in the trunk of *Ceiba* trees in autumn 1991, while ubiquitous gleaners (UGLN) seem to glean from *Lysolima acapulsencis*, herbs, *Ipomoea* sp. and *Conzattia sericea* (Figure 5.12). In spring 1992, this guild was seen foraging for vegetation in the ground as is apparent in the same plot (UGLNP2 is associated with ground).

Granivores (GRAN) were divided by the fourth axis (Figure 5.13). This axis is primary related to ground foraging. Actually, sparrows in autumn 1990 and spring 1992 and ground insectivores (RASC) in 1991 mainly foraged in this substrate, although granivores in 1991 were seen also foraging in the shrubs and trees (*Bursera* sp. *Acacia cymbispina* and herbs). These results might be linked with the fact that sparrows are seen in flocks. Therefore the observations may be biased, since depending on the site in which the flock is observed, most birds will be seen foraging on what is available there. This

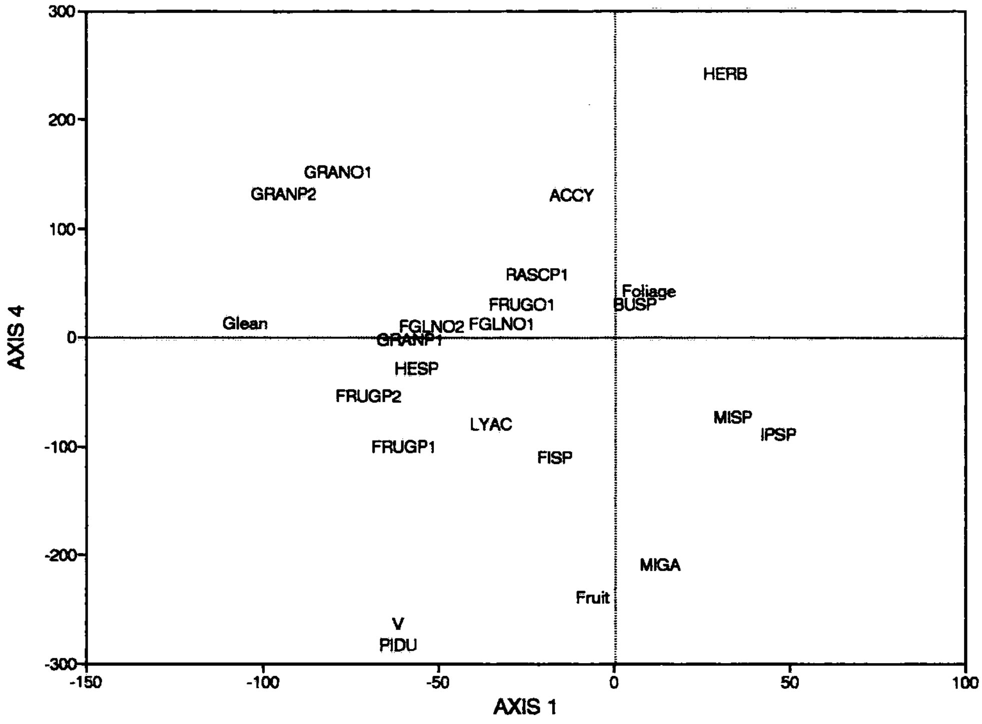


Figure 5.13 (axes 1 and 4). Forest guilds of birds ordinated according to foraging tactics. Bird guild symbols are on Table 5.2. Suffix added correspond to seasons: O1=autumn 1990; O2=autumn 1991; P1=spring 1991; P2=spring 1992. Symbols for plant species are shown in Table 5.3.

might indicate only chance observations of many birds together and not a true preference.

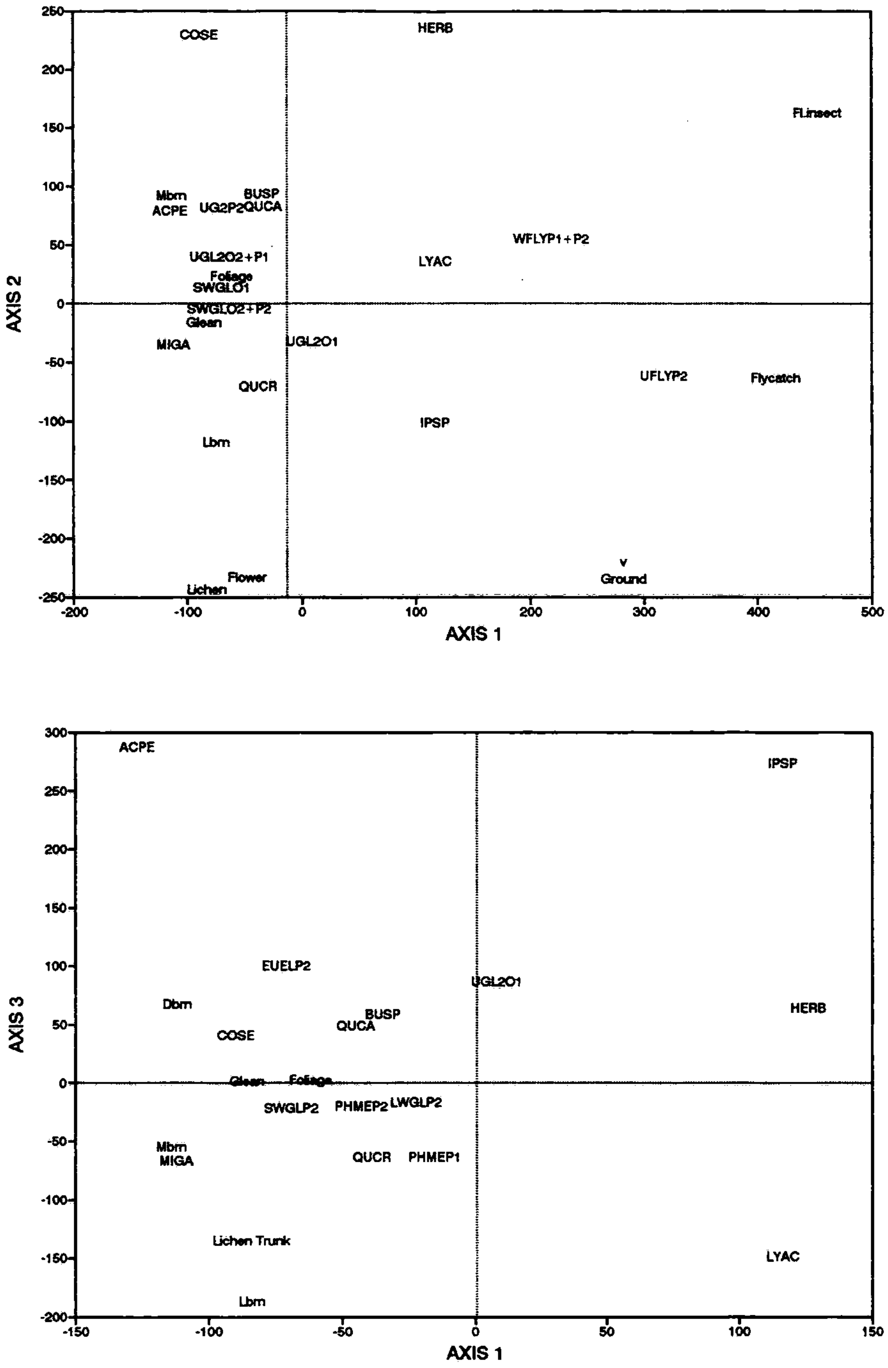
The fourth axis further segregates the spring frugivores (Figure 5.13). Although they still are associated with fruit, they are now related to *Ipomoea* sp., *Mimosa* sp. and *Lysolima acapulcensis*.

Forest gleaners (FGLN) appear near the intersect with respect to all axes. Although this suggest that they are mainly generalists, the third axes show the have a slight preference for *Prosopis juliflora*, *Ficus* sp. and *Guazuma ulmifolia*. The fourth axes also suggest that they may have a partial preference to *Bursera* trees and the shrub *Acacia cymbispina* (the dominant legume in thorn scrub).

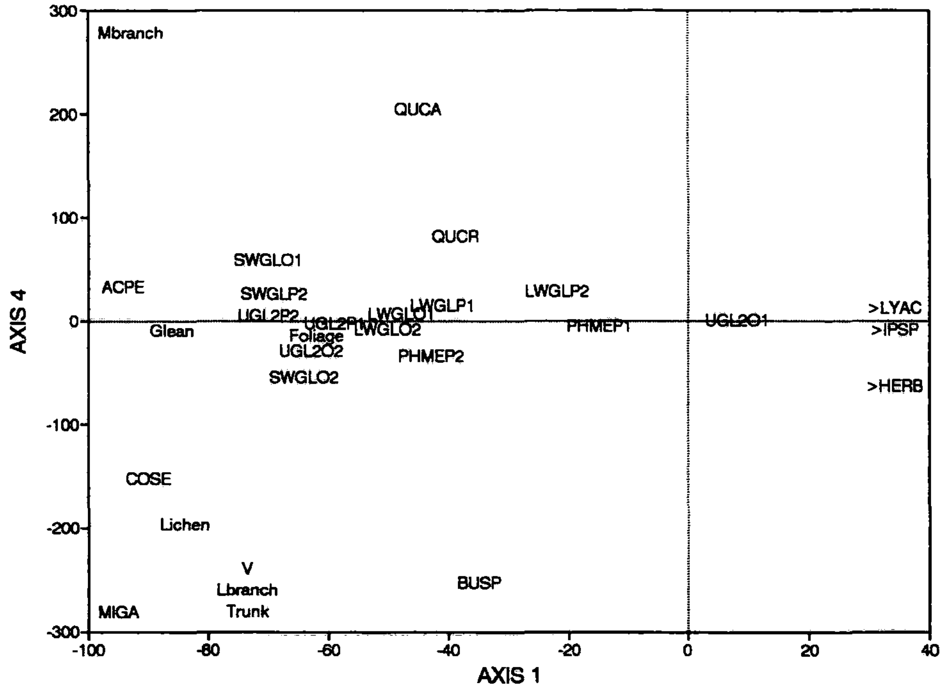
3.5.2.5.4. Woodland Guilds

Figures 5.14 to 5.16 show the ordination of the woodland birds. The first two axes (Figure 5.14) show that the second group of ubiquitous insectivorous (UGL2) forage in the foliage of *Conzatia sericea*, *Bursera* sp. and *Quercus* spp. An interesting exception for this guild is in autumn 1990 in which they looked for *Ipomoea* sp. flowers.

Flycatchers (WFLY and UFLY) also responded to the first two axes. Woodland (WFLY) flycatchers look mainly for flying insects, while ubiquitous



Figures 5.14 (axes 1 and 2) and 5.15 (axes 1 and 3). Woodland guilds of birds ordinated according to foraging tactics. Bird guild symbols are on table 5.2. Symbols for plant species are shown in Table 5.3.



Figures 5.16 (axes 1 and 4). Woodland guilds of birds ordinated according to foraging tactics. Bird guild symbols are on table 5.2. Mnemonics for plant species are shown in Table 5.3.

flycatchers (UFLY) were often seen directing their sallies to the ground. Both groups used mainly *Lysolima acapulsencis* but the second also used *Ipomoea* sp.

Axis three (Figure 5.15) segregated *Euphonia elegantissima* (EUEL) which looked for epiphytes in *Ipomoea* sp. and *Acacia pennatula*. *Pheucticus melanocephalus* in spring 1991 was now linked to *Lysolima acapulsencis* and *Quercus crassifolia* Figures 5.15. The third axis also suggests that most spring insectivores used *L. acapulsencis* to look for food.

3.5.3. Discussion

It is evident that the different guilds tend not only to look for food on different plant species, but also to use differentially the substrates of these plant species. It is also true that some guilds change their foraging preferences between seasons. This would be expected and is more noticeable for those guilds relying heavily on plant phenology (i.e. hummingbirds and frugivores).

The plant preferences (Table 5.3) and the foraging niches obtained by the ordinations (Figures 5.11-5.16) depict a suitable way to describe how foraging resources are used in the study area. Goodnes-of-fit tests obtain the favoured plants but do not include information on the way these plants are used. The ordination is helpful to undersand how food resources are partitioned between bird guilds.

Ipomoea sp. was extensively used by hummingbirds, frugivore-insectivores, hawking flycatchers and ubiquitous insectivores in autumn. Yet, *Ipomoea* sp. was used in diferent ways. Hummingbirds obtained nectar from the flowers, ubiquitous insectivores searched for insects and spiders in the flowers, while hawking flycatchers looked for flying insects and frugivore-insectivores gleaned in the foliage (Figures 5.11 and 5.12). Furthermore, flycatchers use these trees (together with other tall trees) mainly as plataforms for their sallies.

Lysolima acapulcensis, was widely used in spring but contrary to *Ipomoea* sp., it was used in a similar way (gleaning in small branches and foliage) by frugivore-insectivores, ubiquitous insectivores and woodland omnivores. On the other hand, *Pheucticus melanocephalus* and small woodland insectivores looked mainly for arthropods in the lichen of medium branches and trunks (Figure 5.15). *L. acapulcensis* starts to grow leaves in early spring and presumably they attract more arthropods than other plant species. Yet, *Prosopis juliflora*, which is a conspicuous evergreen tree was only used preferentially by frugivore-insectivores in spring 1991 (and not in 1992). The high preference for *L. acapulcensis* in contrast to *P. juliflora* is difficult to explain. Since spring 1991 was the driest year, perhaps birds had to expand their breadth of diet, as predicted by optimal foraging theory (Krebs 1978). Optimal foraging might also explain the fact that *Quercus crassifolia* was preferentially used by woodland insectivores. This species has low arthropod densities (chapter 3.2) but since the relative cover of other plant species (besides herbs) is much lower, perhaps it would by too time consuming for woodland birds to look for food in the other plants present.

The use of vines by hummingbirds in both springs and of *Opuntia* sp. in spring 1991 is explained by the fact that these plants produce large flowers (*Opuntia* sp. had flowers only in spring 1991). *Stenocereus* sp. was preferentially used by forest omnivores, frugivore-insectivores and hummingbirds in spring 1991. This columnar cactus produces large sweet fruits *Stenocereus* sp. (together with *Pithecollobium dulce* and *Ficus* sp. it is associated with fruit in the ordinations) (Figures 5.12 and 5.13) and the three guilds were frequently seen looking for them in this season, which was the only one in which the fruit was ripe.

Conzattia sericea, was other favoured plant used by wood probers (which looked for arthropods in medium branches) and the second group of ubiquitous insectivores (which looked in the foliage and small branches) (Figure 5.12). The bark of *C. sericea* has a rough texture and perhaps more arthropods can be found between the indentations.

Bursera sp. was consistently used by hawking flycatchers. This species produces large amounts of resinous fruits all year around. *Myiarchus cinerascens* and *Empidonax* sp. were seen eating them in all seaons but they were not eaten by other birds (with the exeption of *Guiraca caerulea*, a spring omnivore, which was seen only once eating these fruits). The importance of *Bursera* for ubiquitous and woodland insectivores in autumn 1991 will be discussed in the next chapter.

Finally, the fact that insectivores are only present in forests during autumn (when arthropods are abundant) and are replaced by omnivores (when there are less arthropods but more variety of resources such as fruits, cactus flowers and seeds) in spring suggests that the resources are used according to their availability.

The final chapter will explore the influence of food in bird abundances and distribution. Since only arthropod abundances were estimated, the results will be centered to insectivores.

3.6. The relationship between arthropod densities and foraging preferences for the plant species

3.6.1. Introduction

As early as 1926, Elton emphasized on the importance that food has on the structure of animal communities (Elton 1966). Considering its importance in the organization of bird species distribution and organization, relatively few studies have estimated food abundance and measured its impact at the community level.

There have been mainly two types of studies on food and its influence on the bird community organization. The first group has attempted to explain the relationship between bird densities and food either on a temporal or a spatial scale (Raitt and Pimm 1976, Schluter 1982, Hutto 1985, Poulin *et al.* 1994, Repasky and Schluter 1994). The second group has focused on specific plant foraging preferences.

The importance of individual plants or vegetation layers on the bird species was investigated in detail by Hutto (1985), Holmes and Robinson (1981) and Peck (1989). These authors measured arthropod abundances and found that in general, the favoured plant species were those containing higher densities of the preferred food items.

The issue about the relationship between bird and food abundances has been more difficult to establish. Raitt and Pimm (1976) recognized that although climate and habitat are partially responsible for temporary density fluctuations, food may be the singly most important factor affecting the birds. In their study in the north American Chihuahuan desert, they grouped the birds in three categories (raptors, granivores and insectivores) and they found that many factors interact on the food availability. In the second year of their study, for example, the granivorous bird densities were much higher, even though the seed production had been similar in both years. They investigated the rodent populations and found that their densities were lower in the second year, thus food availability for the birds was therefore higher at this time. Similarly, although less rodents were available in the second year, the lizards were more abundant. This compensation resulted in similar densities of large predator birds in the two years.

At a more general level, Hutto (1985), found a strong correlation between food availability and bird densities in an altitudinal gradient in western Mexico. Schluter (1982) studied the influence of habitat, food and competition on the Galápagos ground finches over an altitudinal gradient. He concluded that food was the factor which best explained the distribution of the birds. Later, Repasky and Schluter (1994) tested the importance of the same factors on wintering sparrows (*Amphispiza belli, A. bilineata* and *Junco hyemalis*) also in the Galápagos but concluded that it was competition which had the strongest influence on the birds' distribution.

Poulin *et al.* (1994), calculated seasonal arthropod abundances using various methods. They found only a weak correlation between the main bird guild abundances and their favoured food on a yearly basis. Abbott *et al.* (1977) determined that only the abundance of one of the three finches they studied was significantly correlated with food availability.

This section will describe first the relationship between the bird species distribution and the food resources, followed by an analysis of the foraging choices in relation to arthropod availability in specific plants. Because only arthropod densities were estimated (and not other food resources), the chapter will be centered on the main arthropod groups and the insectivorous birds. Because of small sample sizes for some individual bird species, guilds will be used as the units of study.

3.6.2. Results

The guild section (chapter 3.5) pointed to the importance fruit had on the plant choices of frugivore-insectivores (particularly during spring) as well as the presence of flowers for the hummingbirds. Wood probers had a preference for trees with rough bark texture and flycatchers favoured tall trees. This section will be centered on the foraging preferences of insectivorous birds.

The arthropod density on the plants present at the study sites was estimated in an attempt to find if the birds responded to food abundance. The arthropod catch during spring was not big enough to establish their relative abundance in the different plants, therefore the analysis will include only the autumn results.

The results of the arthropod densities is presented in section 3.2. Each arthropod group tends to have different distributions between the plant species and therefore it is difficult to say which plants represent better food sources for the bird species; the most profitable plants to explore would be those having the largest densities of those arthropod groups favoured by the birds. The preferences cannot be established *a priori* since arthropod taxa differ in their importance as food resources in different sites. Poulin *et al.* (1994) for example, found that insectivores had high number of ants in the emetic samples she collected in a dry forest in Venezuela. Raitt and Pimm (1976) remarked on the importance of Orthoptera for birds in some north American deserts while Schluter (1982) observed that caterpillars were an important food source for the Galápagos ground finches during the rainy season. Rotenberry (1980) confirmed that ants were one of the main food items on stomach contents, but he also found that Coleoptera, Hymenoptera, lepidopteran larvae, Hemiptera and Orthoptera were important as food resources for the birds in his study sites in shrubsteppe vegetation. Furthermore, different insectivorous bird species tend to chose different invertebrates even in the same area. Robinson and Scott

(1982) for example, analyzed stomach contents and found that although caterpillars were important for vireos and some warblers, other warblers had a stronger preference for homopterans and a tanager preyed mainly on wasps and coleopterans.

In this study, some insects, which has been reported as an important food source for the birds (mainly the hymenopterans, dipterans and orthopterans) were not captured in sufficient numbers to give reliable estimates of their relative abundance on the different plant species. On the other hand, lepidopteran larvae, beetles, hemipterans, homopterans and spiders, which appear frequently on stomach contents of most birds, were satisfactorily sampled.

This section will be focused on the foliage insectivorous guilds since arthropod densities were not estimated on other substrates (i.e. bark, air, soil). Foliage insectivores were divided into the ubiquitous, forest and woodland guilds, depending on their distribution (chapter 3.5). The hawking flycatchers, were also included since they also look for food directly from the foliage.

3.6.2.1. The relationship between arthropod and bird densities

In order to estimate the arthropod abundance per sample unit (the plots on which birds were counted and observed), the cover of each plant present was multiplied by the mean density of the invertebrate groups found on each of them. The results (number of arthropods per plant species) were then added to produce an estimated number of arthropods for each of the vegetation types (chapter 3.1 explains how the vegetation was classified).

3.6.2.1.1. Bird guilds and total arthropod densities

Figures 6.1 to 6.2 show the insectivorous guild densities per vegetation type in autumn 1990 and 1991.

Forest insectivores were found in all dry forest habitats but were particularly dense in huizachales in both years (Figure 6.1). Woodland insectivores had high densities in mixed and mature woodlands. The first group of ubiquitous insectivores differed in densities between years. They were dense in huizachales and coatales in 1990. In 1991 they had higher densities in both huizachales and in mogotes. The second group of ubiquitous insectivores were almost absent in 1990. They were common in most vegetation types in 1991 with the exception of the interface and the mixed woodlands (Figure 6.1).

The hawking flycatchers were ubiquitous in all dry forest habitats and the interface (Figure 6.2). Woodland omnivores had high densities in mature woodlands, nevertheless, in 1990 they had even higher densities in mixed woodlands (Figure 6.2).

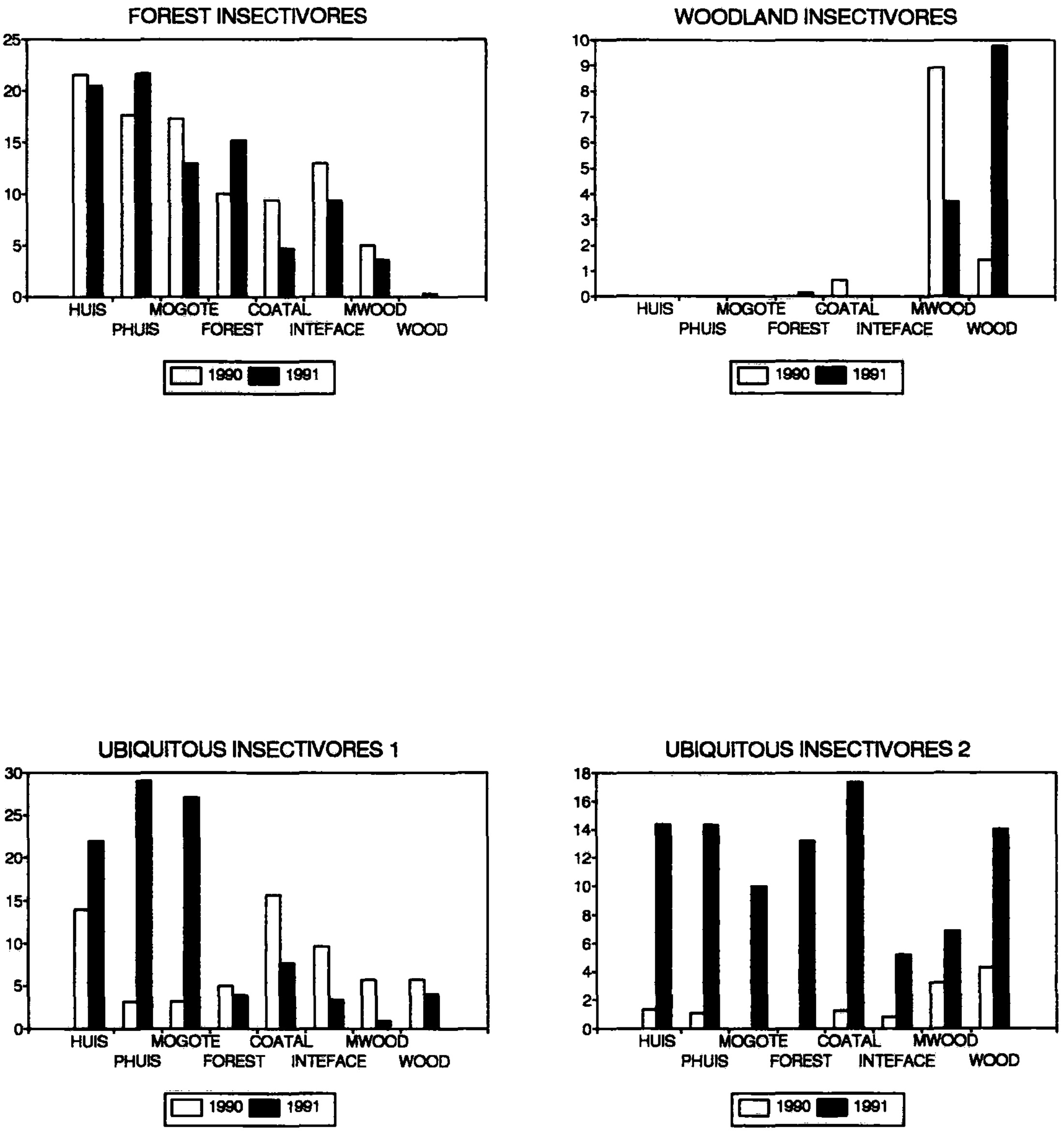


Figure 6.1. Autumn 1990 and 1991 guild densities (numbers per 10 plots) per habitat. PHUIS=Prosopis huizachal, MWOOD=mixed woodland.

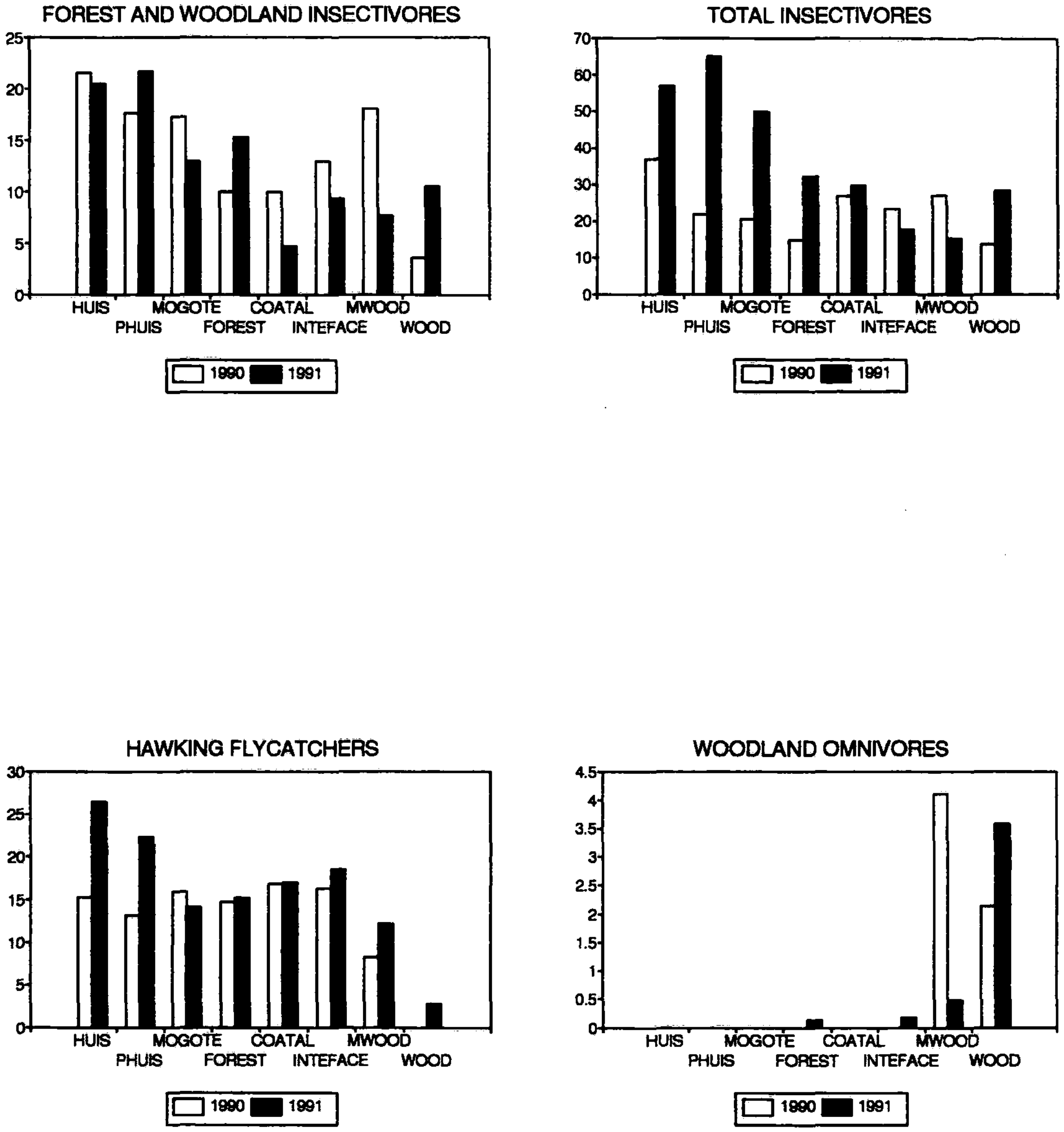


Figure 6.2. Autumn 1990 and 1991 guild densities (numbers per 10 plots) per habitat. PHUIS=Prosopis huizachal, MWOOD=mixed woodland.

The total arthropod densities are shown in Figure 6.3. Densities were higher in those habitats where broad leaved trees predominated (mogotes, forests and coatales). Total density was low in the interface and the mature woodlands and had medium densities in both huizachales and the mixed woodlands (Figure 6.3).

Correlations between the densities of the bird guilds and the total number of arthropods per vegetation type were not significant.

Since birds may have preferences for certain arthropod groups, arthropod were also grouped in five categories which had the highest densities (Coleoptera, Hemiptera, Homoptera, lepidopteran larvae and spiders). The influence of the main arthropod groups densities on those of the bird guild was inspected as well.

3.6.2.1.2. Bird guilds and the arthropod groups densities

The densities of the main arthropod groups differed between vegetation types and with the exception of homopterans, they were remarkably similar between years (Figures 6.3 and 6.4). Coleopterans had high densities in forests, mogotes, coatales and mixed woodlands (Figure 6.3). Hemipterans had high densities in mogotes, forests and coatales, but low in the interface, woodlands and huizachales (Figure 6.3). Homopterans were particularly dense in forests,

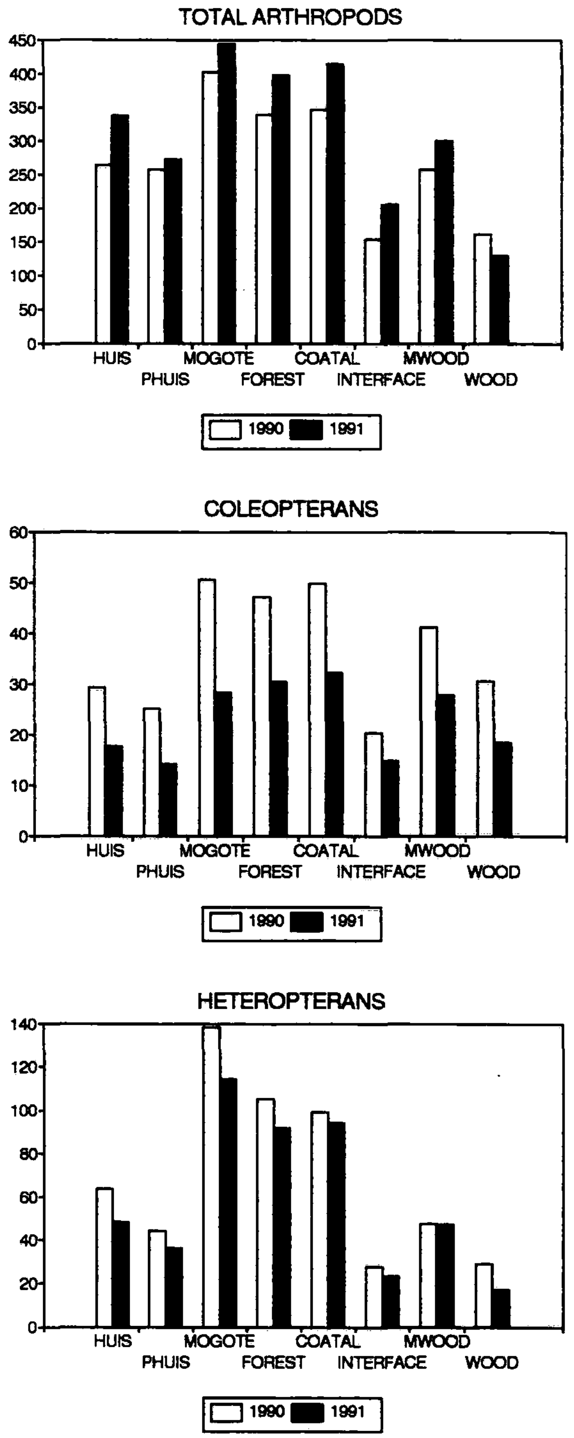
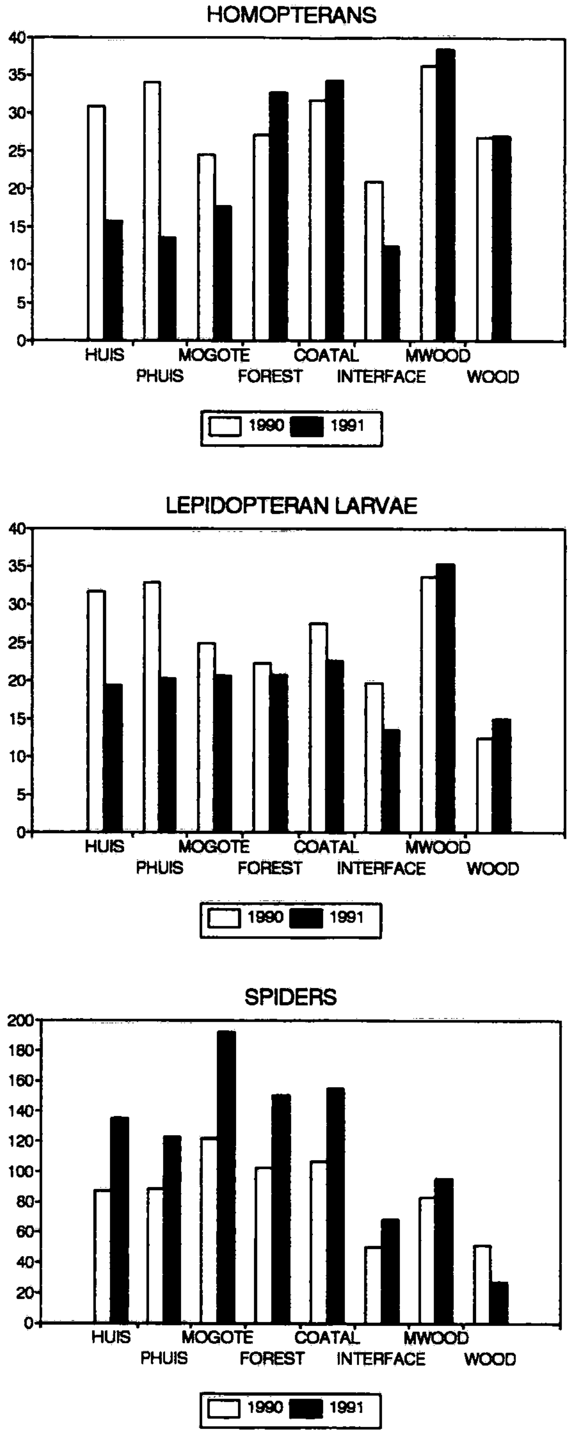


Figure 6.3. Autumn 1990 and 1991 arthropod densities per habitat. PHUIS=Prosopis huizachal, MWOOD=mixed woodland. The figures in the ordinate are number of individuals per plant foliage per sample plot.


HOMOPTERANS

LEPIDOPTERAN LARVAE

SPIDERS

Figure 6.4. Autumn 1990 and 1991 arthropod densities per habitat. PHUIS=Prosopis huizachal, MWOOD=mixed woodland. The figures in the ordinate are number of individuals per plant foliage per sample plot.

coatales and woodlands. Nevertheless, huizachales had high densities in 1990 but low in 1991 (Figure 6.4). Lepidopteran larvae were dense in mixed woodlands, but low in oak woodlands. They also had high densities in huizachales in 1990 (Figure 6.4). Spiders had high densities in mogotes, forests and coatales, and low in the interface and woodlands in both years (Figure 6.4).

In 1990, a positive correlation was found between the abundance of lepidopteran larvae and the total number of gleaning woodland and forest insectivores ($r=0.84$, 6 d.f., $P<0.05$). The regression is shown in Figure 6.5. In the second year, no significant correlations were found.

3.6.2.2. Arthropod densities and foraging plant preferences

Food availability has been suggested as the principal cause of plant foraging preferences (Holmes and Robinson 1981, Peck 1989, Hutto 1985), although foliage structure (Robinson and Holmes 1984) and competition and predator avoidance (Repasky and Schluter 1994) are other factors which may well affect these choices.

Regardless of the effect that arthropod abundances have on the distribution of the bird species, it is clear, as seen in section 3.5. that all bird guilds have marked preferences to forage in certain plant species. At the same time, they also show a strong resistance to look for food in other plant species. This was

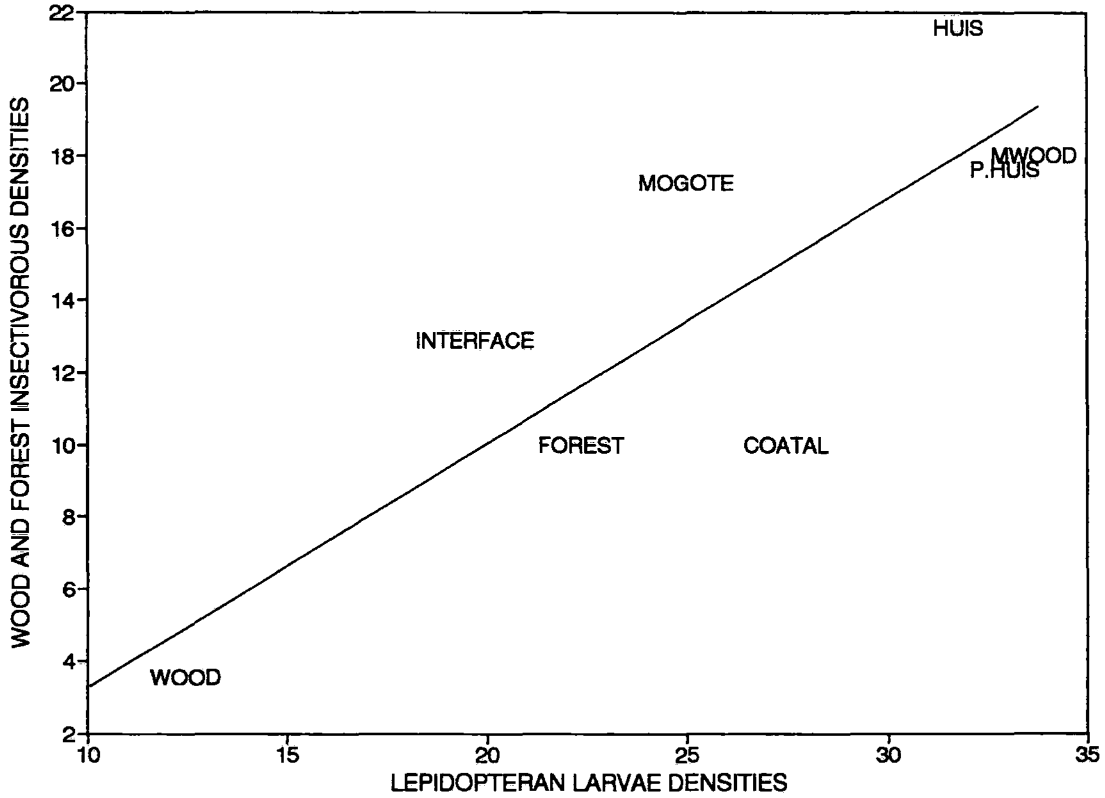


Figure 6.5. Autumn 1990 regression between the densities of lepidopteran larvae and the forest and woodland insectivorous birds in the main habitats of the study area. P.HUIS=Prosopis huizachal, MWOOD=mixed woodland, WOOD=oak woodland.

particularly obvious in the spring of 1991, when those trees with large and conspicuous fruits (*Stenocereus* sp., *Ficus* sp. and *Pithecollobium dulce*) were much favoured by frugivore-insectivores and one of the few species with foliage during the dry season was chosen by hawking flycatchers, frugivore-insectivores and insectivores in both springs. *Stenocereus* sp. was also frequently used by hummingbirds when it had fruit (spring 1991) as were the vines and *Opuntia* sp. when they were flowering. In autumn, the hummingbirds were attracted by the only flowering species (*Ipomoea* sp.). *Ipomoea* sp. was also attractive to individuals of other guilds (hawking flycatchers, forest and ubiquitous insectivores an frugivores) (Table 5.3), while woodprobers had a preference for those trees with rough texture and flycatchers favoured tall trees.

Plant species preferences by the insectivorous guilds will now be reexamined with the tree preference index (TPI) used by Peck (1989):

$$TPI=\frac{O-E}{E}$$

O = the number of birds observed foraging in a plant species, and E = the expected number of birds if they were foraging randomly on the plant species present.

In addition, multiple regressions were performed in which the main arthropod groups densities per plant species (spiders, homopterans, coleopterans, hemipterans and lepidopteran larvae as well as the total arthropod biomass) were entered as the predictive variables and the tree preference index (TPI) as the response variable. The plots from the regressions show the arthropod densities per plant species as well as the tree preference index (in the ordinate). The TPI has negative values when a plant is rejected (used less seldom than expected) and therefore the scale for the ordinate includes negative and positive values.

Figures 6.6 and 6.7 show the TPI for the total number of gleaning insectivores (forest and woodland insectivores) in 1990 and 1991. Besides oaks and *Ipomoea* sp. the birds from this guild, showed a preference for small leaved legumes in both years (*Mimosa* sp., *Lysolima acapulcensis, Prosopis juliflora, Acacia cymbispina, and Conzattia sericea*). The main difference in the foraging preferences between years, was the rejection of *A. macilenta* in 1991 and a strong preference for *Bursera* sp. in the second year.

There was a significant correlation between the insectivorous TPI and the densities of lepidopteran larvae per plant species in both years ($R^2=0.22$, 19 d.f., $P<0.05$ for 1990 and $R^2=0.28$, 20 d.f., $P<0.05$ in 1991). The regression plots are shown in Figure 6.8 and the equations are:

$$Y = -0.22 + 3.61\ (X) \pm 1.58 \text{ for 1990, and}$$

$$Y = -0.32 + 3.09\ (X) \pm 1.09 \text{ for 1991}$$

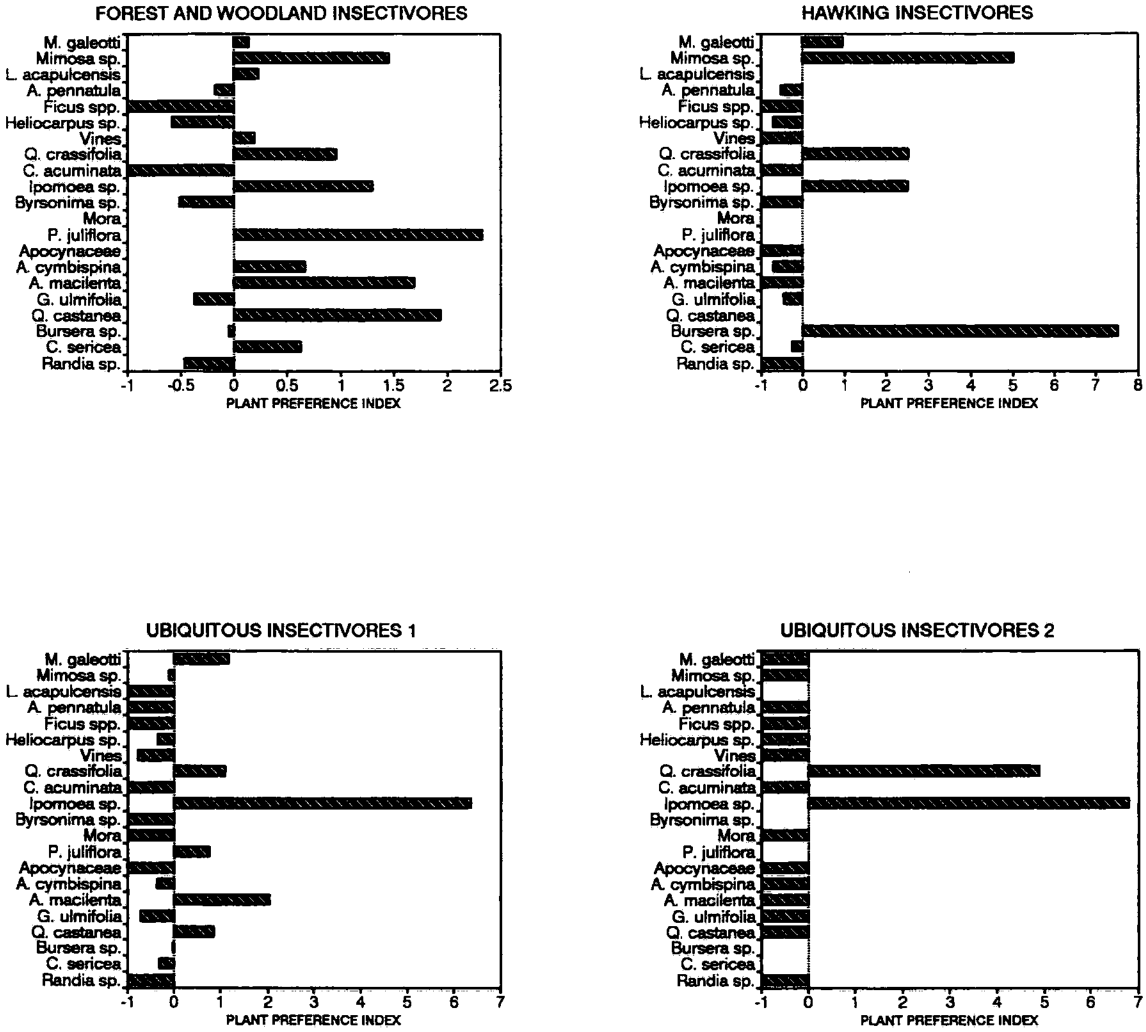


Figure 6.6. Plant foraging preferences by the total gleaning insectivores, hawking flycatchers and ubiquitous insectivores in 1990. The tree preference index was used for the calculations.

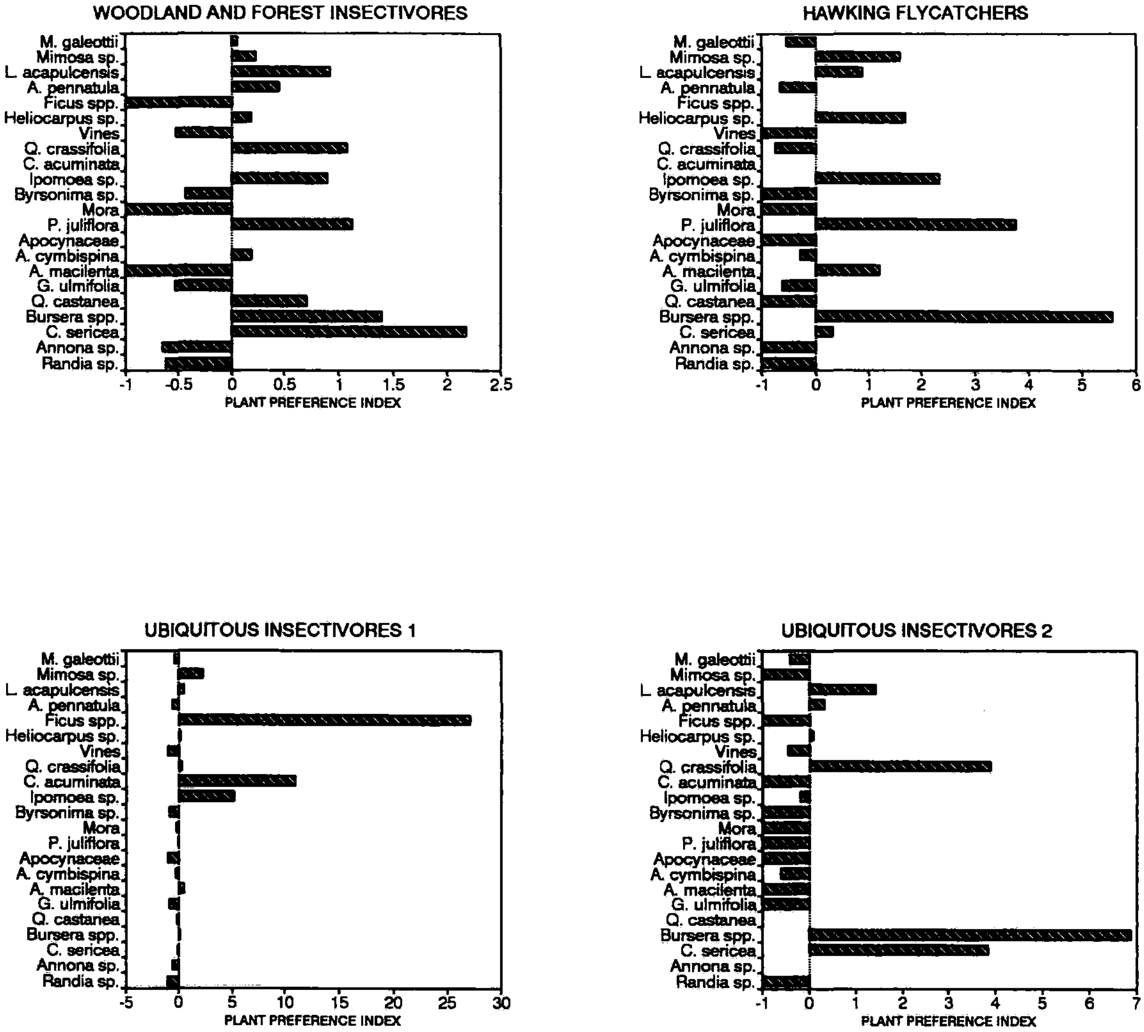


Figure 6.7. Plant foraging preferences by the total gleaning insectivores, hawking flycatchers and ubiquitous insectivores in autumn 1991. The tree preference index was used in the calculations.

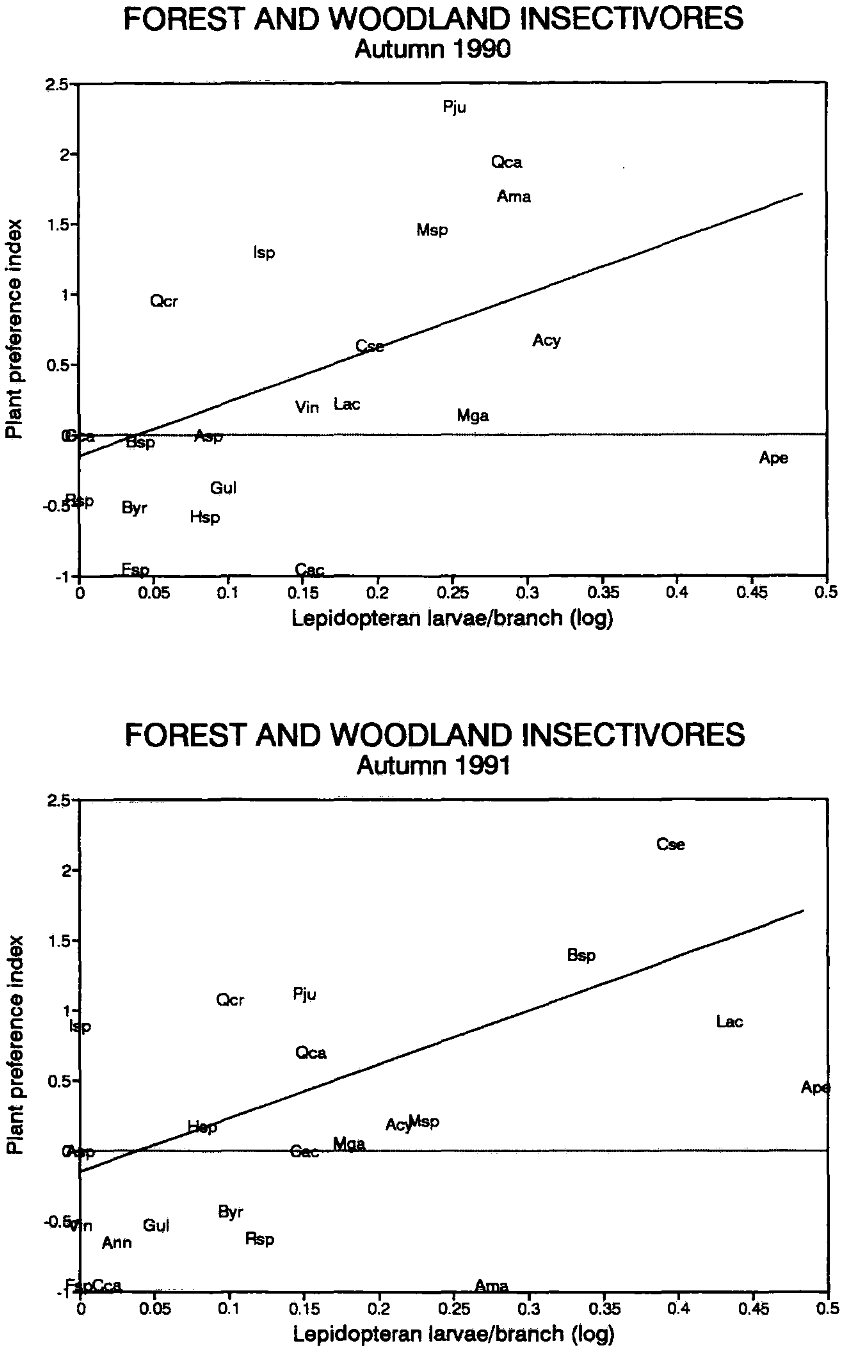


Figure 6.8. Regression between tree preference index of the total gleaning insectivorous birds and the lepidopteran larvae densities per plant species in 1990 and 1991. Mnemonics for plant species are composed from first genus and first two species words. Negative values in the ordinate indicate bird avoidance for the plant species.

Even though the birds did not forage in *Acacia penatula*, which had the highest lepidopteran larvae densities in both years, the favoured species in 1990 (*Prosopis juliflora, Quercus castanea, Acacia macilenta, Mimosa* sp. and *Acacia cymbispina)* had also high larvae densities in that year. Besides a preference for *Prosopis juliflora*, *Quercus castanea, Q. crassifolia* and *Ipomoea* sp., the birds favoured *Lysolima acapulcensis*, *Constantia sericea* and *Bursera* sp. in 1991. Interestingly, these three species had higher lepidopteran larvae densities in this year (=0.1 per branch in 1990 and =1.2 in 1991 for *Bursera,* =0.6 in 1990 and =1.5 in 1991 for *Conzatia sericea* and =0.5 in 1990 and =1.7 in 1991 for *Lysolima acapulcensis*, even though the difference was only significant for the last species: $t=2.81$, 43 d.f., $P<0.01$).

The hawking flycatchers were the only guild which showed a strong preference to forage in *Bursera* sp. in both years (Figure 6.6 and 6.7). They also had a significant preference for *Ipomoea* sp. and in 1991, they also foraged in *Heliocarpus* sp. and *Prosopis juliflora* in addition to *Lysolima acapulcensis* and *Acacia macilenta.* In 1990 they favoured *Mimosa* sp. (Figure 6.7). The results from regression analyses between this guild TPI and the arthropod densities per plant species were not significant.

Ubiquitous insectivores (also in Figures 6.6 and 6.7) were divided into two groups (chapter 3.5). Besides the preference for *Ipomoea* sp. by the first ubiquitous insectivorous group, they differed in their choices with respect to other plants in the two years. In 1990, this guild foraged on *Mimosa galeotti, Acacia macilenta, Quercus crassifolia, Prosopis juliflora* and *Q. castanea* (Figure 6.6). These plants were either unimportant or avoided in the second year in which *Ceiba acuminata*, *Mimosa* sp. and particularly *Ficus* sp. was frequently used (Figure 6.7). No significant relationship was found between the arthropod densities and the foraging preferences of this guild.

The second group of ubiquitous insectivores foraged in *Quercus crassifolia* in both years. The birds from this guild also favoured *Ipomoea* sp. in 1990 (Figure 6.6). In 1991 (Figure 6.7), they favoured *Conzattia sericea*, *Lysolima acapulcensis* and *Bursera* sp.

Even though the regression between the 1991 TPI for this guild and the homopteran densities per plant species was significant ($R^2=0.25$, 20 d.f., $P<0.05$), the relationship does not appear to be linear (Figure 6.9). There appears to be a threshold effect (at about 1.6 homopterans) bellow which plants are not used. Nevertheless, *Lysolima acapulcensis, Conzatia sericea* and *Bursera* sp., the favoured plant species had the highest homopteran densities besides *Annona* sp. *Bursera* sp. which was not used in 1990 had significantly higher homopteran densities in 1991 ($=0.3$ in 1990 and $=1.1$ in 1991; $t=2.11$, 43 d.f., $P<0.05$). On the other hand the ubiquitous insectivores did not use *Annona* sp. which was the plant with highest densities of homopterans in 1991 ($=2.9$, not sampled in 1990). The avoidance of this shrub might have to do

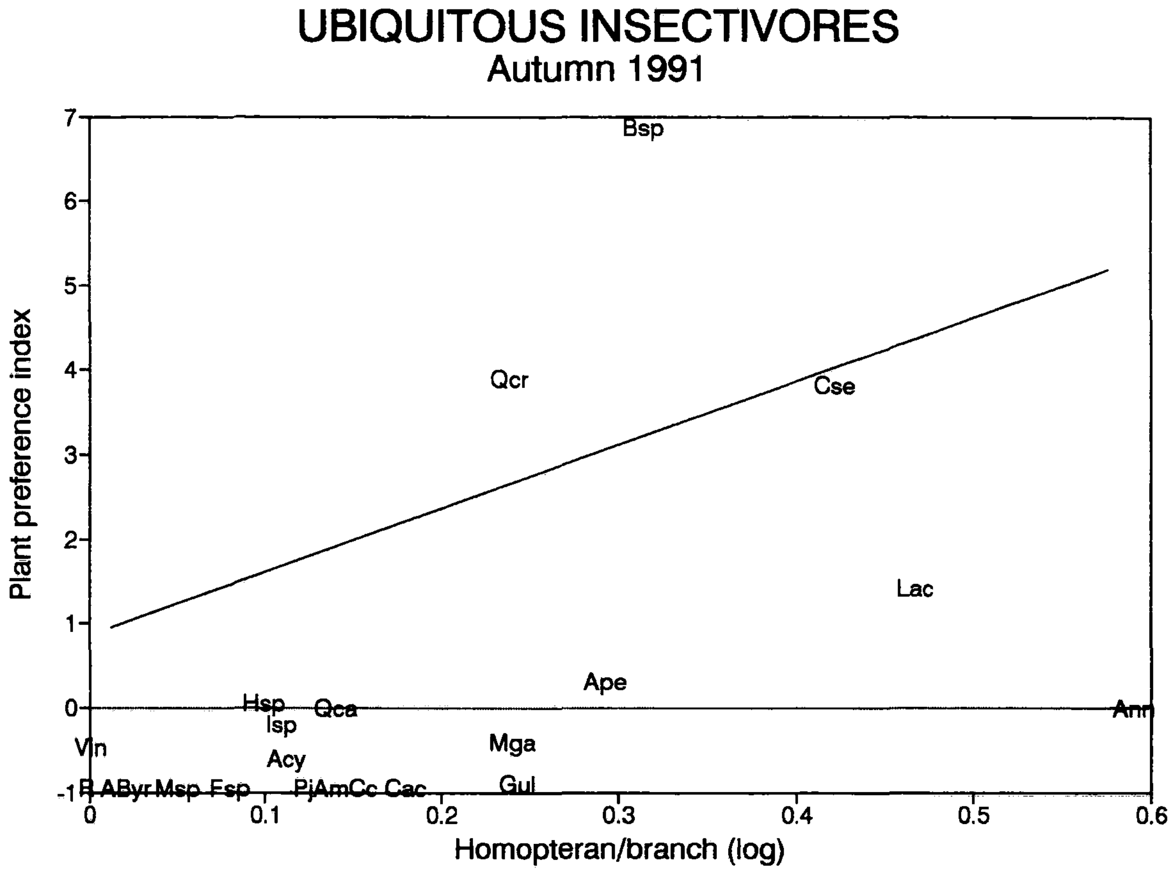


Figure 6.9. Regression between tree preference index of the second group of ubiqutious insectivorous guild and the homopteran densities per plant species in 1991. R=Randia sp., A=Apocynaceae shrub, other mnemonics are composed from first genus and first or first two species words. Negative values in the ordinate indicate bird avoidance for the plant species.

with its low cover (less than 1% of the total plant cover), particularly in woodlands and the edge, were the individuals of these guilds were more commonly found, and will be considered in the discussion.

Woodland omnivores showed a preference for *Quercus crassifolia* and *Lysolima acapulcensis* in both years, and for *Bursera* sp. in the second (Figures 6.10 and 6.11). No significant relationships between their TPI and the arthropod densities was found.

Although the distribution of forest and woodland insectivores is adjacent, it is almost asympatric (Figure 6.1). Therefore, in addition to the analyses above, their foraging preferences were estimated as well by including only those plant species present in their respective habitats.

Forest insectivores were particularly attracted to *Prosopis juliflora, Acacia cymbispina, A. macilenta, Ipomoea* sp. and *Mimosa galeotti* in 1990 (Figure 6.10). They also foraged on the vines, *Conzattia sericea* and *Bursera* sp. In 1991 (Figure 6.11), they showed a strong preference for *P. juliflora, Ipomoea* sp. and *A. cymbispina,* and a slight preference for *Bursera* sp. In both years, they avoided both oak species (*Quercus crasifolia* and *Q. castanea*), *Ficus* sp. and *Guazuma ulmifolia.* There was a significant relationship between the forest insectivores TPI and the lepidopteran larvae densities per plant species in 1991 ($R^2=0.19$, 20 d.f., $P<0.05$), in which:

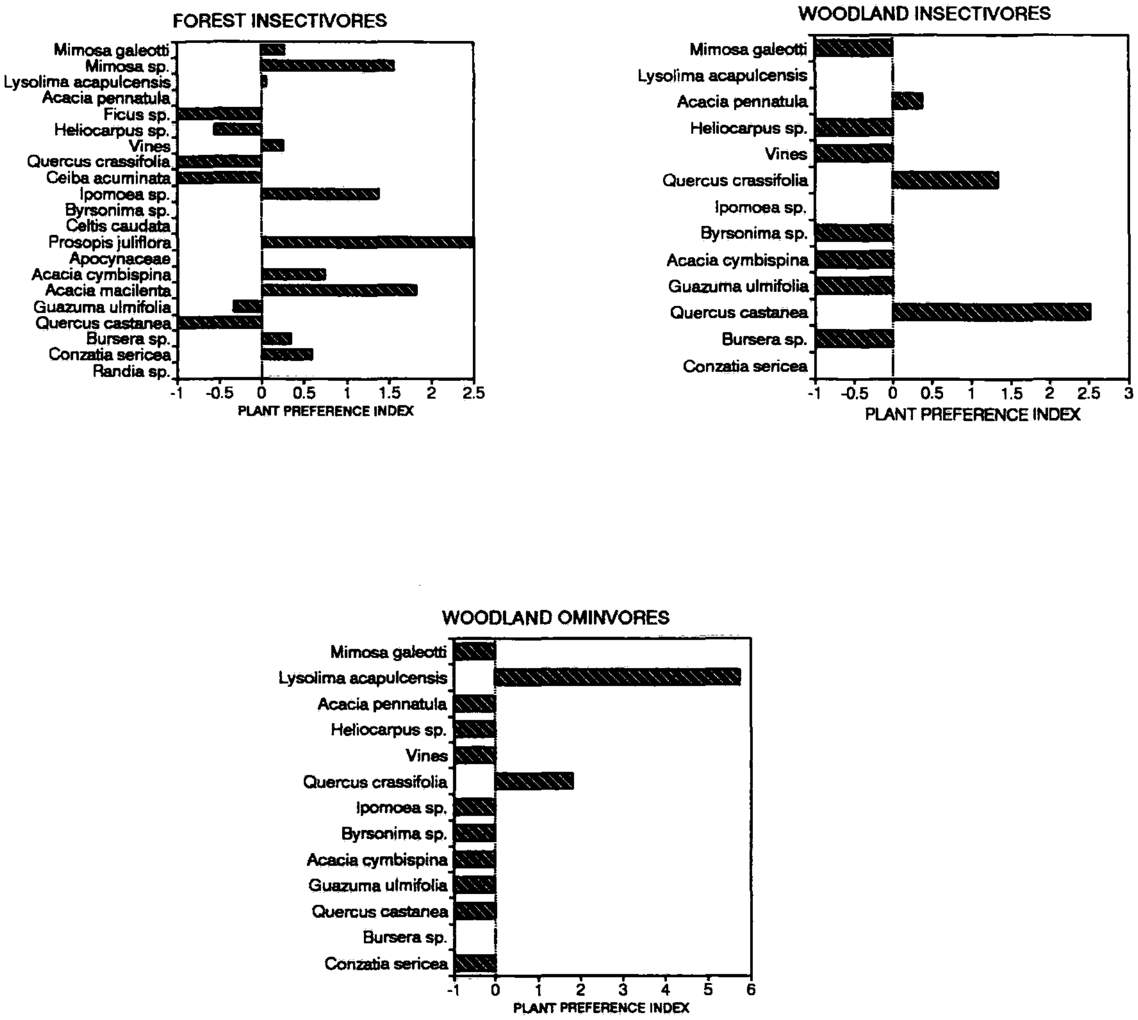


Figure 6.10. Plant foraging preferences by the forest and woodland insectivores and woodland omnivores in 1990. The tree preference index was used for the calculations.

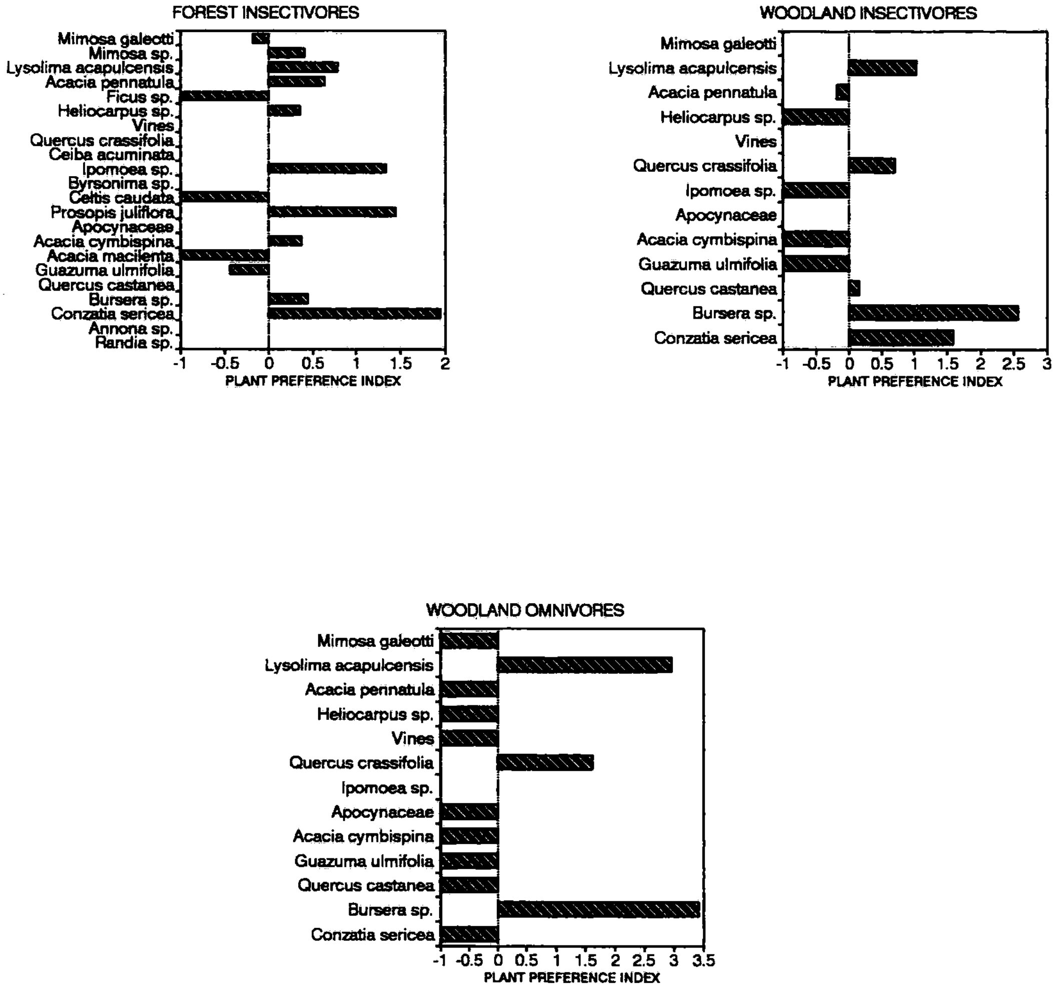


Figure 6.11. Plant foraging preferences by the forest and woodland insectivores and the woodland omnivores in autumn 1991. The tree preference index was used in the calculations.

$$Y = -0.16 + 2.16 (X) \pm 1.01$$

The regression (Figure 6.12) shows that the favoured plants had high lepidopteran larvae densities, while those which were either rejected (*Ficus* sp., *Celtis caudata*, *Guazuma ulmifolia*) or indifferent (*Apocynaceae* shrubs, the vines, *Annona* sp., *Byrsonima* sp.) had low densities. The main exception was *Ipomoea* sp. which was much favoured but contained no lepidopteran larvae. As explained above, this plant was likely to have high densities of unsampled arthropods which could explain why birds showed such a high preference for it.

Woodland insectivores were attracted to *Quercus castanea* and *Q. castanea* in 1990 and to *Bursera* sp., *Conzatia sericea, Q. crassifolia* and *Lysolima acapulcensis* in 1991. The TPI was significantly correlated with the homopteran densities in the second year ($R^2=0.37$, 11 d.f., $P<0.05$). The regression equation is:

$$Y = -0.82 + 4.66 (X) \pm 1.84$$

The plot (Figure 6.12) shows that the three favoured plants in particular (*Lysolima acapulcensis, Consatia sericea* and *Bursera* sp.) were those with highest homopteran densities. The regressions for the first year were not significant.

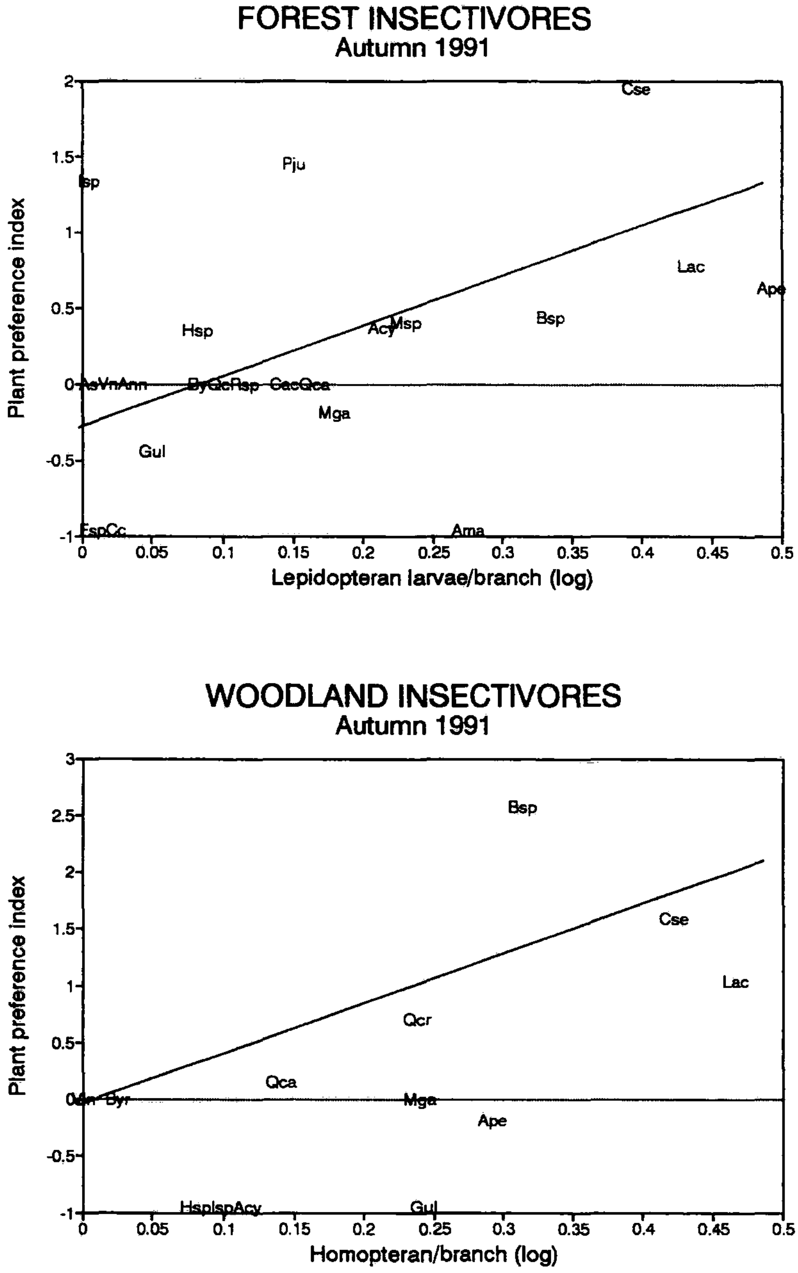


Figure 6.12. Regression between the tree preference index of the forest insectivorous birds and the lepidopteran larvae densities per plant species, and of the woodland insectivores and the homopteran densities per plant species. Mnemonics composed from first genus word and first two species words. Negative values in the ordinate indicate plant avoidance.

In order to further test the foraging preference results of both years, the arthropod densities which were significantly correlated with a particular guild in one year, were forced in a regression with the foraging observations of the other year. The slopes of the two years were then compared in order to test if they were significantly different. The results showed that the slope for the forest insectivores TPI and the lepidopteran larvae as well as the slope for the woodland insectivores TPI and the homopteran densities per plant species in 1990 (which were not significantly different from zero) were not significantly different from the corresponding slopes for 1991 (for whom the regression was significant). In the first case $t=1.68$ with 19 d.f. and in the second $t=1.12$ with 11 d.f. Similarly, even though the regression between the TPI for the second group of ubiquitous insectivores and the homopteran densities was not significant in 1990, its slope was not significantly different from that of the first year (in which the regression was significant: $t=0.31$, 19 d.f.).

The results suggest that in both years, the woodland and ubiquitous insectivores had a preference for those plants with highest homopteran densities while forest insectivores preferred those with high lepidopteran larvae densities.

3.6.3. Discussion

There is some conflicting evidence on the connection between food abundance and the distribution of the bird species in ecological communities (Raitt and

Pimm 1976, Abbott *et al.* 1977, Schluter 1982, Hutto 1985, Repasky and Shluter 1994, Poulin *et al.* 1994).

Arthropod abundance was estimated in this study during autumn 1990 and 1991. Terminal branches of most plant species were sampled and from this, extrapolations were made on the relative arthropod groups in the main habitats. During the first year, there was a positive correlation between the gleaning insectivores and the lepidopteran larvae densities per plant species. There were no significant correlations between any of the arthropod groups and the bird guilds in 1991.

The positive correlation between the arthropods and the bird guilds in the first year supports other studies (Raitt and Pimm 1976, Schluter 1982, Hutto 1985). These studies found that food was one of the main controlling factors affecting bird density and distribution in different communities: north American deserts and vegetation gradients in the Galápagos islands and western Mexico. On the other hand the lack of any significant correlation in the second year, is in accord with Poulin *et al.* 1994 and Repasky and Schluter 1994. Their studies found that the distribution of wintering sparrows in a vegetation gradient in the Galápagos and the monthly abundances of different guilds in dry forests in Venezuela did not respond to their main food sources.

There is evidence that food is only limited at relatively infrequent years of environmental stress, where competition and stabilizing selection would play a fundamental role on the bird community (Grant 1986). At other times it would not be expected of birds to follow their resources closely, due to food superabundance.

According to the hypothesis of occasional environmental stress, conditions (less food or higher temperatures for example) in the study sites should have been more stressful during 1990, where the association between lepidopteran larvae and gleaning insectivorous birds was significant. In fact, precipitation was higher in 1990 (965.3mm in 1990 and 686.5mm in 1991). Although not statistically significant, rainfall in 1990 was also higher than the 15 year mean (761.3mm). The relatively higher precipitation in the first year could have been the cause of higher arthropod densities in the second year but this was not the case.

Perhaps the relationship between food and bird densities is related to the spatial scale of the study. At broad geographical scales (as in the altitudinal gradients Hutto made his studies) containing a variety of vegetation types, the correlations should be high because certain habitats would be more productive, and therefore containing highest arthropod densities. In this study, only three vegetation types were included: huizachales or thorn forests, mature forests and oak woodlands. Furthermore, the first two were very similar in composition (they differed mainly in structural factors) and possibly the addition of more habitats would help to discern with certainty the importance that food has on the bird densities.

In addition to the connection between food abundance and bird densities, this section attempted to find a relationship between the most frequently selected plant species and the arthropod densities that were found in them. Many studies in community ecology have described the plant foraging preferences by the birds species. It is generally assumed that the selected vegetation is a reflection of food availability, even though this supposition is seldom tested (Wiens 1989). In order to determine foraging preference in this study, multiple regressions were used between the arthropod groups densities and the tree preference index per plant species.

It must be recalled that the technique used to estimate arthropod abundances, was not suitable for some groups and therefore it was not possible to estimate their importance in the foraging preferences by the birds. Flies and flying hymenoptera, for example are very active and very likely to escape before falling in the nets. Diet analyzes, frequently find that insect larvae, beetles and homopterans as important food sources for insectivorous birds, but wasps and grasshoppers have also been frequently found in stomach contents. Robinson and Scott (1982), for example, found that even though different arthropods were found in all the bird species he studied, caterpillars were particularly common in vireos and *Dendroica* warblers stomach contents. Other warblers, appeared to prefer homopterans and at least one bird species (a tanager) found in their study sites selected wasps and beetles. Perhaps due to their foraging strategies, the authors found that flies were mainly taken by least flycatchers and redstarts.

Even though no stomach contents analysis were performed in this study, the total number of gleaning insectivores (as well as the forest insectivores in 1991) favoured those plants with higher lepidopteran larvae densities in both years (Figure 6.8). More interesting was the fact that while lepidopteran larvae densities on the plant species differed between years, the birds from these guilds still favoured those plants with the highest larvae densities (*Acacia macilenta, Quercus castanea, Prosopis juliflora* and *Mimosa* sp. in 1990 and *Lysolima acapulcensis, Conztatia sericea* and *Bursera* sp. in 1991). Since the gleaning insectivorous densities were correlated with the densities of lepidopteran densities in 1990, perhaps these insects indeed play an important plant in the distribution of the bird species belonging to this guild.

Gleaning insectivores also had a preference for *Ipomoea* sp. and *Quercus crassifolia* in both years. Neither of this trees had high larvae densities but it must be remembered that the *Ipomoea* sp. flowers presumably attracted flying arthropods which were not properly sampled. *Quercus crassifolia*, on the other hand, are the most abundant tree in the woodlands (57% of the total plant cover). There is some evidence (Nocedal 1984, Hutto 1985) that woodland insectivorous birds tend to forage in the vegetation layers with highest arthropod abundance. Since arthropods were not sampled from the top of the trees, where most gleaners were seen foraging, it might be that the highest *Q. crassifolia* layers had significantly higher arthropod densities.

When gleaning insectivores were divided according to their main distribution (forest and woodland), the forest insectivores still favoured those plants with high lepidopteran larvae in 1991. The woodland insectivores on the other hand (as was the case for the second group of ubiquitous gleaners), favoured those plants with high homopteran densities. Since lepidopteran larvae and homopterans had similar relative densities in the plant species (chapter 2.3), the importance of homopterans for the woodland guild were obscured but when only the plants in their main habitat were included, the homopterans emerged as their most important food choice in multiple regressions.

In 1991, both the lepidopteran larvae and the homopterans appeared to be important; the woodland and the ubiquitous insectivores searched for those plants with higher densities of homopterans, while the forest insectivores favoured those with highest lepidopteran larvae densities.

The woodland insectivores favoured *Bursera* sp., *Conzatia sericea* and *Lysolima acapulcensis*. *Bursera* sp. in particular, which was seldom used by insectivores in 1990, had significantly higher homopteran densities in 1991 (=0.3 in 1990 and $=1.1$ in 1991; $t=2.11$, 43 d.f., $P<0.05$). Furthermore, together with *Bursera* sp., *Conzattia sericea* and *Lysolima acapulcensis* had the highest homopteran densities in 1991.

The ubiquitous insectivores had similar preferences than the woodland insectivores. Although they favoured *Bursera* sp., *Conzatia sericea* and *Lysolima acapulcensis*, they avoided *Annona* sp., which had the highest homopteran larvae densities in 1991. The avoidance of *Annona* sp. may be explained by its low cover (less than 1%) and its physiognomy; being a shrub it is not very conspicuous (there are a few trees with even lower covers, but they are very large and mount above the mean vegetation high). Raitt and Pimm (1976) suggest that food availability might be influenced, among other factors, by sufficient density of food items in order to make exploitation economical. The same statement could be used for the plants in which animals look for food. If they are inconspicuous and have low cover, it is very likely that the birds will overlook them. If it is accepted that inconspicuous plants tend to be avoided regardless of their food abundance then (besides representing a good shelter for invertebrates) homopterans seem to be an important food choice for this guild.

Finally, Robinson and Scott (1982) found that foraging maneouvres were related to the type of food obtained by birds, medium-long hawk insectivores obtained mainly active prey like wasps and flies, while medium hover caught caterpillars and gleaning birds caught often cryptic prey. The hawking flycatchers in this study are mainly medium distance probers and they were not significantly correlated with any of the arthropod group densities. Perhaps they also look for other more active prey which were not adequately sampled. The woodland and forest insectivores, together with the ubiquitous insectivores are mainly gleaners searching for cryptic insects which are well represented by the homopterans and lepidopteran larvae in the sites included in this study.

4. General discussion and conclusions

This thesis explores various aspects of the bird community in a dry forest of western Mexico. It attempts to relate the bird species composition, richness and diversity with the vegetation composition and structure and, in particular for insectivores, with food availability.

A canonical correspondence analysis, was used to relate bird density, richness, diversity and evenness with the plant associations. Multiple regressions helped to identify the plant variables which were associated with the diversity paramters. It was evident that certain habitats support higher number of species and individuals. In particular, those plots where small leaved plants dominated had more species and higher total bird densities. The same habitats had the lowest equitability indices, suggesting that a few of the bird species present had a very high number of individuals; those plots with high equitability indices had no numerically dominating species. This pattern was repeated in both autumns and both springs.

The similarities in bird numbers between years suggests that certain habitats may provide better or more abundant resources (since they support higher bird densities). In fact, those habitats with high covers of small leaved plants, either have more food resources (i.e. higher number of homopterans and lepidopteran larvae were found in small leaved plants such as *Lysolima acapulcensis* and *Acacia cymbispina*) or include plants in which food is more easily accessible (the fruit produced by *Opuntia* sp. and *Stenocereus* sp. or the flowers of *Ipomoea* sp.). The plots in which *Quercus crassifolia*, broad leaved plants (*Guazuma ulmilolia* and *Heliocarpus* sp.), and the >2.5m vegetation cover dominated had low numbers of species and individuals. *Q. crassifolia* was one of the species with fewer arthropods (chapter 3.5) and this may partially explain its negative correlation with bird species abundance. *Guazuma ulmifolia*, together with *Heliocarpus* sp. had few homopterans and lepidopteran larvae (which seem to be the preferred arthropod groups for insectivores) and were rarely used by birds (chapter 3.4). These groups appear to be the preferred insect food for gleaning insectivores as shown in chapter 3.5).

Richness was higher in the vegetation interface but also in thorn forests (particularly in autumn). The high number of species in the vegetation interface was expected since it is usual to find species from both "parent communities" in these habitats (Pianka 1988, Urban and Smith 1989). The high number of species in thorn forests supports Poulin *et al.* (1995) who say that many bird species are opportunistic in Venezuelan dry forests. The food availability provided by those species attracting high total bird densities might also attract a large number of species.

The negative relationship between diversity and equitability is explained by the fact that although these plants attracted many bird species, some of them were particularly abundant and were very efficient in using these plants. As has been found in other studies (Tomoff 1974, Wilson 1974, Nocedal 1984), foliage height diversity was not closely related with bird species diversity.

When the distribution of the bird species was analyzed, it was found that bird ordinations separated the main habitats in each of the four seasons during which the study was conducted. Nevertheless, there were no discreet groups of birds attached to the vegetation types; the segregation of habitats resulted from loose groups of bird species sharing certain groups of habitats. This distribution, which follows the individualistic distribution of the bird species (Gleason 1926), was expected and has been documented in the gradient studies conducted by Bond (1957), Terborgh (1977) and Navarro (1992).

Hutto (1985) suggests that birds respond to certain habitat cues at regional scales, particularly when the vegetation types differ markedly. In fact, when an attempt was made to identify the individual variables explaining the bird species distribution, it was clear that those species characteristic of vegetation types (dry forests and woodlands) were those appearing in the results. With the exception of *Acacia cymbispina* those species which were often seen used by birds were not important in the ordination results. The herbs, both oak species (*Quercus crassifolia* and *Q. castanea*) and *Acacia pennatula* were particularly common in woodlands and had the highest negative scores in the ordinations, while *Croton ciliato-glandulosae*, *A. cymbispina* and *Byrsonima* represent dry forests and had high positive scores

(Table 4.1).

The bird species ordination not only segregated the woodland from the dry forests. Different habitats corresponding to the main associations within the predominant vegetation types (i.e. huizachales, mogotes and mature forests may be regarded as different associations belonging to dry forests) became obvious in further axes of the analyses. The segregation of these associations was more difficult to anticipate because the composition between them is similar. Mixed woodlands were segregated from oak woodlands and mature forests from thorn forests in all seasons. The interface between forests and woodlands was also differentiated.

Rotenberry (1985) found it likely that those plants to which the variation in bird densities are likely to respond at local scales are those which provide more food. It was therefore expected that those plants offering better food resources would become obvious in the ordinations.

Although some of the significant variables simply seem to represent the plant associations (as in the separation between the main vegetation types), others are used by birds directly (*Ipomoea* sp. in the first year and the small leaved thorny trees in both years). On the other hand, the fact that these plants (particularly the small leave thorny trees) are typical of certain associations makes the results difficult to interpret (do these plants actually attract birds because they offer more food or do they appear in the ordinations because they represent a particular vegetation type?). Poulin *et al.* (1995) found that the distribution of the bird species guilds in a Venezuelan dry forest was not linked to the abundance of those plants offering the main source of foods for the different guilds. Perhaps the same pattern occurs in the dry forests of western Mexico.

Nevertheless, even though the importance of the plants preferred by the birds was ambiguous in the ordinations, there seems to be a connection between bird composition and food availability. Insectivores and hummingbirds, for example were more common in autumn, when there are flowers and more arthropods. In spring, where more fruit is to be found, frugivores and opportunistic species were more abundant.

At local levels (i.e. within the plant associations present in dry forests), the distribution of the birds may be in part related to their foraging behaviour. The forest insectivores, represented by *Polioptila caerulea* and *Vermivora celata* were particularly dense in huizachales and the interface, were they had a preference to forge in small leaved shrubs where high densities of lepidopteran larvae and homopterans were found. Hummingbirds were also numerous in the interface and huizachales, where more flowers are provided by *Ipomoea* sp. The hawking flycatchers like *Empidonax* sp., *Myopatis viridicata, Camptostoma imberbe* and *Myiarchus cinerascens* were frequent in both huizachales and mature forests. These species look for active prey within the foliage (Robinson and Scott 1982) and seem to be less attached to plants with a particularly growth form. Frugivore-insectivores like *Icterus pustulatus* were common in mogotes where *Ficus* sp. (which produces large amounts of edible fruit), is very common. The fact that the densities of the different groups of birds and those plants which provide their favoured food sources were not correlated seems to indicate that birds evidently occupy those habitats where their main food supply is abundant, but the cues to occupy those habitats are not the food resources themselves. The lax correspondence between bird densities and food abundance is not surprining. Since plant phenology (which eithter directly or indirectly controls bird food resources) is largely fluctuating between years (Murphy and Lugo 1986), it would be detrimental for the bird populations to follow the food resources very closely. Birds have to be flexible in variable environments.

In order to explore the ability of birds to look for the resources available, their plant preferences were analyzed. All the birds were first grouped into guilds (because not enough observations could be made at the species level). What was attempted was to see if, once inside their chosen habitat, birds looked in particular for those plants offering the highest (or most adequate) food densities.

Chapter 3.5 examined the plant species preferences by the different guilds. The food availability for nectarivores, granviores and frugivores was not measured and the importance of the plants was only inferred.

The different guilds had a preference for those plants corresponding to their foraging strategies and their main diet predisposition. It was also clear that some guilds change their diets depending on availability. Granivore-insectivores and frugivore-insectivores searched for arthropods in the foliage in autumn but were seen looking in the floor (presumably for seeds) and eating fruit respectively during spring. Hummingbirds were also seen looking for arthropods in spring but fed mainly on nectar during autumn.

Some trees, such as *Ipomoea* sp. were used in different ways by different guilds. Hummingbirds searched for nectar in the flowers, while insectivores searched for arthropods. Flycatchers used *Ipomoea* sp. as platforms and picked up flying insects from the air and woodpeckers were seen probing in the bark in search for buried prey. The foliage of *Conzattia sericea* was used by gleaning insectivores, but the trunk and large branches were favoured by wrens (bark gleaners).

The phenological phase of some plants determined the way it was used. Besides the flowers of *Ipomoea* sp., *Opuntia* sp. and the vines (which were used by hummingbirds in autumn and spring respectively), *Lysolima acapulcensis* was favoured by different guilds in spring 1991 because its leaves were starting to appear when at a time when most other plants were still deciduous (where higher densities of arthropods could presumably be found). On the other hand, *Prosopis juliflora*, which is a conspicuous evergreen tree was only favoured by frugivore-insectivores in spring 1991.

The scarce attention *P. juliflora* received in spring 1992 can only be explained because in 1992 was an extremely wet season (because of El Niño effect) and other plants were green (therefore birds had more plant choices where they could look for food).

Bursera sp. was the only species which was consistently used by hawking flycatchers. This species produces resinous fruits which are eaten by *Myiarchus cinerascens* and *Empidonax* sp. Further studies are needed in order to understand why these fruits are particularly appealing to these flycatchers. *Bursera* sp. was also widely used by insectivores during autumn 1991. Interestingly the foliage of this tree supported high densities of homopterans and lepidopteran larvae during autumn 1991 but not in 1990 when birds did not forage on this tree.

Robinson and Scott (1982) found that foraging maneouvres were related to the type of food obtained by birds, medium-long hawk insectivores obtained mainly active prey like wasps and flies, while medium hover caught caterpillars and gleaning birds caught often cryptic prey. The hawking flycatchers in this study are mainly medium distance probers and had no significant preference for any plant species with particular high densities of any of the arthropod groups. Perhaps they look for more active prey which was not adequately sampled.

The case of the hawking flycatchers illustrates the fact that food and certain habitat components are combined and that their individual influence may be difficult to dissociate. Nevertheless, it is clear that, besides looking for conspicuous items such as fruits and flowers, birds also learn to recognize those plants with higher densities of concealed food sources, represented by certain arthropod groups (Heinrich and Collins 1983). This is reinforced by the preference of gleaning insectivores to look for food in those plants with highest densities of lepidopteran larvae and homopterans in this study.

It is true that the estimation of the different food types is time consuming and laborious. Nevertheless, besides being the source of basic studies, the importance of food and its relationship with plant structure and composition on the bird species distribution, is essential in managing and conservation strategies.

Appendix 2.1. Autumn 1990 mean number of invertebrates in plant terminal branches.

	Randia sp.	Mimosa galeottii	Bursera sp.	Quercus castanea	Guazuma ulmifolia	Vines	Acacia macilenta	Acacia cymbispina	Apocynaceae shrub	Prosopis juliflora
GASTEROPODA			0.05		0.02		0.05	0.02		
ISOPODA										
COLLEMBOLA	0.17	0.02		0.14						0.14
PHALANGIDA	0.33									
THYSANURA										0.18
ODONATA		0.02								
ORTHOPTERA										
Acrididae					0.02		0.05			0.05
Gryllidae				0.05			0.09		0.11	0.05
Blattidae		0.16			0.14		0.14	0.02	0.22	0.14
Mantidae		0.02						0.02		
DERMAPTERA		0.07	0.18	0.27	0.16	0.22	0.16	0.25	0.11	0.09
THYSANOPTERA	0.33			0.09	0.02	0.13		0.05		0.14
PSOCOPTERA	0.17	0.07		0.18	0.02					
HETEROPTERA										
Miridae	0.33	0.11	0.27	0.14	0.02	0.04	0.18	0.18	0.22	0.27
Alydidae				0.05	0.02			0.07		0.05
Piesmidae										
Reduviidae	0.33	0.11	0.32		0.07		0.23	0.11		0.59
Tingidae		0.20	0.45	1.45	1.48	0.13	0.14	0.50	0.56	0.05
Lygaeidae		0.05			0.05			0.02		
Coreidae					0.02					0.09
Corimelaenidae		0.05			0.02			0.02		
Pentatomidae	0.33		0.05	0.05	0.02	0.09		0.11		
Other Heteroptera	0.17	0.02			0.02	0.04				
HOMOPTERA										
Delphacidae		0.02			0.02					
Dictyopharidae										0.05
Membracidae		0.77	0.05	0.23	0.11		0.55	0.59		0.18
Cercopidae		0.05	0.09		0.11			0.02		0.05
Cicadellidae	0.33	0.80	0.18	0.59	0.18		0.23	0.30		0.18
Flatidae										0.05
Issidae			0.05	0.09				0.02		
Psyllidae		0.07		0.05	0.02		0.23	0.30		0.36
Aphididae			0.05	0.05	0.02	0.04	0.14	0.39		0.14
Coccoidea		0.07			0.02	0.26		0.07	0.22	
NEUROPTERA		0.07		0.14			0.05	0.02		0.05
COLEOPTERA										
Staphylinidae										0.05
Lathrididae				0.32						
Carabidae				0.05						
Malachidae			0.05		0.05			0.05		
Dermestidae		0.16								
Nitidulidae		0.09	0.05	0.27	0.02			0.02		
Coccinellidae		0.02		0.09	0.05					
Tenebrionidae		0.02		0.05	0.02					
Bosthrichidae		0.07			0.02					
Chrysomelidae		0.02	0.05	0.14	0.05					
Cassinidae	0.17				0.02	0.04		0.02		
Hispinae					0.09					
Bruchidae	0.33	0.02	0.05		0.20		0.09	0.05		0.23
Curculionidae	0.17	0.18	0.23	0.32	1.48	0.09	0.41	0.59		0.05
Scolytidae		0.20		0.59	0.02					
Other Coleoptera	0.17	0.02					0.05	0.05		
TRICHOPTERA		0.05		0.09	0.07			0.02		
LEPIDOPTERA	0.17									0.23
Geometrid larvae		0.23		0.14	0.02	0.13	0.14	0.41		0.05
Bristly larvae		0.05		0.09	0.05	0.04		0.02	0.11	0.09
Other larvae		0.57	0.14	1.05	0.34	0.30	1.18	1.18	0.33	0.68
DIPTERA		0.11	0.09	0.05	0.09	0.22	0.05	0.07	0.00	0.18
Larvae		0.02		0.05		0.13	0.27	0.05		0.14
SYPHONAPTERA					0.02					
HYMENOPTERA										
Vespoidea					0.02					
Apidae										
Braconidae		0.02			0.05		0.09	0.02		
Formicidae	0.17	0.11			2.34	0.70	0.59	0.61	0.78	0.68
Other Hymenoptera		0.02		0.18			0.05	0.09	0.22	
ACARINA	0.33	0.18	0.14	0.14	0.23	0.26	0.64	0.45	0.33	0.36
PSEUDOESCORPIONIDA									0.11	
ARANEAE										
Uloboridae			0.05		0.07					
Mimetidae		0.05			0.05			0.05		
Oxypidae	0.17	0.48	0.09	0.23	0.03	0.17	0.23	0.27		0.23
Thomisidae		0.25			0.32	0.17	0.64	0.41	0.11	0.32
Saltacidae	0.83	0.77	0.09	0.59	0.52	0.65	0.77	1.14	0.11	1.05
Peucetia sp.			0.05			0.04	0.05	0.07		
Other spiders	1.50	2.50	1.00	2.05	1.75	0.96	0.73	1.68	1.56	0.86

Appendix 2.1 (cont.). Autumn 1990 mean number of invertebrates in plant terminal branches.

	Celtis caudata	Byrsonima sp.	Ipomoea sp.	Ceiba acuminata	Quercus crassifolia	Heliocarpus sp.	Ficus sp.	Lysiloma acapulcensis	Mimosa sp.	Acacia pennatula	Conzattia sericea
GASTEROPODA											
ISOPODA								0.03		0.03	
COLLEMBOLA					0.14	0.03		0.09		0.03	
PHALANGIDA						0.03		0.03			
THYSANURA							0.13		0.06		
ODONATA											
ORTHOPTERA											
Acrididae						0.03					
Gryllidae		0.06			0.14	0.05					
Blattidae		0.13	0.13	0.14		0.13	0.63	0.06	0.53	0.06	0.04
Mantidae						0.05	0.13				
DERMAPTERA	0.40	0.06	0.25	0.43	0.38	0.28	0.63	0.09		0.09	
THYSANOPTERA	0.20	0.06	0.06	0.14	0.05		0.88	0.06		0.06	
PSOCOPTERA		0.13			0.33	0.03					
HETEROPTERA											
Miridae			0.19			0.21	0.38	0.24		0.33	0.26
Alydidae		0.06				0.10					0.04
Piesmidae						0.03		0.06			
Reduviidae					0.10		0.50	0.09	0.18	0.12	0.11
Tingidae		8.69	0.69	0.57	0.76	7.69	0.25	0.85	0.18	1.79	1.70
Lygaeidae						0.05		0.03			
Coreidae	0.20										
Corimelaenidae								0.03		0.03	
Pentatomidae			0.44		0.05	0.21		0.06		0.03	0.07
Other Heteroptera					0.05	0.13				0.09	
HOMOPTERA											
Delphacidae										0.03	
Dictyopharidae											
Membracidae					0.05			0.12		0.03	
Cercopidae						0.03					
Cicadellidae			0.63		0.76	0.08		0.42	0.06	1.09	0.70
Flatidae											
Issidae					0.14			0.09	0.06	0.06	
Psyllidae						0.10	0.38	0.09			0.04
Aphididae		0.63	0.06		0.05	0.03		0.03	0.18	0.06	
Coccoidea			0.06			0.05		0.06		0.27	0.04
NEUROPTERA		0.06				0.03		0.03	0.06	0.06	
COLEOPTERA											
Staphylinidae	0.20				0.05		0.13			0.03	
Lathrididae					0.10				0.53		
Carabidae											
Malachidae					0.05		0.13	0.09		0.24	0.07
Dermestidae		0.06									
Nitidulidae					0.19	0.03				0.52	0.04
Coccinellidae					0.05	0.08				0.03	0.04
Tenebrionidae	0.40		0.19		0.05	0.03	0.13	0.09			0.04
Bosthrichidae							0.25	0.03	0.06	0.03	0.04
Chrysomelidae					0.14	0.05		0.15		0.33	0.19
Cassinidae			0.06								
Hispinae		0.06	0.06			0.92					
Bruchidae		0.06	0.06	0.14		0.26		0.06	0.18		0.04
Curculionidae		0.50	0.06		0.29	0.41	0.13	0.67	0.29	1.06	1.37
Scolytidae					0.05	0.03					
Other Coleoptera			0.06		0.10	0.03	0.13			0.03	
TRICHOPTERA								0.06		0.06	0.11
LEPIDOPTERA											0.04
Geometrid larvae			0.06	0.14		0.03		0.03	0.12	0.64	0.19
Bristly larvae			0.13			0.05	0.13	0.06	0.06		0.11
Other larvae		0.13	0.38	0.29	0.19	0.28	0.13	0.91	1.29	2.12	1.04
DIPTERA	0.00	0.00	0.06	0.14	0.05	0.10	0.00	0.12	0.00	0.15	0.04
Larvae				0.14						0.06	0.04
SYPHONAPTERA											
HYMENOPTERA											
Vespoidea					0.05					0.03	
Apidae								0.03			
Braconidae											
Formicidae		0.56	0.38	2.00	0.33	0.10	0.25	0.12	0.24	0.30	0.04
Other Hymenoptera						0.08	3.25	0.09		0.12	0.04
ACARINA		0.06	0.13	0.14	0.05	0.10		0.21	0.24	0.15	0.48
PSEUDOESCORPION			0.06								
ARANEAE											
Uloboridae					0.10						
Mimetidae									0.06		
Oxypidae		0.19	0.25	0.29	0.24	0.31	0.38	0.18	0.88	0.24	0.19
Thomisidae		0.19	0.06	0.14	0.05	0.05		0.21	0.65	0.42	0.22
Saltacidae		0.31	0.31	0.14	0.33	0.79	0.50	0.27	1.00	0.70	0.52
Peucetia sp.					0.05	0.05	0.13	0.03		0.03	0.04
Other spiders	0.20	1.69	0.63	0.43	1.00	2.36	1.50	1.24	2.00	2.24	1.63

Appendix 2.2. Autumn 1991 mean number of invertebrates in plant terminal branches.

	Randia sp.	Annona muricata	Mimosa galeottii	Bursera sp.	Croton sp.	Quercus castanea	Randia sp.	Guazuma ulmifolia	Vines	Acacia macilent	Acacia cymbispina	Apocynace shrub	Prosopis juliflora
GASTEROPODA								0.17					
THYSANURA				0.04									
ORTHOPTERA													
Tettigonidae													
Acrididae					0.09								
Gryllidae				0.04		0.08		0.08			0.04		
Blattidae		0.17		0.09		0.17		0.17					0.08
DERMAPTERA		0.17		0.17				0.58	1.67			0.33	
THYSANOPTERA						0.42		0.17		0.17	0.08		
PSOCOPTERA		0.42	0.13	0.04				0.08					0.08
HETEROPTERA													
Miridae		0.25	0.04		0.91	0.08		0.75		0.50	0.08		0.25
Piesmidae													
Anthocoridae						0.08							
Berytidae		0.08											0.08
Rhopalidae													
Nabiidae		0.08	0.08								0.04		
Reduviidae			0.13	0.09		0.08		0.08			0.25	0.17	2.00
Tingidae		0.25	0.08		0.09	0.08		0.08	0.17				
Lygeidae		0.08	1.71	2.04		3.50							
Coreidae			0.04							0.17			
Corimelaenidae		0.08									0.04		
Pentatomidae		0.25		0.13						0.17	0.13		
Other Heteroptera								0.17			0.04		
HOMOPTERA													
Membracidae		0.08	0.46		0.18			0.08		0.33	0.04		
Cixiidae											0.13		0.25
Cercopidae			0.04			0.08							
Cicadelidae		3.33	0.33	0.09	2.45	0.17		0.67			0.13		0.08
Flatidae													
Derbidae													
Issidae													
Psyllidae										0.17	0.17		
Aphididae		0.25	0.04			0.25							
Coccoidea													0.17
NEUROPTERA		0.08	0.04	0.04	0.18	0.42							
COLEOPTERA													
Larvae	0.20	0.08	0.08	0.09		0.08	0.20						
Staphylinidae													
Latthridiidae													
Erotylidae				0.04									
Carabidae		0.08	0.04	0.09					0.17				
Dermestidae			0.04										
Nitidulidae													
Phalacridae			0.04			0.17		0.17					
Coccinellidae			0.13					0.17					
Melandryidae		0.08				0.08							
Tenebrionidae											0.04		
Anobiidae													
Cerambicidae													
Chrysomelidae			0.04	0.04	0.09			0.08		0.33	0.04		
Hispinae		0.25	0.17		0.09	0.17		0.08					
Bruchidae	0.20	0.25	0.04	0.70		0.08	0.20	0.17			0.21		0.50
Curculionidae		0.08	0.04	0.22				0.17		8.50	0.04	0.33	
Scolytidae			0.08										
Other Coleoptera	0.20	0.33	0.17				0.20				0.04		
LEPIDOPTERA													
Geometrid larvae			0.08	0.04		0.08		0.08		0.83	0.42		0.25
Bristly larvae			0.04	0.04	0.09						0.08		
Other larvae	0.40	0.08	0.46	0.04	0.09	0.42	0.40	0.08		0.50	0.54		0.25
Tineoidea	0.40	0.33		0.13	0.09		0.40	0.17					
DIPTERA		0.08	0.04	0.13		0.08		0.08			0.08		0.08
HYMENOPTERA													
Vespoidea		0.08											
Apidae													
Braconidae		0.17		0.04									0.08
Formicidae		0.17	0.08			0.08		0.17	0.50	0.50	0.17		0.08
Other Hymenoptera		1.00	0.13		0.09			0.17			0.04		0.17
ACARINA	2.00	0.25	0.08	0.09		0.08	2.00	0.42	0.17	0.33	0.58	0.17	1.25
PSEUDOESCORPIONID						0.08							
ARANEAE													
Mimetidae	0.20		0.08	0.04			0.20				0.04		
Uloboridae		0.08				0.17		0.08					
Saltacidae		3.75	1.17	0.26	0.73	0.58		0.50	0.17	1.67	1.38	0.33	0.83
Thomisidae	0.40	0.50	0.29	0.09	0.64	0.17	0.40	0.75		3.00	0.83	0.17	0.42
Oxipidae		0.50	0.38	0.35	4.55	0.17		0.25	0.17	0.67	0.38	0.33	0.17
Other spiders	0.80	5.42	1.63	2.96	0.91	1.08	0.80	2.75	0.67	1.50	2.08	0.50	0.67

Appendix 2.2 (cont.). Autumn 1991 mean number of invertebrates in plant terminal branches.

	Celtis caudata	Byrsonima sp.	Senecio sp.	Ipomoea sp.	Ceiba acuminata	Quercus crassifolia	Heliocarpus sp.	Ficus sp.	Acacia pennatula	Lysiloma sp.	Mimosa sp.	Conzattia sericea	Herbs
GASTEROPODA	0.17												
THYSANURA										0.08			
ORTHOPTERA													
Tettigonidae		0.08											
Acrididae			0.11										
Gryllidae		0.08	0.06								0.08		0.08
Blattidae	0.17	0.08	0.06	0.18									
DERMAPTERA			0.89	0.47	0.17				0.18				0.08
THYSANOPTERA			0.11	0.06		0.17			0.06	0.08		0.08	
PSOCOPTERA	0.17	0.33	0.11			0.17							
HETEROPTERA													
Miridae	0.17	0.17	0.33	0.06		0.17	0.64		0.06		0.17	0.75	
Piesmidae									0.06				
Anthocoridae				0.24					0.06			0.08	0.08
Berytidae											0.08		
Rhopalidae			0.06				0.09						
Nabiidae			0.28										
Reduviidae		0.17	0.17	0.12		0.17				0.08	0.08		
Tingidae	0.33	5.33	0.11	0.41			4.45	0.33	0.65	0.17			
Lygeidae			0.39			0.17	0.09	0.17	0.06			0.17	0.33
Coreidae			0.17								0.08		
Corimelaenidae			0.06					0.17					
Pentatomidae			0.39	0.29			0.55			0.25			0.17
Other Heteroptera			0.61										
HOMOPTERA													
Membracidae			0.11	0.12		0.33			0.06				0.17
Cixiidae	0.17								0.06		0.08		
Cercopidae	0.33								0.06				
Cicadelidae			0.83	0.29	0.67	0.50	0.27	0.17	0.94	3.58	0.08	1.00	0.08
Flatidae		0.08											
Derbidae			0.22										
Issidae													0.08
Psyllidae									0.06	0.83			
Aphididae			0.17			0.17	0.09						
Coccoidea			0.11					0.17				0.08	0.08
NEUROPTERA		0.08	0.17						0.12		0.33	0.08	0.08
COLEOPTERA													
Larvae				0.06	0.17								
Staphylinidae			0.39										
Latthridiidae													0.08
Erotylidae	0.17		0.06										
Carabidae		0.08	0.11	0.06					0.06				
Dermestidae						0.17							
Nitidulidae						0.17							
Phalacridae		0.08	0.33			0.17			0.06			0.08	1.75
Coccinellidae			0.11	0.18	0.17								
Melandryidae			0.06					0.17		0.08			0.08
Tenebrionidae				0.35					0.06				
Anobiidae						0.17							0.08
Cerambicidae				0.06									
Chrysomelidae			0.11				0.27	0.17	0.18			0.17	
Hispinae			0.06				0.64		0.06	0.08			
Bruchidae	0.67	0.08	0.28	0.12			0.09	0.17	0.12		0.08	0.17	0.08
Curculionidae	0.17		0.56	0.06				0.17	0.76	0.42	0.08		
Scolytidae							0.09						
Other Coleoptera		0.08		0.06					0.12	0.08		0.17	
LEPIDOPTERA													
Geometrid larvae			0.06		0.17		0.09		0.24	0.17	0.42	0.42	
Bristly larvae				0.06		0.17		0.83	0.12	0.17			
Other larvae		0.33	0.28		0.17	0.33	0.18		2.65	2.00	0.42	0.25	0.08
Tineoidea		0.08	0.11				0.09						
DIPTERA			0.22	0.12	0.17	0.17	0.09		0.18			0.33	0.08
HYMENOPTERA						0.17							
Vespoidea													
Apidae													
Braconidae	0.17		0.06										
Formicidae			0.06	0.06			0.09		0.12	0.17	0.08		0.08
Other Hymenoptera		0.08	0.39	0.06			0.09		0.06		0.08		0.33
ACARINA	1.00	1.00	0.28	0.06		0.17	0.18			0.08	0.50	0.83	0.33
ARANEAE													
Mimetidae		0.08							0.06			0.08	
Uloboridae								0.17			0.08		
Saltacidae	0.83	1.42	2.33	1.29	0.17	0.17	1.91	0.33	1.12	0.67	1.33	1.50	1.00
Thomisidae	0.17	0.42	1.39	0.41			0.36	0.17	0.47	0.25	0.50	0.25	1.25
Oxipidae	0.33	0.33	0.28	0.18			0.09	0.17	1.29	0.50	0.58		
Other spiders	2.17	3.58	3.89	1.76	0.50	0.33	2.82	0.33	1.88	1.08	1.17	1.17	1.00

Appendix 3.1. Relative abundance and breeding status as well as main distribution in America of the bird species in the study area.

TAXONOMIC GROUP	ENGLISH NAME	*RA*	*FA*	*BS*	*MS*	*AD*
TROGONIDAE						
Trogon elegans	Elegant Trogon	C	R	y	S	NA
CUCULIDAE						
Piaya cayana	Squirrel Cuckoo	C	R	y	B	SA
TROCHILIDAE						
Amazilia beryllina	Berylline Hummingbird	C	R	y	A	CA
Calothorax lucifer	Lucifer Hummingbird	C	R	y	A	NA
Cynanthus latirostris	Broad-billed Hummingbird	C	R	y	B	NA
Amazilia violiceps	Violet-crowned Hummingbird	C	R	y	B	NA
Lampornis clemenciae ?	Blue-throated Hummingbird	F	R	y	B	NA
Eugenes fulgens	Rivoli's Hummingbird	C	R	?	B	CA
Archilocus alexandrii	Black-chinned Hummingbird	C	MB	n	A	NA
Selasphoros rufus	Rufous Hummingbird	C	M	n	A	NA
PICIDAE						
Centurus aurifrons	Golden-fronted Woodpecker	C	R	y	B	NA
Centurus uropygialis	Gila woodpecker	C	R	y	B	NA
Picoides stricklandi	Strickland's Woodpecker	C	R	y	S	M
Picoides scalaris	Ladder-backed Woodpecker	C	R	y	B	N-CA
TYRANNIDAE						
Pitangus sulphuratus	Great Kiskadee	C	R	y	B	N-SA
Tyrannus vociferans	Cassin's Kingbird	C	R	y	S	N-CA
Myiarchus cinerascens	Ash-throated Flycatcher	F	MB	y	B	N-CA
Contopus pertinax	Greater (Jose Maria) Pewee	C	R	y	B	CA
Contopus sordidulus ?	Western (Wood) Pewee	F	MB	?	B	N-SA
Pyrocephalus rubinus	Vermilion Flycatcher	C	R	y	B	SA
Myopagis viridicata	Greenish elaenia	C	R	y	B	SA
Empidonax affinis?	Empidonax flycatcher	C	R	?	B	NA
Camptostoma imberbe	N.Beardless Flycatcher	C	R	y	B	N-CA
CORVIDAE						
Aphelocoma ultramarina	Mexican Gray-breasted Jay	C	R	y	B	NA
PARIDAE						
Parus wollweberi	Bridled Titmouse	C	R	y	B	NA
AETHITHALIDAE						
Psaltriparus minimus	Bushtit	C	R	y	B	NA
CERTHIIDAE						
Certhia americana	Brown Creeper	C	R	y	S	N-CA
TROGLODYTIDAE						
Tryomanes bewickii	Bewick's Wren	C	R	y	B	NA
Catherpes mexicanus	Canyon Wren	C	R	y	B	NA
Salpinctes obsoletus	Rock Wren	C	R	y	S	N-CA
Campylorhynchus gularis	Spotted Wren	C	R	y	B	M
SYLVIIDAE						
Regulus calendula	Ruby-crowned Kinglet	C	MW	n	B	NA
Polioptila caerulea	Blue-gray Gnatcatcher	C	MB	?	A	N-CA
Polioptila nigriceps	Black-tailed Gnatcatcher	C	R	?	S	NA

RA=world relative abundance; FA=frequency in study area; BS=breeding status; AD=main distribution in America. R=resident; MB=migrant but breeds in area; MW=Winter migrant; S=found only in spring in study area; A=found only in autumn in study area; B=all year resident in study area; NA=North America; CA=Central America; SA=South America; M=endemic of Mexico; C=common; F=frequent; R=rare.

Appendix 3.1. (Cont.)

TAXONOMIC GROUP	ENGLISH NAME	RA	FA	BS	MS	AD
TURDIDAE						
Catharus guttatus	Hermit Thrush	F	MW	n	B	N-CA
Catharus aurantiirostris	Orange-billed Thrush	C	R	y	B	SA
Turdus migratorius	American Robin	C	R	y	S	NA
MIMIDAE						
Melanotis caerulescens	Blue Mockinbird	C	R	y	S	M
Toxostoma curvirostrae	Curve-billed thrasher	C	R	y	B	NA
PTILOGONATIDAE						
Ptilogonys cinereus	Gray-silki Flycatcher	C	R	y	S	MG
VIREONIDAE						
Vireo solitarius	Solitary Vireo	F	MW	n	B	N-CA
PARULINAE						
Vermivora celata	Orange-crowned Warbler	U	RW	n	A	N-CA
Vermivora ruficapilla	Nashville Warbler	C	RW	n	A	N-CA
Vermivora virginianae	Virginia's Warbler	C	RW	n	A	NA
Mniotilta varia	Black-and-white Warbler	C	RW	n	B	N-SA
Dendroica coronata	Yellow-rumped Warbler	C	MB	y	B	N-CA
Dendroica nigrescens	Black-throated Warbler	C	MW	n	B	NA
Dendroica townsendi	Townsend's Warbler	C	MW	n	A	N-CA
Dendroica petechia	Yellow Warbler	C	MB	?	B	N-SA
Icteria virens	Yellow-breasted Chat	F	MR	y	B	N-CA
Myoborus pictus	Painted Redstar	C	R	y	B	N-CA
Peucedramus taeniatus	Olive warbler	C	R	?	?	N-CA
THRAUPIDAE						
Euphonia elegantissima	Blue-hooded Euphonia	C	R	?	S	CA
Piranga flava	Hepatic Tanager	C	R	y	B	N-SA
Piranga ludoviciana	Western Tanager	U	MW	n	S	N-SA
ICTERIDAE						
Molothrus aenus	Brown-headed Cowbird	C	R	y	B	N-CA
Quiscalus mexicanus	Great-tailed Grackle	C	R	y	S	N-SA
Icterus pustulatus	Streaked-backed Oriole	C	R	y	B	CA
EMBERIZIDAE						
CARDINALINAE						
Pheuticus chrysopeplus	Yellow Grosbeak	C	R	?	A	MG
Pheuticus melanocephalus	Black-headed Grosbeak	C	R	y	B	NA
Guiraca caerulea	Blue Grosbeak	C	R	y	S	NA
Passerina cyanea	Indigo Bunting	C	MW	n	S	N-CA
EMBERIZINAE						
Melozone kieneri	Rusty-crowned sparrow	C	R	y	S	M
Pipilo fuscus	Brown Towhee	C	R	y	B	NA
Spizella atrogularis	Black-chinned Sparrow	C	R	n	S	NA
Chondestes grammacus	Lark Sparrow	C	RW	n	B	N-CA
Aimophila ruficeps	Rufous-crowned sparrow	C	R	y	B	NA
FRINGILLIDAE						
Carpodacus mexicanus	House Finch	C	R	y	B	NA
Carduelis psaltria	Lesser Golfinch	C	R	?	S	N-SA

RA=world relative abundance; FA=frequency in study area; BS=breeding status; AD=main distribution in America. R=resident; MB=migrant but breeds in area; MW=Winter migrant; S=found only in spring in study area; A=found only in autumn in study area; B=all year resident in study area; NA=North America; CA=Central America; SA=South America; M=endemic of Mexico; C=common; F=frequent; R=rare.

Appendix 3.2. Bird species inluded in the analyzes. Densities (number of birds per 10 plots) are given for main vegetation types. F=dry forests; I=vegetation interface; W=woodlands.

	AUTUMN 1990			AUTUMN 1991			SPRING 1991			SPRING 1992		
BIRD SPECIES	F	I	W	F	I	W	F	I	W	F	I	W
Trogon elegans									0.9			0.8
Piaya cayana				0.1	0.2		1.8	0.3	0.3	1.0	0.2	
Amazilia beryllina	0.2	5.0	4.5	0.5	12.0	3.7						
Calothorax lucifer	3.1	3.5	1.0	1.6								
Cynanthus latirostris	9.8	2.0	0.3	3.6	1.7	1.3	0.7			1.1	1.8	
Amazilia violiceps	5.1	9.0	1.3	5.8	10.0	2.4	0.5			1.0		
Lampornis clemenciae	1.3	0.5		1.1	0.5		1.6		0.3	0.7		
Eugenes fulgens	0.8	1.5	0.5				0.2					
Archilocus alexandrii	7.8	10.0	1.8	8.8	0.3	1.4						
Selasphoros rufus	0.1	1.0	0.0	2.8	11.3	0.5						
Centurus aurifrons	1.1	0.5	0.1	0.4			2.4	0.3	0.1	1.2	0.2	0.2
Centurus uropygialis	+			+			+			+		
Picoides stricklandi									0.5			0.2
Picoides scalaris	0.6	1.5	0.5	0.4	1.0	0.6	3.5	2.3	0.9	1.7	1.0	1.2
Pitangus sulphuratus	3.9	0.3		0.5			0.6	0.8		0.2	0.3	
Tyrannus vociferans										1.0	0.2	0.3
Myiarchus cinerascens	15.7	9.0	2.3	10.0	6.3	2.2	5.5	3.3	4.1	5.4	6.5	1.8
Contopus pertinax					0.7	0.4			0.1		1.5	1.3
Contopus sordidulus ?	0.1	0.5	0.9	0.1	2.0	0.8		1.3	3.0	0.2	2.7	1.9
Pyrocephalus rubinus				0.1								0.2
Myopagis viridicata	0.5	1.5	0.5	0.7		0.6	0.5	0.8		2.3	1.5	1.3
Empidonax sp.	5.8	3.0	1.0	5.0	5.0	3.9	6.6	7.8	2.9	3.0	1.7	0.9
Camptostoma imberbe	5.0	4.0	1.0	4.6	2.3		1.6	0.3	2.0	4.3	5.8	1.3
Aphelocoma ultramarina			0.5			0.3			0.3			0.8
Parus wollweberi						3.0			2.1			1.6
Psaltriparus minimus	0.2		0.8				0.2	1.3	2.0	0.9	2.7	2.8
Certhia americana												0.1
Tryomanes bewickii	2.2	2.8	0.6	1.9	4.4	2.0	3.5	6.0	3.9	3.5	4.4	2.5
Catherpes mexicanus	1.5	1.8	0.8	0.3			0.6	0.3		0.9	0.3	
Salpinctes obsoletus							0.3	0.5		0.1		
Campylorhynchus gularis						0.1			0.3			
Regulus calendula			1.5			2.6			0.1		1.2	0.5
Polioptila caerulea	21.9	11.0	2.0	15.2	8.7	0.6				0.2		
Polioptila nigriceps							0.5		1.8	0.1		
Catharus guttatus			0.5	0.1	0.2		0.1	0.3		0.2	0.7	0.3
Catharus aurantiirostris			0.4					2.0	1.0			0.1
Turdus migratorius					0.3	0.2				0.1	0.3	2.7
Melanotis caerulescens							0.3	2.3	0.3	0.4	1.0	0.2
Toxostoma curvirostrae	0.8	1.5		0.2	1.3		7.3	6.3	2.4	3.1	3.5	0.8
Ptilogonys cinereus										0.1	0.7	0.8
Vireo solitarius	0.1	0.5	1.3	0.1	0.3	0.7	0.1	1.3	1.9			1.3

Appendix 3.2 (cont.)

	AUTUMN 1990			AUTUMN 1991			SPRING 1991			SPRING 1992		
BIRD SPECIES	F	I	W	F	I	W	F	I	W	F	I	W
Vermivora celata	0.8			0.5								
Vermivora ruficapilla	1.9	7.0	0.3	1.5	1.3	0.1						0.3
Vermivora virginianae	0.8		0.3	0.4						0.1		
Mniotilta varia						0.3				0.2	0.3	0.5
Dendroica coronata	8.3	3.5	4.3	12.5	1.0	10.3		0.5	0.4	3.9	0.3	1.3
Dendroica nigrescens	0.1	5.0	4.3		0.7	2.3						1.0
Dendroica townsendi						0.8						
Dendroica petechia	0.2			0.2			1.7	2.0		0.1	0.3	0.3
Icteria virens	0.3			0.1	0.2		0.8	6.5	0.6		2.5	0.2
Myoborus pictus		0.8	0.8						0.8			
Peucedramus taeniatus									1.0			
Euphonia elegantissima								1.5		0.2		0.5
Piranga flava		0.5	2.9		0.3	1.3	0.0	0.5	3.9		0.7	4.1
Piranga ludoviciana										0.2		0.5
Molothrus aenus				1.1			1.1	2.0	0.6	0.5	1.7	0.3
Quiscalus mexicanus							0.3	1.3				
Icterus pustulatus	4.7	2.0	0.6	2.5	3.3	1.3	22.4	12.0	1.8	9.2	8.3	1.4
Pheuticus chrysopeplus				0.1								
Pheuticus melanocephalus	0.4				0.3	0.3	1.3	1.3	2.8	1.3	3.2	7.1
Guiraca caerulea							6.5	4.3	0.5	5.0	3.3	1.4
Passerina cyanea										0.4		1.4
Melozone kieneri							2.0	2.5			0.8	
Pipilo fuscus	0.2	4.0	0.5	0.4	2.0	0.5	8.9	9.0	3.9	2.7	6.0	4.9
Spizella atrogularis											7.7	0.1
Chondestes grammacus	1.3				1.5					2.2		
Aimophila ruficeps	2.8	1.0	0.5	6.3	8.3	4.0	0.3			6.6	1.0	4.3
Carpodacus mexicanus				0.3	1.3	1.3	0.5		0.8	0.1		
Carduelis psaltria										0.1		

Appendix 5.1. A priori guild classification of bird species. Season in which species was present is indicated.

GUILD/	AUTUMN		SPRING	
species	1990	1991	1991	1992
HUMMINGBIRDS				
Amazilia beryllina	X	X		
Amazilia violiceps		X	X	X
Archilocus alexandrii	X	X		
Calothorax lucifer	X	X	X	X
Cynanthus latirostris	X	X	X	
Eugenes fulgens	X			
Lampornis clemenciae	X	X	X	X
Selasphoros rufus	X	X		
GRANIVORE-INSECTIVORES				
Aimophila ruficeps	X	X	X	X
Chondestes grammacus	X	X		X
Passerina cyanea				X
Spizella atrogularis				X
GROUND INSECTIVORES				
Pipilo fuscus	X	X	X	X
Atlapetes sp.			X	X
FOREST OMNIVORES				
Euphonia elegantissima		X	X	X
Guiraca caerulea			X	X
Melanotis caerulescens			X	X
Molothrus aenus		X	X	X
Piaya cayana		X	X	X
Quiscalus mexicanus			X	
FOREST INSECTIVORES				
Polioptila caerulea	X	X		X
Polioptila nigriceps			X	X
Vermivora virginianae	X	X		X
WOOD PROBERS				
Catherpes mexicanus	X	X	X	X
Campylorhynchus gularis			X	
Certhia americana				X
Salpinctes obsoletus			X	X
Tryomanes bewickii	X	X	X	X
WOOD PECKERS				
Dendrocopus stricklandi			X	X
Melanerpes aurifrons	X	X	X	X
Picoides scalaris	X	X	X	X

Appendix 5.1. (cont.)

GUILD/	AUTUMN		SPRING	
species	1990	1991	1991	1992
FRUGIVORE-INSECTIVORES				
Icterus pustulatus	X	X	X	X
Toxostoma curvirostrae	X	X	X	X
FLYCATCHING HAWKERS				
Camptostoma imberbe		X	X	X
Empidonax	X	X	X	X
Myiarchus cinerascens	X	X	X	X
Myopagis viridicata	X	X	X	X
UBIQUITOUS FLYCATCHERS				
Pitangus sulphuratus	X	X	X	X
Pyrocephalus rubinus		X		X
Ptilogonys cinereus				X
Tyrannus vociferans				X
WOODLAND FLYCATCHERS				
Contopus pertinax		X	X	X
Contopus sordidulus ?	X	X	X	X
UBIQUITOUS INSECTIVORES 1				
Carduelis psaltria				X
Dendroica coronata	X	X	X	X
Dendroica petechia	X	X	X	X
Icteria virens	X	X	X	X
Pheuticus chrysopeplus		X		
Vermivora celata	X	X		
Vermivora ruficapilla	X	X		X
Pheuticus melanocephalus	X	X	X	X
UBIQUITOUS INSECTIVORES 2				
Psaltriparus minimus	X		X	X
Regulus calendula	X	X	X	X
Vireo solitarius	X	X	X	X
WOODLAND INSECTIVORES				
Dendroica nigrescens	X	X		X
Dendroica townsendi		X		
Mniotilta varia		X		
Myoborus pictus	X		X	X
Parus wollweberi		X	X	X
Dendroica fusca			X	
WOODLAND OMNIVORES				
Aphelocoma ultramarina	X	X	X	X
Catharus guttatus	X	X	X	X
Catharus aurantiirostris	X	X	X	X
Piranga flava	X	X	X	X
Piranga ludoviciana				X
Trogon elegans			X	X
Turdus migratorius				X

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