The abundance of four bird guilds and their use of plants in a Mexican dry forest-oak woodland gradient in two contrasting seasons

Pablo Corcuera Martínez del Río
Departamento de Biología, UAM-Iztapalapa, A.P. 55-535, C.P. 09340, México D.F. E-mail: pcmr@xanum.uam.mx

Resumen

Abundancia de cuatro gremios alimentarios de aves y su uso de plantas en un gradiente ambiental (bosque seco – bosque de encino) mexicano en dos temporadas contrastantes.

Se hizo una comparación entre la abundancia de cuatro gremios de aves, su preferencia por buscar alimento en distintas plantas y el suministro de alimento proporcionado por éstas. El estudio se llevó a cabo en un gradiente de vegetación que abarca selva baja y bosque de encino en dos estaciones contrastantes -la época seca y la época húmeda- y en dos años consecutivos. Las aves fueron agrupadas, atendiendo a las maniobras de forrajeo y a las plantas preferidas, como: colibríes, papamoscas de follaje, pizcadores de selva y pizcadores de bosque. Para identificar a estos gremios se emplearon clasificaciones y para identificar las variables que pudieran caracterizar a cada uno de éstos, se utilizó un análisis de correspondencia sin tendencia. Se realizaron censos en 67 parcelas de diámetro fijo. En cada parcela se estimó la cobertura de las plantas y se emplearon correlaciones simples para determinar cuales plantas estaban asociadas con las densidades de cada gremio de aves en las distintas estaciones de los dos años. Las preferencias de búsqueda se estimaron por medio de pruebas de bondad de ajuste. La mayoría de las plantas que estuvieron significativamente correlacionadas con los gremios no fueron las preferidas para buscar alimento, salvo en el caso de los colibríes; éstos estuvieron significativamente correlacionadas con *Ipomoea wolcottiana,* un árbol con flores muy visitado por estas aves. En el otoño, que es la época húmeda, ni los pizcadores de follaje ni los papamoscas (fundamentalmente insectívoros en esta estación) utilizaron las plantas con mayores densidades de artrópodos. Esto podría deberse a que las densidades totales de artrópodos no necesariamente reflejan las presas más utilizadas. Además, las aves podrían tener una preferencia por aquellas plantas con alimento fácilmente accesible y no necesariamente por aquellas con mayor cantidad de alimento. El que las plantas con mayores coeficientes de correlación en los dos años hayan sido similares en las dos estaciones (independientemente del alimento que proporcionan) también sugiere que éstas representan más a los hábitats preferidos que al alimento disponible. En la época seca sólo en el primer año las densidades de los colibríes estuvieron asociadas con las plantas más utilizadas. Los resultados coinciden con otros estudios realizados en selvas bajas, en donde las plantas preferidas están sólo parcialmente correlacionadas con la distribución de las aves.

Palabras clave: ecología de comunidades, estrategias de forrajeo, gremios de aves.

Abstract

I classified the bird community of a Mexican dry forest and oak woodland into foraging guilds, and studied the effect of food availability on guild distribution in a gradient of vegetation (three communities) at two contrasting seasons of two consecutive years. Bird species were grouped into hummingbirds, foliage flycatchers, and forest and woodland gleaners based on their foraging manoeuvres and plant preferences. A classification was used to group the birds and a detrended correspondence analysis was used to identify the variables that characterized each guild. Bird densities were obtained by means of 67 circular plots of a fixed radius. The cover of the plant species was obtained in each of the these plots and simple correlations were used to determine which plant species were associated with the bird guild densities. Plant foraging preferences were assessed by goodness of fit tests. Gleaners and flycatchers (mainly insectivores during autumn) did not use preferentially those plants with higher arthropod densities nor were their favoured plants correlated with their abundance. This in part might be attributed by the fact that total densities might not reflect the favoured prey. Also, birds might favour plants from which food is more easily accessible, which are not necessarily those with higher food availability. In addition, some plants with high correlation coefficients for forest ans woodlands gleaners, such as *Acacia tortuosa* and *Quercus crassifolia* were significant in the two seasons, suggesting that they were likely to be representative of the main vegetation types, regardless of the bird species food requirements. Hummingbird abundance was significantly correlated with the density of *Ipomoea wolcottiana* in autumn, a tree that produces large flowers and is much visited by members of this guild. For gleaners and foliage flycatchers, my results agree with other dry forest studies in which the favoured food supply was only weakly associated with the bird species. Hummingbirds consist of a more specialized group, which at least in autumn, is significantly associated to the plants which provide nectar.

Key words: bird guilds, foraging strategies, community ecology.

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A feeding guild is a group of species that feed on the same food in similar proportions (Poulin et al. 1994). 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). Guild studies are valuable to identify the resources that determine the structure of animal communities (Terborgh and Robinson 1986). Poulin et al. (1993) used this approach to determine the influence of the change in resources in the bird structure throughout the year. Ekhardt (1979) used guilds as a tool in order to study the ways in which insectivore birds capture their prey. He suggested that every species fits into adaptive syndromes, manifested, among other characteristics, as particular foraging tactics. These syndromes may be shared by a number of species which, regardless of their taxonomic differences, belong to the same guild.

Many authors have found that food have a definite influence on the abundance of insectivorous and nectarivorous bird species. Hutto (1985) gives examples of causal relationships between food availability and nectarivorous and insectivorous bird species densities, while Peck (1989) found that plots which included trees supporting high numbers of arthropods also had higher densities of insectivorous birds. On the other hand Poulin et al.(1993) only found a weak correlation between the abundance of food resources and the densities of the birds belonging to each guild found in a Venezuelan dry forest.

In this study I assessed the relationships established between the bird guild abundances, food resources presents on plants (insects, fruit and flowers) and plant preferences by birds in a dry forest in Western Mexico. The study was done in two contrasting seasons in two consecutive years. I asked the question: Do favoured plant species influence the abundances of birds? To do that, I considered four bird guilds: nectarivores, foliage flycatchers, woodland gleaners, and a miscellaneous group of frugivorous and insectivorous gleaners. Woodpeckers, wrens and aerial flycatchers were not included because I only assessed the types of fruit and flowers produced by the plants and the arthropods associated with the foliage (i.e. I did not measure densities of aerial insects or arthropods on wood).

Methods

Study sites

The study was conducted in a landscape located in Western Mexico. It is situated around Estipac, Jalisco (20°20'N and 103°35'W; 1355-1995 m a.s.l). Mean temperature in the area is 20.3°C and annual rainfall 826 mm, with T/P ratio of 2.4. Most of the rain falls between mid-June to mid-September and there are from 6 to 8 dry months each year.

The landscape has a vegetation gradient that change from dry forest (or "huizachal") to dry oak woodland (tropical deciduous woodland and oak woodland, respectively, according to Rzedowski, 1978). Within the dry forests, the gradient includes different combinations of plant species. Based on the general appearance (physiognomy), it is possible to recognize broad-leaved deciduous forests, small-leaved deciduous forests and *Ipomoea* forests. A detailed description of the site is given in Corcuera and Butterfield (1999).

I selected 67 circular plots of 60 m diameter in which the field work was conducted. The plots were intercperced throughout the vegetation gradiant and distance between plots was at least 200 m. Plant variables and densities and foraging manoeuvres of the bird species registered were measured in these plots (see below).

Plant Species Composition

Plant species cover and composition per plot was estimated during November and December 1990. For plants less than 2.0 m tall, a 2 mm x 2 m 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. This was done by tracing two 60 m lines. One of them with a N-S and the other with a E-W orientation. The two lines crossed each other at the centre of each plot and the rod was placed at 3 m intervals. For higher vegetation an optical square marked with two perpendicular axes was used (adapted from Montaña and Ezcurra 1980). The results (number of touches by either the rod or the optical square per plant species) were used to estimate the relative cover of each plant species. A species-area (or number of touches in this case) curve was drawn for ten random plots (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. Plants were identified at the Herbario Metropolitano (UAMIZ, México D.F.).

Food resources

In each season I estimated percent of flowers and fruits and densities of arthropods in the foliage of the most common plant species.

Each season every plant species was categorized in a phenological phase (fruiting, flowering or growing) when at least 80% of all individuals presented fruits, flowers or leaves, respectively. If more than 20% but less than 80% of green leaves were present, I considered the plant to be semideciduous.

To characterize flowers I used form (brush, tube or cup) and corolla size (*sensu* Arizmendi and Ornelas

1990). Fruits were classified as capsules (dry fruits enclosing the seeds), drupes (a large seed surrounding by a fleshy endocarp), legumes (various seeds in an elongated pod), and fleshy fruits (such as those produced by many cacti species and which are readily eaten by birds and mammals) (*sensu* Standley 1926, Lawrence 1971). In addition to these, *Ficus* sp. produces a typical convoluted inflorescence (syconium) which, at least for mammals and birds, could be regarded as a fleshy fruit. I measured the relative cover of the plant species and counted the foraging visits each bird made to each plant species. This information allowed me to establish the preference to look for food in each plant species by the bird guilds.

Arthropod density samples on plants were obtained by placing muslin bags over 30 cm terminal branches and sprayed the branches with insecticide. After 10 minutes, all of the arthropods on the branch and within the bag were removed and preserved in 70% ethanol. For each of the 13 commonest trees and shrubs, 22 replicate samples were taken, each from a different tree. *Ficus* sp. was also examined, but it was scarce and branches from only eight individual plants were sampled. The sampling was repeated 15 days after the first, to compensate for possible temporal variations in the arthropod abundance within the study period. In practice, such temporal variations were small. In a regression of mean arthropod numbers on the plants for the two samples the slope did not differ significantly from unity and $r^2=0.49$ ($P<0.005$). Accordingly, the results presented have been pooled for the two sets of samples and the values presented here are based on 44 replicate samples for each of the 13 common plant species, with 16 samples for *Ficus*.

Bird Guilds

The guild densities were based on ~~e~~ counts of the individual bird species obtained in the 67 plots in autum (September and December of 1990 and 1991) and spring (March and April of 1991 and 1992). Each plot was visited three times after a two trial visits. Each count lasted 10 min.

Guild determination was based on the foraging behaviour of the birds (following Holmes et al. 1979). Each time a bird was seen, its activity was recorded as a "spot" observation. If the bird moved to another plant species or foraging substrate, the activity was recorded again. The foraging activities were grouped in four categories: 1) foraging manoeuvre, 2) substrate of attack, 3) foraging height and 4) plant species in which the bird was seen foraging.

The registered foraging manoeuvres (modified from Holmes et al. 1979, Rabenold 1978) were: a) glean, in which a stationary item is picked from a substrate by a standing bird; b) flycatch, in which the bird flies into the air to catch a flying prey; c) hop, which is a short sally, usually within the foliage; d) hover, in which a stationary item is picked by a flying bird, and; e) probe, in which a bird searches for a subsurface prey (i.e. in coarse bark).

The substrate of attack was defined as the type of substrate in which the food item was obtained by the bird. The substrates were: flower, fruit, flying insect, ground, mistletoe, foliage, and lichen (some bird species foraged in branches with lichens). I included the diameter of the trunk or branch if it was being used, and then categorized it as medium (*ca*. 20-80 mm in diameter) or large (>80 mm). Smaller branches were often difficult to discern from the foliage and therefore <20 mm diameter branches and leaves were categorized as foliage.

Foraging height was recorded by the position of the bird in five classes: forest/woodland floor, the herb layer, the shrub layer, the mid tree canopy and the upper canopy.

The last category included the plant species used by the birds (modified from Sabo and Whittaker 1979, Sabo and Holmes 1983, Holmes et al. 1979). As in other studies (*e.g.*, Sabo and Holmes 1983), the frequencies of use for every group of variables belonging to each of the four categories were transformed to percentages.

The scientific and English bird names are based on the AOU (1983) check-list.

Statistical analyses

In order to formally determine the guilds, I used multivariate classifications (following to Holmes et al. 1979, Landres and MacMahon 1980, Recher and Holmes 1985). In this study an R type matrix (Ludwig and Reynolds 1988) was constructed. Bird species were represented by rows, and columns represented the foraging strategies. The cosine distance was used for the classification as suggested by Ludwig and Reynolds (1988). To classify the birds into guilds I pooled the data from the four study seasons (*sensu* Holmes et al. 1979).

I used ordinations to associate each guild with the foraging manouevre, substrate of attack, height and plant species in each season (*sensu* Sabo and Whittaker 1979, Sabo and Holmes 1983, Poulin et al. 1993). I used detrended correspondence analysis (Hill 1979) and assumed that guilds were groups of bird species related with those variables that had (i) high ordination scores and (i) were located nearby (i.e. had similar coordinates) in the ordination plot. The data matrix containing the foraging manoeuvres for each species was used to perform the ordinations. Each bird species was considered a case and the foraging manoeuvres were the variables.

Simple correlations were used to relate the guild densities and plant densities, and goodness of fit tests were used to determine foraging plant preferences (the null hypothesis would be that birds use each plant species according to their relative cover). Analysis of variance was used to test the inter-seasonal differences between: (i) the mean density of the bird guilds and (ii) the arthropod density by plant species by season.

Results

Food resources

The name, family, life form and code of the plant species found in the area is shown in Appendix 1. There were many vine species in the study area. I could only identify those which had flowers (*Clystoma binatum* and *Ipomoea*

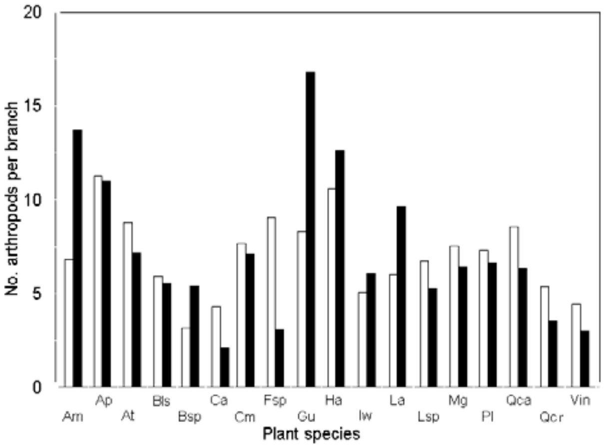

Figure 1. Number of arthropods per branch in 18 plant species in autumn 1990 (black bars) and 1991 (clear bars). Code names for plants are in Appendix 1.

quamoclit). The percentage cover of the plants shows that *Croton ciliatoglanduliferus*, *Acacia tortuosa* and *Quercus crassifolia* dominated the study area, while *Ceiba aesculifolia*, *I. quamoclit*, *Stenocereus* sp. and a *Ficus* species were the more rare (Appendix 1).

The phenological phase of the plant species changed between spring and autumn (Appendix 1). Most plants had shed their leaves at spring, the dry season. The main exception was *Prosopis laegivata,* which was the only evergreen tree present in the study area. *Acacia tortuosa*, *A. pennatula, Lysiloma acapulcense* and *Lysiloma* sp. retained at least 20% of their foliage during the two springs(Appendix 1) and can be considered as semideciduous species.

Six plant species were registered producing flowers during summer, and one of them (*Ficus* sp.) extended this period to autumn. *Ipomoea quamoclit* and *I. wolcottiana* produced relatively large tubular flowers in autumn (Appendix 1). The two species of cacti (*Opuntia* sp. and *Stenocereus* sp.) and the plants of *C. binatum* produced flowers in the spring of 1991 (Appendix 1). The flowers of the vine (30 mm long) and *Stenocereus* sp. (50 mm long) were tubular, while those of *Opuntia* sp. (50 mm long) had the form of a cup. *Stenocereus* flowers were open at night (when they were visited by bats and nocturnal insects) and remained open throughout the morning when they were visited by hummingbirds. *Ficus* sp. presented large amounts of syconia during the autumn (Appendix 1). *Acacia tortuosa, Guazuma ulmifolia* y *C. ciliatoglanduliferus* presented flowers in the form of cups or brushes that were too small to be visited by birds (Appendix 1).

With the exception of *Stenocereus* sp., fruits were produced mainly during autumn (Appendix 1). Thirteen tree and shrub species showed legume and capsule fruits, that sometimes some granivorous birds opened to eat the seeds. In spring 1991, *Stenocereus* sp. produced large conspicuous fruits that were avidly consumed by many bird species. The *Bursera* trees had drupes in both springs (Appendix 1).

Arthropod densities were significantly different at least in a plant species ($F_{17,380}$=6.06, P<0.001 in 1990). A multiple comparison test using least significance difference showed that *G. ulmifolia* had significantly (P<0.05) higher density of insects and spiders than the other plant species during autum 1990. The vines, *C. aesculifolia, Q. crassifolia* and the *Bursera* spp. had the lower densities (Figure 1). In addition, in 1990 *A. tortuosa* and *A. pennatula* and in 1991 *L. acapulcense* and *Acacia macilenta* had high arthropod densities, while *I. wolcottiana* in 1990 and *Ficus* sp. in 1991 had low densities.

Bird guilds

From a total of 68 bird species seen in the study period, 38 were present during the autumn of 1990, 47 in the autumn of 1991 and 46 and 56 during the springs of 1991 and 1992. Only those species for which more than 20 observations were available (n=23) were included in the analysis of the bird guilds. These included 75% of the total number of birds records in the autumn of 1990, 62% of those registered in the autumn of 1991 and 40% and 44% of those in the springs of 1991 and 1992, respectively. The seasons in which each of the 23 species were present, as well as their seasonal densities are shown in Appendix 2.

At the 50% dissimilitude coefficient of cosine distance four groups of birds were recognized: hummingbirds (all of which fed mainly on relatively large nectar producing flowers), foliage flycatchers (which collected food by giving short sallies or jumps within the foliage of trees and shrubs as opposed to gleaners which swept the plant substrate in search of insects), a miscellaneous group of woodland gleaners, and a group of forest gleaners (which are frugivorous and insectivorous and foraged mainly in dry forests; Figure 2).

The first two axes of the ordinations segregated four groups of birds and agreed with the classification by cosine distance (Figure 3a). The only exception was the Bushtit (*Psaltriparus minimus*) which appeared in the same cluster as the forest gleaners but was nearest to the woodland gleaners in the ordination. A discriminant analysis grouped this species with the forest gleaners (Wilk's lambda=0.243, P^2=16.97, d.f.=1, P<0.001 with 100% of the cases correctly classified).

The first axis separated the woodland gleaners from the hummingbirds and the second axis separated the foliage flycatchers from the forest gleaners. (Figures 3a and 3b). If the two plots are overlaid the relationship between the variables and the bird groups (guilds) becomes apparent; the woodland gleaners were associated with both *Quercus* species and *A. pennatula*, while the hummingbirds were associated with hovering, *Opuntia* sp., flowers, the vines and *Stenocereus* sp.. Foliage flycatchers were associated with hawking and the *Bursera* sp. trees, while forest gleaners were related to ground search (forest

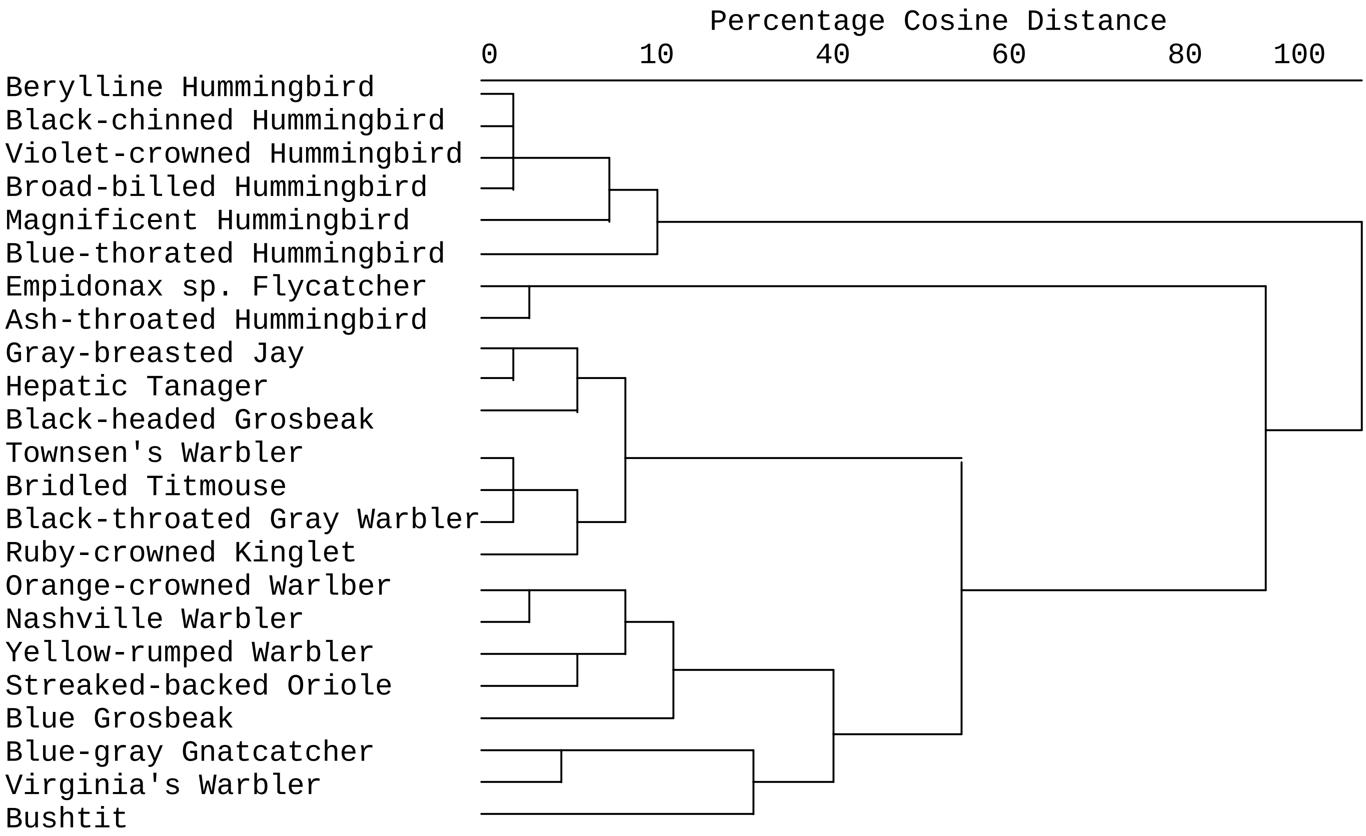

Figure 2. Classification of bird species based on foraging strategies and plant preferences.

gleaners sometimes looked for insects in the litter). The Woodland gleaners consisted of insectivorous birds (Townsend's Warbler [*Dendroica townsendi*], Bridled Titmouse [*Parus wollweberi*], and Black-throated Warbler [*Dendroica nigrescens*]) and other species (Black-headed Grosbeak [*Pheucticus melanocephalus*], Hepatic Tanager [*Piranga flava*]) which are more omnivorous in other areas. Most individuals looked for arthropods in the foliage and small twigs in autumn and in larger branches with lichen and other epyphites in spring.

The list of birds in the forest gleaner guild included insectivorous and omnivorous birds. For example, Streaked-backed Oriole (*Icterus pustulatus*) and the Blue Grosbeak (*Guiraca caerulea*) have a broader diet than Blue-grey Gnatcatcher (*Polioptila caerulea*), which is mainly insectivorous. This is explained by the fact that the species present in autumn were mainly insectivorous, while those present in spring either were omnivorous and were not present in autumn (Blue-Grosbeak) or were much more omnivorous in spring (Streaked-backed Oriole and Yellow-breasted Chat [*Icteria virens*] which eat fruit in spring.

Guild densities

The main difference in bird densities between the two years consisted of significantly higher densities of hummingbirds and foliage flycatchers in autumn (Appendix 2). The changes in feeding guilds densities between seasons can reflect, in a broad way, the changes in resource availability.

Hummingbird ($F_{3,264}$=80.82, P<0.001) and Foliage Flycatcher ($F_{3,264}$=17.21, P<0.001) densities were significantly higher in the two autumns than in the two springs (densities in the same season but different years were not significantly different). Woodland gleaners densities did not vary significantly between seasons ($F_{3,264}$=2.02, P>0.05), while Forest gleaners were higher in the two autumns than in the spring of 1991($F_{3,264}$=5.93, P<0.001), but not more than in the Spring 1992. Figure 4 shows the bird guild densities (mean number per plot) in the four seasons.

Resource exploitation of the bird guilds

The distribution (abundance) of the birds in the ordination plot is explained by those variables with the highest scores for the ordination axes. What the ordination does not establish is if the plant species included in the analysis are those favoured by the birds (i.e. some of the species might be used only because they are very abundant but not because there is a true preference for them). In order to determine which plants were significantly favoured a goodness of fit tests was used.

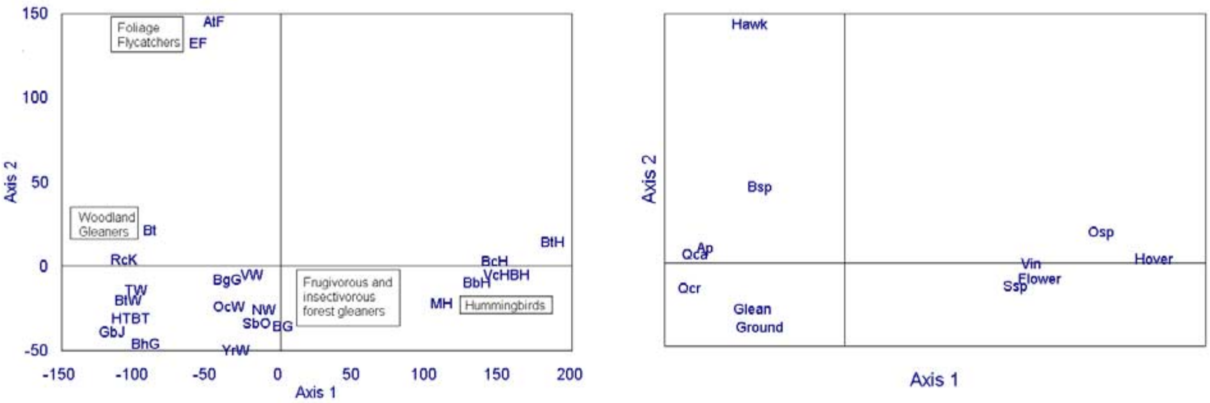

Figure 3. Ordination of bird species (a) and associated plant variables (b). Axis 1 separates hummingbirds from gleaners and flycatchers while axis 2 separates flycatchers from the other bird guilds (3a). The gleaners are clustered in two groups (forest and woodland gleaners) which agree with the bird guild classification. The position of the variables used to identify the bird guilds indicates their relationship with the bird groups when the two plots are overlaid (3b). Hawk is associated with the flycatchers; *A. pennatula, Q. castanea* and *Q. Crassifolia* are associated with the woodland gleaners; glean and ground are related to the forest gleaners, and the vines, flowers, *Stenocereus* sp., *Opuntia* sp. and hover are associated with the hummingbirds.

All guilds avoided *Croton ciliatoglanduliferus,* the herbs, and the broad-leaved shrubs in all or at least three of the four seasons (Appendix 3). Hummingbirds favoured *Ipomoea wolcottiana* in the two autumns. This guild also was attracted to *Opuntia* sp., *Stenocereus* sp. and the vines in spring 1991 and to *Lysiloma acapulcense* in autumn 1990. *Ipomoea wolcottiana* was favoured by Foliage Flycatchers and Foliage gleaners in the four seasons and the same two guilds foraged in *L. acapulcense* in the two springs. In addition, Foliage Flycatchers favoured *Bursera* trees in the four seasons while Foliage gleaners foraged in *Prosopis laegivata* in the two autumns and spring 1991 and in *Ficus* sp. in the two springs and autumn 1991.

Woodland gleaners searched for food in the two *Quercus* species (*Q. crassifolia* and *Q. castanea*) and favoured *L. acapulcense* in the four seasons. They ignored *A. tortuosa* and *Guazuma ulmifolia* in addition to *C. ciliatoglanduliferus* (Appendix 3).

The relationship between bird guild densities and the vegetation

Hummingbirds were significantly correlated with *I. wolcottiana* in the two autumns (Appendix 4). In Autum 1990 and spring 1991, they were associated to *A. tortuosa* and *Stenocereus* sp., respectively; and with *Opuntia sp.* and *C. ciliatoglanduliferus* in 1992. They were negatively correlated with *Q. crassifolia* in autumn (Appendix 4).

Foliage flycatchers were positively correlated with *C. ciliatoglanduliferus*, *A. tortuosa* and *I. wolcottiana* in autumn and with *Heliocarpus appendiculatus* in spring. They had a negative correlation with *Q. crassifilia* in autumn (Appendix 4). The results indicate that the abundance of woodland gleaners was significantly correlated with the vegetation cover of *Q. crassifolia* in the four seasons and with *C. multiflora* in three of them (Appendix 4). In autumn 1990, the birds of this guild were also associated with the herbs and were negatively correlated in three or two seasons with typical forest plants such as *C. ciliatoglanduliferus*, *A. tortuosa, Opuntia* sp. and *H. appendiculatus* (in the two springs).

Forest gleaners were positively correlated with *A. tortuosa* in all seasons, with *Stenocereus* sp. in Autum and with *Opuntia* sp. in spring. They were negatively correlated with the herbs and *Q. crassifolia* in the four seasons and with *Q. castanea* and *C. multiflora* in autumn (Appendix 4)

Discussion

There was a relationship between the bird guild densities and the resources available. In autumn, nectar producing flowers and hummingbirds were abundant but in spring both, flowers and hummingbirds were scarce. Furthermore, forest and woodland gleaners were mostly insectivorous in autumn -when insects were more

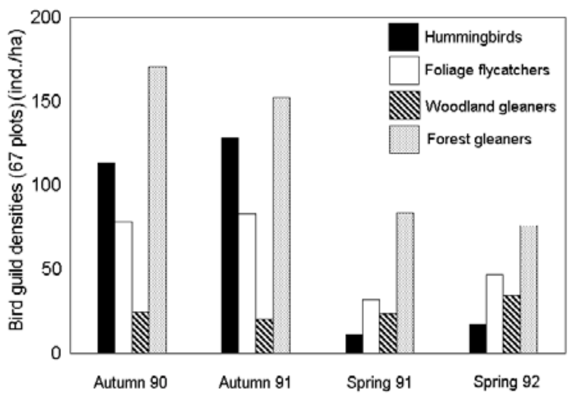

Figure 4. Number of individuals per bird species guilds in autumn 1990 and 1991 and spring 1991 and 1992.

abundant- but became mostly omnivorous during sping - when insects were scarce and a variety of other food resources such as fruit and seeds were available. Nevertheless, a more detailed inspection shows that the relationship between favoured plants, food availability and guild densities is complex. In this section I will first discuss the use of the plants which provided food for the four guilds and then reflect on the possible reasons why, regardless of their arthorpod densities, or flower or fruit type, certain plants were frequently used.

During autumn, many flowers, particularly those of *I. wolcottiana* were abundant. Hummingbirds extensively used this species. *Ipomoea wolcottiana* was a very common flowering tree, flowering profusely in autumn, while *Stenocereus* sp. and most vines flower in spring but were scarce. Furthermore, *I. wolcottiana* was positively correlated with the distribution of Hummingbird densities in both autumns. Hummingbirds were also associated with *Stenocereus* sp. in spring 1991 (and autumn 1990). This plant flowered during spring 1991 and together with the vines and *Opuntia* (which were also flowering in spring 1991 but not in 1992) was a favoured plant in this season. Therefore the distribution of the hummingbird guild was related to the abundance of their favoured flowering plants in the study area.

Deciduous plants have not yet shed their leaves in autumn and support higher arthropod densities in this season than in spring. The food supply for forest gleaners (arthropods in particular) was therefore much higher in autumn. Some species of this guild migrate in spring (most warblers) while other species become omnivorous during spring (the Yellow-rumped Warbler and the Streaked-backed Oriole). Spring 1992 was a very wet season because of the effect of El Niño. Unusually, many plants had leaves during the "dry" season of this year. Since rainfall and plant foliage might reflect the availability of certain arthropod groups, it is possible that food was available and sustained the relatively high densities during this season (when densities were not significantly lower than in the two autumns).

Forest gleaners also favoured *I. wolcottiana*, *Ficus* sp. (in three seasons) and some small leaved species such as *L. acapulcense* and *P. laegivata*. Their density was related to *A. tortuosa* in all seasons but this plant was only used preferentially in autumn 1990. The plant cover of *Stenocereus* sp. was correlated with the forest gleaners densities in the two autumns but this plant was not used by this guild. In spring 1991, the cover of *P. laegivata* was correlated to the densities of this guild and was also used preferentially. Nevertheless, in all other cases, excepting *A. tortuosa* in 1990, the relationship between favoured plants and bird densities was not significant.

Foliage flycatcher densities were correlated with *I. wolcottiana* in all seasons and with *C. ciliatoglanduliferus* in three of them. Nevertheless, this guild only favoured *I. wolcottiana* in the two autumns and ignored *C. ciliatoglanduliferus* in all seasons. Foliage flycatchers consistently used *Bursera* sp. This species produces large amounts of resinous fruits all year around. *Myiarchus cinerascens* and *Empidonax* sp. were seen eating them in all seasons. Other birds (with the exception of *Guiraca caerulea* which was seen only once eating these fruits) did not eat them.

Nevertheless it is unlikely that *Bursera* fruits were the main food supply of this guild, since even frugivorous birds are seldom specialists of a single fruit (Whelan et al. 1998). Since fruits and insects were scarcer during the two springs, the densities of birds in the foliage flycatcher guild were expected to be lower at this time of the year.

Robinson and Holmes (1982) found that the foraging manoeuvres were related to the type of food obtained by birds. Insectivorous birds conducting medium to long hawking manoeuvres obtained mainly active prey like wasps and flies, while medium distance hovering birds caught mostly caterpillars, and gleaning birds obtained often cryptic prey. The species of foliage flycatchers in this study conducted mainly medium distance sallies. Perhaps their favoured plants had higher densities of active insect species (which were not properly sampled with the technique I used).

Woodland gleaners were scarce in the four seasons. As in the case of forest gleaners some insectivorous warblers in this guild became scarcer in spring (*e.g.*, Black-throated Grey Warbler), while more generalist species became more abundant (*e.g.*, Black-headed Grosbeak). The birds from this guild favoured *Q. crassifolia* and *L. acapulsence* in the four seasons and *Q. castanea* in three of them (*Q. crassifolia* had relatively low arthropod densities). The abundance of the woodland gleaners was also highly related with the oaks. 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 is possible that the highest *Q. crassifolia* layers had higher arthropod abundances.

The common use of certain plants such as *I. wolcottiana* and *L. acapulcense* suggests an opportunistic nature of gleaners and flycatchers. The white racemes of *I. wolcottiana* attract a large number of highly mobile, and therefore conspicuous insects. These insects could be easily available to different guilds. In spring, the direct consumption of either the exposed seeds or of insects feeding on them could not be seen, but the open capsules certainly offer some kind of food to gleaners and flycatchers.

L. acapulcense is a semideciduous large tree. The presence of green leaves suggests that this species could have more insects than deciduous plants. The large size of *L. acapulcense* could also make it conspicuous, despite its relative scarceness (Appendix 1), and therefore attractive to birds of different guilds. The vegetation cover of this plant was not significantly correlated to the spring ordination axes, which is the season when it was used by birds.

The lack of a direct link between the bird species abundance and the abundance (cover) of their (presumably) favoured plant food sources as well as the evident opportunism showed by the bird species in both seasons coincides with what Poulin et al. (1993) found in dry forests in Venezuela. On the other hand, changes in resource availability appear to have an influence on a the abundances (as well as foraging behaviour) of the different guilds.

Conclusion

A conclusion can be addressed by answering to the question stated in the introduction: do favoured foraging plants determine the bird guild abundance in the study area? The answer is that even though marked plant phenological changes do have an effect in both, bird guild densities and foraging behaviour, favoured plant densities are only occasionally correlated with bird guild densities. With the exception of hummingbirds, which is the most specialized guild in the study, birds might choose their microhabitats based on visual cues, independently of the food supply in each of them. In addition, this study supports the opportunistic nature of most birds found in similar ecosystems elsewhere.

Literature cited

AOU (American Ornithologist's Union). 1983. Checklist of North American birds. 6th Edition. AOU, Washington D.C.

Arizmendi, M.C. and Ornelas, J.F. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. Biotropica 22:172-180.

Corcuera, P. and Butterfield, J.E.L. 1999. Bird communities of dry forests and oak woodland of western Mexico. *Ibis* 141:240-255.

Ekhardt, R.C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky mountains. Ecological Monographs 49:129-149.

Grieg-Smith, P. 1983. Quantitative Plant Ecology. Blackwell Scientific Publications, Oxford.

Hill, M.O. 1979. DECORANA-A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University. Ithaca, N.Y.

Holmes, R.T., Bonney, R.E. Jr. and Pacala, S.W. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60:512-520.

Hutto, R.L. 1985. Habitat selection by nonbreeding, migratory land birds. *In* Cody, L.C. (Ed.), Habitat Selection in Birds. Academic Press, New York.

Landres, P.B. and MacMahon, J.A. 1980. Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. Auk 97:351-65.

Lawrence, G.H.M. 1971. Taxonomy of Vascular Plants. The MacMillan Company. Indianapolis, IN, U.S.A.

Ludwig, J.A. and Reynolds, J.F. 1988. Statistical Ecology. John Wiley and Sons, New York.

Montaña, C. and Ezcurra, E. 1980. Simple instrument for quick measurement of crown projections. J. Forest. 78:699.

Nocedal, J. 1984. Estructura y utilización del follaje de las comunidades de pájaros en bosques templados del Valle de México. Acta Zool. Mex. No.6.

Peck, D.M. 1989. Tree species preferences shown by foraging birds in forest plantations in Northern England. Biol. Conserv. 48:41-57.

Poulin, B., Lefebvre, G. and McNeil, R. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. Ibis 135:432-441.

Poulin, B., Lefebvre, G. and McNeil, R. 1994. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. Biotropica 26:187-197.

Rabenold, D.N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. Ecological Monographs 48:397-424.

Recher, H.F. and Holmes, R.T. 1985. Foraging ecology and seasonal patterns of abundance in a forest avifauna. *In* Keast, A., Recher, H.F. and Saunders, D. (Eds.), Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management. Surrey Beatty & Sons, Chipping Norton, NSW.

Robinson K.L. and Holmes, R.T. 1982. Foraging behavior of forest birds: the relationship among search tactics, diet, and habitat structure. Ecology 63:1918-1931.

Rzedowski, J. 1978. Vegetación de México. Ed. Limusa, México.

Sabo, R.S. and Holmes, R.T. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85:121-138.

Sabo, S.R. and Whittaker, R.H. 1979. Bird niches in a subalpine forest: an indirect ordination. Nat. Acad. Sci. Proc. (USA) 76:1338-1342.

Standley, P.C. 1926. Trees and Shrubs of Mexico. Smithsonian Institution, Washington.

Terborgh, J. and Robinson, S. 1986. Guilds and their utility in ecology. *In* Kikkawa, J. and Anderson, D.J. (Eds.), Community Ecology. Pattern and Process. Blackwell Sci. Pub.

Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn, W.J. and Diger, S. 1998. Are bird-consumed fruits complementary resources? Oikos 83:195-205.

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Appendix 1. Main plant species, by life form, registered in that study. To every species is indicated family, code, relative cover (% total value), qualitative phenological status, and characteristics of flowers and fruits.

Plant name	Code	% value	Foliage season[a]	Flowering season	Flower or inflorecence	Corolla size (mm)	Fruiting season	Fruit type
Small-leved deciduous shrubs								
Acacia macilenta (Leguminosae)	At	8.5	A,s_{91}	-	-	-	A,S	Legume
Acacia tortuosa (Leguminosae)	Am	1.4	A,s	S	Brush	<10	A	Legume
Small-leaved deciduous trees								
Acacia pennatula (Leguminosae)	Ap	4.8	A,s	-	-	-	A	Legume
Conzattia multiflora (Leguminosae)	Cm	6.4	A,s_{91}	-	-	-	A	Legume
Lysiloma acapulcense (Leguminosae)	La	3.6	A,s	-	-	-	A	Legume
Lysiloma sp. (Leguminosae)	Lsp	2.1	A,s	-	-	-	A	Legume
Mimosa galeottii (Leguminosae)	Mg	2.7	A	-	-	-	A,S	Legume
Small-leaved evergreen tree								
Prosopis laegivata (Leguminosae)	Pj	0.7	A,S	-	-	-	A,S	Legume
Broad-leaved deciduous trees								
Bursera sp. (Burseraceae)	Bsp	2.9	A,s_{91}	-	-	-	A,S	Drupes
Ceiba aesculifolia (Bombacaceae)	Ca	0.4	A	-	-	-	A	Capsule
Guazuma ulmifolia (Betulaceae)	Gu	6.2	A,s_{91}	S	Cup	<10	A	Capsule
Heliocarpus appendiculatus (Tiliaceae)	Hsp	6.4	A	-	-	-	A	Plumose
Ipomoea wolcottiana (Convolvulaceae)	Iw	7.2	A,s_{91}	A	Tube	40	A	Capsule
Ficus sp. (Moraceae)	Fsp	0.3	A,s_{91}	A,S	Syconium	-	A	Syconium
Quercus crassifolia (Fagaceae)	Qcr	8.3	A	-	-	-	A	-
Quercus castanea (Fagaceae)	Qca	1.7	A	-	-	-	A	-
Broad-leaved shrub								
Croton ciliatoglanduliferus (Euphorbiaceae)	Ccg	8.4	A,s_{91}	S	Brush	<10	A	Capsule
Other broad-leaved shrubs	Bls	4.6						
Herbs	Her	18.8						
Succulent plants								
Opuntia sp (Cactaceae).	Osp	2.9	-	S_{91}	Cup	50	-	-
Stenocereus sp. (Cactaceae)	Ssp	0.3	-	S_{91}	Tube	50	S_{91}	Fleshy fruit
Vines								
Clystoma binatum (Bignoniaceae)	Vin	0.4	A	S_{91}	Tube	30	A	Capsule
Ipomoea quamoclit (Convolvulaceae)	Iqu	1.0	A	A	Tube	35	-	-

[a] A capital letter in foliage season indicates that the plant species had *ca.* 80% of the foliage present, a lower case letter indicates that the species had *ca.* 20% of its foliage.
A=autumn, S=spring, S_{91}=only in spring 1991, s=semideciduous.
A hyphen is included when concept does not apply (i.e. foliage for cactaceae) or when plant had no fruit or flowers at time of visit (usually they produce flowers or fruits during summer).

Appendix 2. Bird species, by feeding guild, detected in this study. To every species is give scientific and common name, code, and relative densities by season (Ind./ha). Relative densities are based on 67 plots of 60 m diameter each one. Numbers in parenthesis indicate proportion of the total birds present in the study area which were included in the study. Au = Autum, Sp = Spring.

Bird species/guild		Code	Season			
			Au90	Au91	Sp91	Sp92
Hummingbirds						
Amazilia beryllina	Berylline Hummingbird	BH	14.0	21.5		
Archilocus alexandrii	Black-chinned Hummingbird	BcH	43.5	38.5		
Amazilia violiceps	Violet-crowned Hummingbird	VcH	23.5	37.9	2.8	4.0
Cynanthus latirostris	Broad-billed Hummingbird	BbH	24.0	18.8	2.5	6.2
Eugenes fulgens	Magnificent Hummingbird	MH	4.5	6.2	1.3	
Lampornis clemenciae	Blue-throated Hummingbird	BtH	4.0	4.8	4.5	7.2
Foliage Flycatchers						
Empidonax sp.	Empidonax sp.	EF	23.0	32.3	2.0	15.3
Myiarchus cinerascens	Ash-throated Flycatcher	AtF	55.5	50.8	30.0	31.5
Woodland Gleaners						
Aphelocoma ultramarina	Gray-breasted Jay	GbJ	1.0	0.3	0.5	1.4
Piranga flava	Hepatic Tanager	HT	63.0	2.0	83.0	7.5
Pheuticus melanocephalus	Black-headed Grosbeak	BhG	1.0	0.9	103.0	19.1
Dendroica townsendi	Townsen'd Warbler	TW		1.5		
Parus wollweberi	Bridled Titmouse	BT		4.8	43.0	2.3
Dendroica nigrescens	Black-throated Gray Warlber	BtW	13.5	5.3		2.0
Regulus calendula	Ruby-crowned Kinglet	RcK	3.0	5.2	3.0	2.2
Forest Gleaners						
Vermivora celata	Orange-crowned Warbler	OcW	3.0	2.2		
Vermivora ruficapilla	Nashville Warbler	NW	16.0	7.3		0.7
Dendroica coronata	Yellow-rumped Warbler	YrW	54.5	54.5	1.3	18.2
Icterus pustulatus	Streaked-backed Oriole	SbO	15.8	15.7	60.3	47.7
Guiraca caerulea	Blue Grosbeak	BG			16.8	25.8
Polioptila caerulea	Blue-gray Gnatcatcher	BgG	74.5	70.8		0.7
Vermivora virginianae	Virginia's Warbler	VW	5.0	1.7		0.3
Psaltriparus minimus	Bushtit	Bt	1.5		5.5	11.9
Total number of species			38 (50)	47 (43)	46 (30)	56 (32)
Total number of records			525 (75)	618 (62)	376 (40)	468 (44)

Appendix 3. Significant plant foraging preferences by bird guilds. Results are based on goodness of fit tests. Preferences are indicated by "+", rejections by "-". Number of signs indicates probability level: 1, $P<0.01$, 2, $P<0.05$, 3, $P<0.001$. Au = Autum, Sp = Spring.

PLANT	Hummingbirds				Foliage flycatchers				Woodland gleaners				Forest gleaners			
	Au90	Au91	Au90	Au90	Au91	Sp91	Sp92	Au91	Sp91	Sp92	Sp91	Sp92	Au90	Au91	Sp91	Sp92
Small-leaved shrubs	--	---	-	--	---	--	---			--				-	--	--
Small-leaved deciduos shrub																
Acacia tortuosa			--	+		--	-	---	-	---	-	-			-	
Small-leaved deciduos trees																
Acacia pennatula		-			+++		+	+++								++
Conzattia multiflora	-			--				++		-						
Lysiloma acapulsence		+++	+++		+	+++	+++	+++	+++	+++					+++	+++
Small-leaved evergreen tree																
Prosopis laegivata				+++	++	+++					+			++		
Broad-leaved deciduous trees																
Bursera sp.					++			+++					+++	+++	+++	+++
Ipomoea wolcottiana	+++	+++		+++	+++	+++	+++	--					+++	+++	++	++
Ficus spp.					+++	+++	+++									+++
Quercus crassifolia		-	+++					+++	+++	+++			+++		++	
Quercus castanea			+++				+++	+++		+++						+++
Broad-leaved shrub																
Croton ciliatoglanduliferus	--	---	---	---	---	---	---	---	--	---	--	--	--	--	---	--
Herbs	---	---	--	---	---	---	---	---	--	---	--	--	--	--		
Succulent plants																
Opuntia sp.		--		--	--	-	--				+++					
Stenocereus sp.						+++					+++					
Vines					--	-				-	+++					

Appendix 4. Significant correlations between plant variable and bird guild densities (65 degrees of freedom). Au = Autum, Sp =Spring.

PLANT	Hummingbirds				Foliage flycatchers				Woodland gleaners				Forest gleaners			
	Au90	Au91	Sp91	Sp92	Au90	Au91	Sp91	Sp92	Au90	Au91	Sp91	Sp92	Au90	Au91	Sp91	Sp92
Small-leaved deciduos shrub																
Acacia tortuosa	.263			.471	.321	.367	-.332			-.252	-.284	-.284	.378	.573	.412	.358
Small-leaved deciduos trees																
Acacia pennatula							.368							-.253		
Conzattia multiflora				-.311	-.287				.462	.444		.318	-.318	-.449		-.249
Lysiloma acapulcense							.371									
Lysiloma sp.														.550		
Small-leaved evergreen tree																
Prosopis laegivata														.345	.286	
Broad-leaved deciduous trees																
Heliocarpus appendiculatus	-.253						.263	.244			-.267	-.303				
Ipomoea wolcottiana	.395	.409			.332	.290				-.272	-.329	-.298	.249			
Quercus crassifolia	-.361	-.376		-.291	-.488	-.360		-.438	.246	.558	.581	.476	-.320	-.383	-.483	-.397
Quercus castanea												.427	-.274	-.304		
Broad-leaved shrub																
Croton ciliatoglanduliferus				.278	.359	.257		.522	-.342	-.352	-.433	-.392		.284		.248
Herbs				-.436	-.268	-.322			.294				-.345	-.528	-.256	-.313
Succulent plants																
Opuntia sp.				.269	.296					-.268	-.277	-.287			.287	.508
Stenocereus sp.		.293	.446			.299							.276	.295		