Effects of landscape pattern and resource distribution on frugivorous bird species in the central andes of colombia: setting ecological thresholds

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Abstract

Understanding wildlife distributional patterns and their relationship with landscape characteristics (cover and configuration) and resource distribution is key for their conservation, especially in transformed landscapes. Theoretically, in some cases there are threshold values in habitat amount and configuration, below which species persistence is compromised. I analyzed the relationship of forest frugivorous bird species to the distribution of key fruiting trees (*Cecropia, Ficus* and *Miconia*) and landscape characteristics of forest patches at three different spatial scales, local (3 ha), intermediate (312 ha) and landscape (2500 ha), in the Central Andes of Colombia to look for indication of statistically significant ecological thresholds (e.g. non-linear relationships between species presence and habitat). I used data from four 2,500 ha rural landscapes with different fragmentation levels (80%, 46%, 25% and 20% forest cover) between 1 700 and 2 100 m on the western slope of the Central Andes. In general, the distribution of frugivorous bird species was better explained at local and intermediate scales by landscape characteristics, especially forest cover, than fruit resources distribution. At local scale, I established 27 species-specific occurrence thresholds in four landscape characteristic variables and in one fruit resources variable, for 13 forest frugivorous bird species. At intermediate scale I detect nine occurrence thresholds in two landscape characteristic variables and one fruit resource distribution variable for seven bird species. At landscape scale, not significant relationships were found because were not enough replicates. At local and intermediate scales the species which exhibiting the highest discrimination between presence and absence based on landscape characteristics to indicate ecological thresholds were large-bodied frugivorous. However, their use must be done carefully to avoid mis-interpretations in decision-making processes which could lead major negative implications for conservation.

Key words: Habitat Amount, Key Fruiting Trees, Landscape Configuration, Occurrence Thresholds, ROC Curves, Species Distribution.

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Introduction

As land uses increase in intensity and extension it is important to understand the role of landscape pattern in preserving, altering or eliminating biological communities (Miller et al. 1997). The effects of habitat transformation on wildlife depends on interaction between the scale at which the organisms function in the landscape, the patterns of distribution and abundance of organisms in the landscape, and how they are altered by habitat transformation (Kattan & Murcia 2003). Understanding these changes and their consequences on biodiversity are relevant issues especially in megadiverse countries where the deforestation rate is increasing.

Food abundance varies through time and space, but may directly influence abundance of organisms present (Block & Brennan 1993). The distribution of these resources will condition habitat quality, resulting in source – sink relationships (Pulliam 1988) among other relationships. Severe transformation caused by habitat loss can negatively affect the distributional patterns of resources especially for certain guilds as frugivorous and insectivorous (Sodhi et al. 2004) and produce changes in the composition of all species communities. Distribution of frugivores is important for tropical forest conservation, because loss of plant-animal mutualisms like loss of seed-dispersing species will potentially have large impacts on patterns of seed deposition and future distribution and conservation of many plant species. Furthermore, lack of disperser will increase local extinctions of plant species (Groom 1998; Amaraskare 1998; Bodin et al. 2006), especially of populations with low densities. Over time, these changes may cause synergic effects on community structure and function of the native forests (Loiselle & Blake 2002).

Certain plant genera could be considered as key-species for frugivores due to the fact that they provide fruits not only during periods of high abundance of fruits, but also during scarcity periods of fruits. In Andean forests *Cecropia* (Cecropiaceae), *Ficus* (Moraceae) and *Miconia* (Melastomataceae) are genera with several species, not only characteristics from open areas and secondary forests but also from interior habitats (Vargas 2002), and with asynchronical phenology patterns (Ríos 2005; Ríos & Kattan in prep.; Valenzuela & Kattan in prep.). This means that they could be considered as key resources for frugivores, not only birds but also a broad variety of taxa (Luck & Daily 2003; Loiselle & Blake 1999; Poulin et al. 1999; Lambert & Marshall 1991; Loiselle & Blake 1990; Estrada et al. 1984). However, only the local habitat conditions may be inadequate to explain species presence or abundance; the significant effect of boundary shape or characteristics of the surrounding landscape must be considered (Turner 2005), because some species might be favored more than others in their distribution and also they can affect other functions such as relationships between species (i.e. predator – prey interactions).

Studies exploring the effects of landscape context and patch characteristics to establish relationships with the structure and composition of faunal communities have been conducted for different taxa and landscape types (see Mazerolle & Villard 1999). The most important landscape characteristics influencing species richness and abundance are patch size (Martinez-Morales 2005; Cornelius et al. 2000; Abensperg-Traun et al. 1996; Vos & Stumpel 1995), patch shape (Martinez-Morales 2005); edge extent and nature (Watson et al. 2004; Campi & MacNally 2001; Restrepo et al. 1999); land cover and landscape configuration (Bishop & Myers 2005; Watson et al. 2005; Westphal et al. 2003; Flather & Bevers 2002; Steffan-Dewenter et al. 2002; Trzcinski et al. 1999; McGarical & McComb 1995; Villard et al. 1999). In many cases, a single study found significant relationships with more than one on these characteristics. However, a common problem in many studies is incorrect extrapolations of results from small scales to large scales (McGarical & Cushman 2002).

One tool that has been suggested for assessing the consequences of landscape transformation is setting threshold values in ecological processes (Fahrig 2001; Hugget 2005; Lindenmayer et al. 2005; Radford et al. 2005). Ecological thresholds are critical values of an independent variable around which the system flips from one state to another (Muradian 2001). Thresholds have been established using both empirical and simulation data (Fahrig 2002; Dykstra 2004). Examples of threshold values are, extinction thresholds (Tilman et al. 1994; Fahrig 2001, 2002), fragmentation thresholds (Andrén 1994, 1999), connectivity thresholds (With & Crist 1995; Metzger & Décamps 1997; Schultz & Crone 2005), and occurrence thresholds (Hansen et al. 1995; Bütler 2004; Guénette & Villard 2004, 2005). Threshold values can provide information to define sensitivity of species to processes that threaten many ecological processes having potential utility in conservation and management (Hugger 2005).

In Colombia, the Andean region has a high variety of biophysical environments due its high topographical complexity. This has generated great diversity and endemism, in a limited space (Etter & van Wyngaarden 2000; Kattan et al. 2004) reflected in high beta diversity values for many taxa such as birds and plants (Kattan et al. 2006; Mendoza et al. in prep.). However, historically this region is one of the most fragmented areas in the country because of the population growth and the spreading of coffee crops and cattle ranching during the first decades of 20th Century. Since then, majority of forest patches are on private lands and very few policy instruments have been implemented to promote forest and species conservation within the landowners' community. As a consequence of this long-term forest fragmentation 30% of forest bird species are currently extinct in sub Andean forests (Renjifo 1999). Large-bodied canopy frugivores and understory

insectivores are the most sensible guilds to habitat fragmentation in the tropics (Kattan et al. 1994; Kattan 1992).

I investigated the species/habitat relationships using landscape characteristics and fruit resource variables which are supposed to influence the forest frugivorous bird species assemblages. Also I investigated a gradient of habitat transformation and fruit resource distribution to explore threshold values for species occurrence. The questions I addressed were, (1) How well does the abundance and distribution of fruiting trees (gen. *Cecropia, Ficus* and *Miconia*) explain the distribution of frugivorous bird species?; (2) How well do landscape variables explain the distribution of frugivorous bird species?, and (3) Are there ecological thresholds for landscape variables and abundance and distribution of fruiting trees affecting the frugivorous bird distribution?

Study Area and Methods

I conducted my study in four 2 500-ha rural landscapes with different amounts of native forest, between 1 700 and 2 100 m.a.s.l. on the western slope of the Central Andes of Colombia. From north to south they are (Fig 1): 1) Mid Chambery River watershed (henceforth Chambery) (75°30'5" W, 5°16'34" N), Municipality of Aranzazu, Caldas, with 20% forest cover; 2) Otún River watershed (Otún) (75°33'8" W, 4°42'43" N), Municipality of Pereira, Risaralda, 80% of native forest cover; 3) Barbas River Canyon (Filandia) (75°35'42"W 4°40'48"N) Municipality of Filandia, Quindío, 46% of native forest cover; and 4) Mid Nima River watershed (Nima) (76°9'1" W, 3°30'41" N), Municipality of Palmira, Valle del Cauca, 25% forest cover. All these areas are characterized by Sub-Andean forest, with mean annual temperature and rainfall of 19°C and 2 000 to 3 000 mm. The main land-uses in all landscapes are livestock pastures and forestry plantations of exotic species (*Pinus, Cupressus* and *Eucalyptus*).

In 2002 – 2005 the Alexander von Humboldt Institute (AvHI) conducted biodiversity characterizations in the same area within the Project "Conservation and sustainable use of biodiversity in the Colombian Andes" (IAvH 2007). These landscapes were selected in agreement with regional authorities and local communities according to their conservation priorities, and because they were considered as representative samples of sub-Andean landscapes with different amount of native forest to evaluate contribution of different habitats to regional diversity and potential effects of habitat loss in species diversity. In each landscape different habitats were sampled (native forest, grasslands, forestry plantations and crops). Sampling sites were selected according to their vegetal structure aiming at a representative picture of each habitat. Within each habitat a sampling unit was located, this was composed by two bird count points and four transects for vegetation survey (Fig. 2). In total

138 sampling units were made (40 in Chambery; 22 in Otún; 40 in Filandia and 36 in Nima) and species richness and abundance of birds, trees and ants (not considered here) species was recorded.
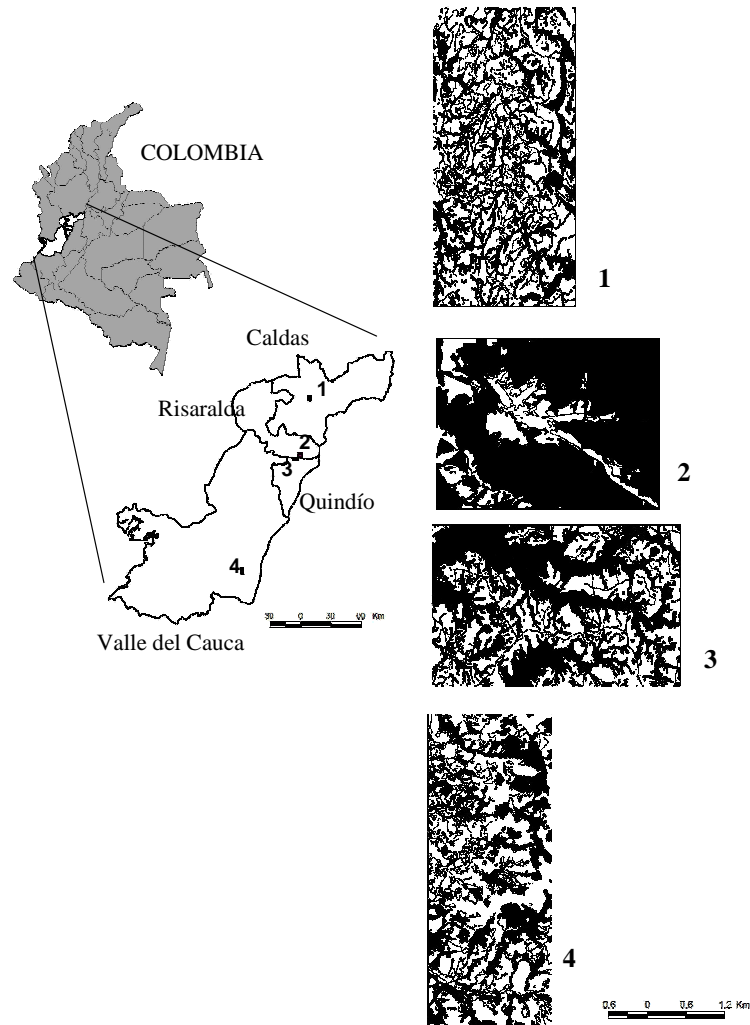

Fig. 1: Map of the study area in the Central Andes of Colombia. 1. Mid Chambery River watershed (20% forest cover). 2. Mid Otún River watershed (80%). 3. Barbas River Canyon (46%). 4. Mid Nima River watershed (25%), Black areas represent native forest land-cover.

Bird Survey

The sampling method for birds was point counts (50m radius, two per each site, equivalent to 523,3 m^2, separate one each other 50 m Daily et al.,2001) using visual observation and vocalization recordings within the 50 m radius. Each site was sampled for three repetitions consecutive days between 06h00 and 10h00 during 15 minutes (except windy or rainy days; Renjifo 1999). The

combination of methods attempted to consider differences in detectability among the species (Mendoza et al. in press).

Trees Sampling

For trees data four transects 50x4m (800 m^2) were made adjacent to each bird sampling site. Because parallel transects were not independent one to each other (5 m), for the analysis the data from transect one and three, and two and four were pooled (Fig. 2). All tree individuals with dbh ≥ 5cm were counted (Mendoza et al. in press).
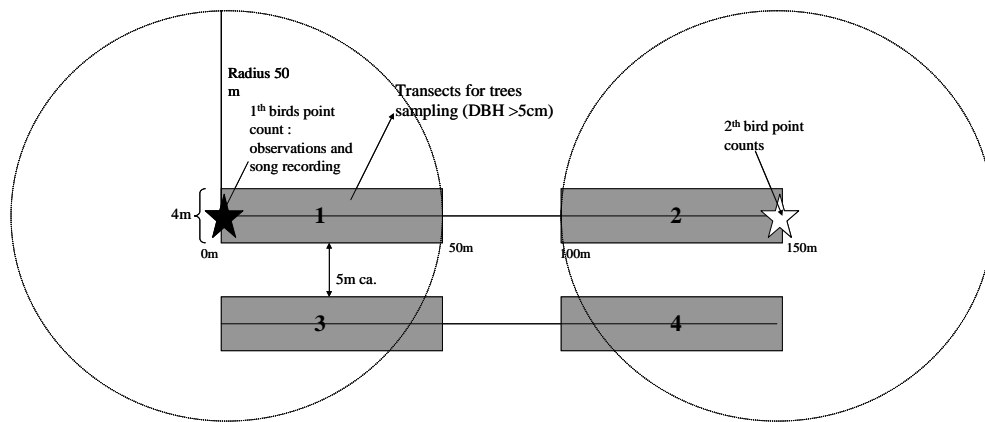
Fig. 2: Diagram of sampling units for birds and trees used to data recording by the Humboldt Institute (Modified from Mendoza et al. in press).

From those data bases and because my aims were related to forest species, I chose for my study only the information from native forest habitats (n = 76; distributed: 16 in Chambery; 16 in Otún; 20 in Filandia and 24 in Nima) (Fig. 1), and data of species richness and abundance of forest frugivorous bird species and *Ficus, Cecropia* and *Miconia* trees. In total 58 bird species (excluding migratory species), and 33 fruiting tree species were selected (Table 1, Appendix 1).

Table 1: Frugivorous bird species recorded in four landscapes of sub Andean forest in Central Andes of Colombia and their frequency of occurrence. In bold the species which met the criterions of abundance: species only present on ≥ 10% or ≤ 90% of the 76 sites; and the criterion of are considered as negatively affected species by habitat transformation according to DCA and CCA results.

Abbreviation	Scientific name	Frequency of Occurrence (mean ± SD)	Landscape Chambery	Filandia	Nima	Otún
Aabur	*Aburria aburri*	(5.26 ± 0.22)		X		X
Amerc	*Amazona mercenaria*	(6.58 ± 0.24)	X	X	X	
Aflav	**Anisognathus flavinucha**	**(30.26 ± 0.46)**	X	X	X	X
Awagl	***Aratinga wagleri***	**(17.11 ± 0.37)**		X		X
Ahaem	***Aulacorhynchus haematopygus***	**(52.63 ± 0.50)**	X	X	X	X
Apras	***Aulacorhynchus prasinus***	**(35.53 ± 0.48)**	X	X	X	X
Bmont	*Buthraupis montana*	(2.63 ± 0.16)			X	
Cgoud	***Chamaepetes goudotii***	**(19.74 ± 0.40)**		X	X	X
Cniti	*Chlorochrysa nitidissima*	(3.95 ± 0.19)		X		X
Cspiz	*Chlorophanes spiza*	(6.58 ± 0.24)	X			
Ccyan	*Chlorophonia cyanea*	(1.32 ± 0.11)				X
Ccani	***Chlorospingus canigularis***	**(10.53 ± 0.30)**	X		X	X
Copht	*Chlorospingus ophthalmicus*	(7.89 ± 0.27)	X	X	X	X
Cfasc	***Columba fasciata***	**(17.11 ± 0.37)**	X	X	X	
Dalbi	*Diglossa albilatea*	(1.32 ± 0.11)		X		
Dcyan	*Diglossopis cyanea*	(1.32 ± 0.11)		X		
Ebour	***Eubucco bourcierii***	**(31.58 ± 0.46)**	X	X		X
Emusi	***Euphonia musica***	**(34.21 ± 0.47)**	X	X	X	X
Exant	***Euphonia xanthogaster***	**(36.84 ± 0.48)**	X	X		X
Hcris	*Habia cristata*	(5.26 ± 0.22)	X			X
Hfron	*Hemispingus frontalis*	(1.32 ± 0.11)				X
Hsupe	***Hemispingus superciliaris***	**(22.37 ± 0.41)**			X	X
Hguir	*Hemithraupis guira*	(1.32 ± 0.11)	X			
Mchry	*Masius chrysopterus*	(6.58 ± 0.24)		X		X
Moliv	***Mionectes olivaceus***	**(10.53 ± 0.30)**	X	X		X
Mstri	***Mionectes striaticollis***	**(10.53 ± 0.30)**	X	X		X
Mrall	***Myadestes ralloides***	**(78.95 ± 0.41)**	X	X	X	X
Mychry	***Myiodynastes chrysocephalus***	**(42.11 ± 0.49)**	X	X	X	X

Omomo	*Ortalis motmot*	(28.95 ± 0.45)	X		X	
Ppiti	*Parula pitiayumi*	(67.11 ± 0.47)	X	X	X	X
Ppers	*Penelope perspicax*	(17.11 ± 0.37)		X		X
Pauri	*Pharomachrus auriceps*	(10.53 ± 0.30)		X	X	X
Pchal	*Pionus chalcopterus*	(17.11 ± 0.37)		X	X	X
Ptumu	*Pionus tumultuosus*	(6.58 ± 0.24)		X		X
Pmela	*Pipraeidea melanonota*	(11.84 ± 0.32)		X	X	X
Prief	*Pipreola riefferii*	(1.32 ± 0.11)				X
Pleuc	*Piranga leucoptera*	(5.26 ± 0.22)				X
Plleucs	*Platycichla leucops*	(1.32 ± 0.11)		X		
Pscut	*Pyroderus scutatus*	(15.79 ± 0.36)		X		X
Rflam	*Ramphocelus flammigerus*	(10.53 ± 0.30)	X	X	X	
Salbic	*Saltator albicollis*	(19.74 ± 0.40)	X	X	X	
Satri	*Saltator atripennis*	(52.63 ± 0.50)	X	X	X	X
Salbo	*Sericossypha albocristata*	(2.63 ± 0.16)				X
Tarth	*Tangara arthus*	(61.84 ± 0.48)	X	X	X	X
Tcyan	*Tangara cyanicollis*	(5.26 ± 0.22)	X			X
Tgyro	*Tangara gyrola*	(15.79 ± 0.36)	X	X	X	X
Thein	*Tangara heinei*	(50 ± 0.50)	X	X	X	X
Tlabr	*Tangara labradorides*	(5.26 ± 0.22)			X	X
Tnigr	*Tangara nigroviridis*	(9.21 ± 0.29)	X	X		X
Tvasso	*Tangara vassori*	(1.32 ± 0.11)	X			
Tvitr	*Tangara vitriolina*	(38.16 ± 0.48)	X	X	X	X
Txant	*Tangara xanthocephala*	(2.63 ± 0.16)	X			X
Tepis	*Thraupis episcopus*	(10.53 ± 0.30)	X	X		X
Tpalm	*Thraupis palmarum*	(5.26 ± 0.22)	X	X		
Tfusc	*Turdus fuscater*	(14.47 ± 0.35)	X	X		
Tigno	*Turdus ignobilis*	(17.11 ± 0.37)	X	X	X	X
Tserr	*Turdus serranus*	(2.63 ± 0.16)			X	
Zviri	*Zimmerius viridiflavus*	(90.79 ± 0.29)	X	X	X	X

I evaluated the relationships between frugivorous bird species to landscape characteristics and fruit resources distribution, at three ecological scales, local, intermediate and landscape. I measured the landscape characteristic variables (Table 2) using the land-cover interpretations in vector format of each study area produced by the GIS Unit of the AvHI. To generate those maps aerial photographs (scale 1:25 000; yrs. 1986 and 1990) and Quick Bird satellite images (1 m resolution, yrs. 2002 and 2003) were used. At local scale, I made a buffer ring with 100 m radius over each sampling point to use the same area to measure the explanatory variables (Table 2), 76 units were considered. For

intermediate scale, each landscape was divided in eight quadrants (312 ha), having 32 units. For landscape scale was the 2 500 ha window (n=4).

Because some sampling points which are closer together have a tendency to be more similar that things that are farther apart, is a lack of independence among observations creating spatial auto-correlation (SA) (Dale & Fortin 2002). Spatial autocorrelation creates apparently significant results more often than in fully independent data. Then, before the statistical tests are running, the magnitude and structure of SA needs to be determinate. I found significant spatial autocorrelation (SA) in my variables (abundance and richness of bird and tree species). I evaluated SA using the Moran's coefficient in correlograms (I = between 0.55 to -0.85 for trees and 0.22 to -0.19 for birds). Moran coefficient (I) describes the degree of correlation between the values of a variable as a function of spatial locations (Fortin 1999). Moran's I indicates positive autocorrelation with positive values (usually 0 to 1), negative autocorrelation with negative values (0 to -1), and the absence of autocorrelation is close to 0 (Legendre 1993; Rosenberg 2001). Because the individual coefficients of the correlogram are not independent from one another I deemed the correlogram as significant if the significance level of at least one individual coefficient was lower than the α' level ($\alpha' = 0.004$), using the Bonferroni adjustment (Fortin 1999). I made 12 distance classes. Because SA I used a conservative measure level of significance ($\alpha = 0.01$) in the analysis (Guénette & Villard 2005). Adjusting the α level does not correct SA per se but does provide some assurance that significant results detected are indeed significant (Dale & Fortin 2002). However, marginally significant values ($\alpha = 0.02$) were considered for logistic regression models and threshold calculations, ROC curves (see below).

To establish if richness and abundance of frugivorous birds were related to richness and abundance of key fruiting trees within each landscape and among landscapes, I used a Mantel test (Fortin 1999; Fortin & Dale 2005). This test was selected because my bird and fruiting trees data were collected in the same sites, and the objective of the Mantel Test is to look for correlation between spatially autocorrelated data (Fortin & Dale 2005). I built the distance matrices of species richness and abundance using Euclidean distance. For significance evaluation I used Monte Carlo test randomizations (5000). I evaluated the relationship between patch area and total abundance of fruiting tree species (*Cecropia, Ficus* and *Miconia*) using Spearman Correlation.

I related the frugivorous bird species abundance with the selected explanatory variables (Table 2) at three different ecological scales (local, 3 ha; intermediate, 312 ha and landscape, 2500 ha) using Canonical Correspondence Analysis (CCA). The aim of canonical ordination is to detect the main pattern in the relations between the species and the explanatory environment or habitat variables (ter Braak 1986, 1987). I assessed individual variables in the final

model by calculating the intraset correlations. This gave me the correlation between a landscape variable and an axis, which is a measure of the relative importance of that particular variable to the axis. The graphical output resulting from an ordination is a bi-plot. Vector in the bi-plot represents the correlation between an explanatory variable and the CCA axes (ter Braak 1986; Coppedge et al. 2001). The significance was evaluated by conducting Monte Carlo randomizations on the frugivorous bird – explanatory variables relationship. As I had different sampling effort among quadrants and landscapes, I used mean abundance of frugivorous bird species and key fruiting trees. To establish the key fruiting tree richness in each quadrant and landscape, I used rarefaction individual – based (for intermediate scale I compare among quadrants using n = 20 individuals; and for landscape scale using n = 150 indiv.) (Gotelli & Colwell 2001).

Table 2: Explanatory variables selected to evaluate the relationship between landscape characteristics and key resource distribution in the Central Andes of Colombia. *To avoid pseudoreplication effects, Patch Area variable was only considered for logistic regression analysis because in some cases we had a big patch (>200 ha) with more than one sampling points. Then all samplings in one big fragment were summarized in one sample using presence – absence data of the species and only one area value.

Ecological Scale	Abbreviation	Variable
Local (3 ha)	Patch_Area*	Patch area
	Num_LC	Numbers of land-covers within the 100m buffer ring
	HA100	Suitable amount of habitat (Forest) within the 100m buffer ring
	EL100	Forest edge length within the 100m buffer ring
	Treerich	Key fruiting trees total richness
	Treeabun	Key fruiting trees total abundance
	Abu_Ficu	Abundance of *Ficus*
	Abu_Cecr	Abundance of *Cecropia*
	Abu_Mico	Abundance of *Miconia*
Intermediate (312 ha) and	Suit_Am_Habit	Suitable amount of habitat (Forest)
Landscape (2500 ha)	Num_LC	Numbers of land-covers
	Num_Patch	Number of forest patches
	EL	Forest edge length
	Treerich	Key fruiting tree richness (n=20 and 150 indiv.)
	Treeabun	Key fruiting trees (mean abundance)
	Abu_Ficu	Mean abundance of *Ficus*
	Abu_Cecr	Mean abundance of *Cecropia*
	Abu_Mico	Mean abundance of *Miconia*

Selection of species for threshold analyses was made using two criterions: First, species only present on $\geq 10\%$ or $\leq 90\%$ of the 76 sites, were included because, threshold effects cannot be derived for very rare or very common (Trzcinski et al. 1999; Gutzwiller & Barrow 2001). Second, species negatively

affected by habitat transformation (Mönkkönen & Reunanen 1999; Guénette & Villard 2004). In case of presence/absence data focusing on focal species is recommended for management purposes (Mönkkönen & Reunanen 1999), because for instance in the case of negatively affected by habitat transformation species their major habitat requirements could encapsulate those of less sensitive species found in the same guild. These negatively affected species were identified through a detrended correspondence analysis (DCA) using a scatter diagram (ter Braak 1987) (Fig. 3) and the CCA results. Species related to the landscapes with higher amount of forest cover and which were not present in highly fragmented landscapes were considered as negatively affected by habitat transformation. Thirty two three species met both criterions (Table 1).
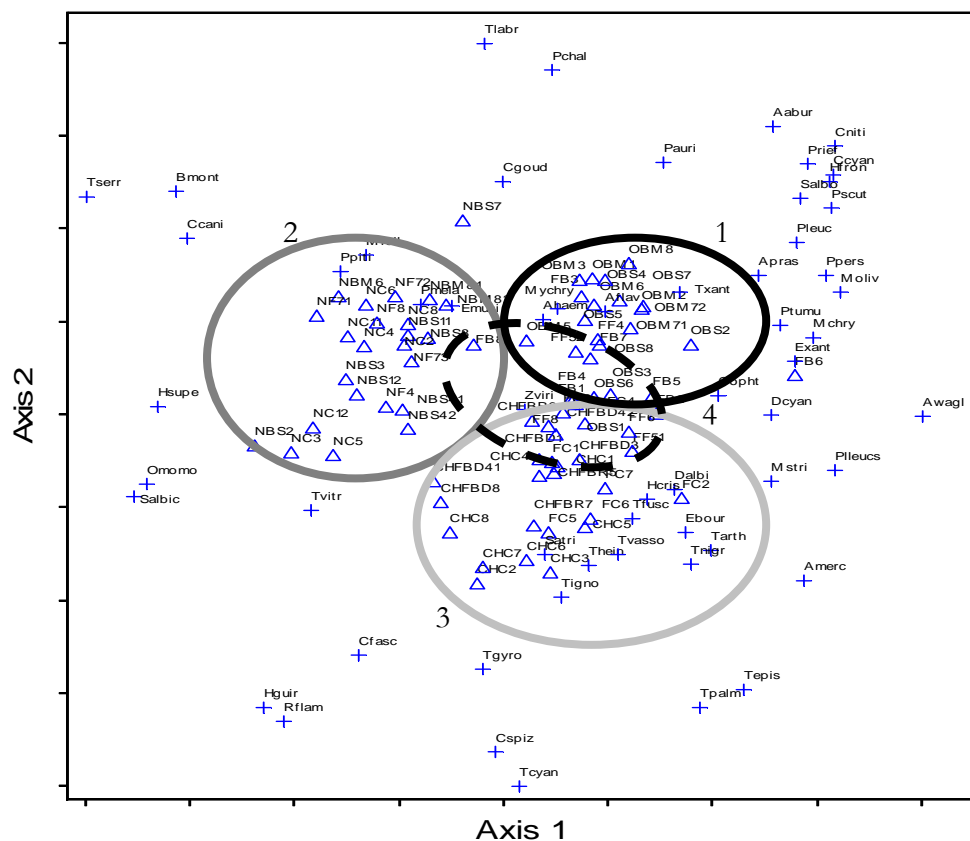
composition in the Central Andes of Colombia using DCA. Crosses are bird species. Full bird names are in Table 1. Triangles are sites (starting with CH are from Chambery; F from Filandia; O from Otún and N from Nima). Solid line circles number 1, 2 and 3 correspond to Otún, Nima and Chambery respectively, dashed line circle number four grouping the Filandia's sites.

I used stepwise (forward) logistic regressions to evaluate relationships between the presence and absence (P/A) of single species with the explanatory variables (landscape and key fruiting resource variables). This approach is based on the probability of Wald statistic ($p < 0.001$ for enter and $p > 0.10$ for removal (Guénette & Villard 2005). I ran the logistic regressions for local scale, intermediate and landscape scales. To establish species-specific ecological thresholds I used single specific explanatory variables (Table 2). I transformed the data using logarithmic transformations (Zar 1984).

To assess the performance of the regression models and identify the threshold values, I used threshold-independent receiver operation characteristic (ROC) curves (Guénette & Villard 2004, 2005). Each point on the ROC plot represents a sensitivity/specificity pair corresponding to a particular decision threshold. A test with perfect discrimination (no overlap in the two distributions of results) has a perfect sensibility (1.0) and perfect specificity (0.0) (Zweig & Campbell 1993). Area under curve values (AUC) with significances higher than 0.02 were arbitrarily considered non different of 0.5 (0.5 AUC values corresponds to the theoretical plot for a test with no discrimination between the two distributions of results). To identify the optimum probability threshold I used the maximum accuracy method, the point at which the sum of sensitivity and specificity is maximized (Manel et al. 2001; Guénette & Villard 2005). The ROC curves method appears as one of the best methods to establish ecological thresholds compared with others approaches (Manel et al. 2001; Liu et al. 2005). Usually, AUC values of $0.5 – 0.7$ are taken to indicate low accuracy, values of $0.7 – 0.9$ indicate useful applications and values of > 0.9 indicate high accuracy (Manel et al. 2001). I evaluated the model fit to each scale comparing the area under curve (AUC) and Nagelkerke's R^2, though Spearman correlation (Gutzwiller & Barrow 2001; Guénette & Villard 2005). I ran this test using SigmaPlot 10.

To validate the threshold values the sites where each species is present and where is absent, according with the value obtained for the explanatory variable, were recorded. For variables which have a negative relationship with forest and forest – edge species, below the threshold the presence of the species is expected. For variables with positive relationship with the species above the threshold the presence is expected. However, in all cases some false negatives (absence of the species in sites where their presence was expected) and some false positives (presence in sites where their absence was expected) occurred, but in less proportion of the true positives and negatives (Zweig & Campbell 1993).

Results

Relationship between abundance and richness of birds and resources

Among landscapes the richness and abundance distribution of frugivorous birds were positively correlated with the richness and abundance of fruiting trees of genera *Ficus, Cecropia* and *Miconia* (Mantel test; r = 0.184 and 0.119 respectively; p≤0.001). Within each landscape separately the correlations were not significant, even though for Nima and Otun landscapes which significance values could motivate further research to explore these relationships (Table 3).

Table 3: Mantel test results for each one of the relationships evaluated between frugivorous bird species abundance/richness and key fruiting trees (*Ficus, Cecropia* and *Miconia*) abundance/richness on local scale in the Central Andes of Colombia.

Landscape	Relationship evaluated	Standard Mantel Statistic (r)	p-value
All landscapes	Frut. trees richness vs. Frug. birds richness	0.184	0.0002
n = 76	Frut. trees abundance vs. Frug. birds abundance	0.119	0.0006
Chambery	Frut. trees richness vs. Frug. birds richness	0.09	0.17
n = 16	Frut. trees abundance vs. Frug. birds abundance	0.10	0.26
Filandia	Frut. trees richness vs. Frug. birds richness	0.07	0.31
n = 20	Frut. trees abundance vs. Frug. birds abundance	-0.16	0.18
Nima	Frut. trees richness vs. Frug. birds richness	0.20	0.03
n = 24	Frut. trees abundance vs. Frug. birds abundance	0.08	0.21
Otún	Frut. trees richness vs. Frug. birds richness	-0.24	0.04
n = 16	Frut. trees abundance vs. Frug. birds abundance	0.22	0.13

Birds – explanatory variables relationship

At local scale (3.14 ha) and for abundance data of frugivorous bird species the three first CCA axes accounted for 42.8% of the total variance in the species data (axis 1: 24.9%; axis 2: 17.8% and axis 3: 0.1%), and 84% of the extracted variance in the species – explanatory variables relationship. The Monte Carlo test of relationships showed that both the first CCA axis (p<0.01) and the overall analysis (p<0.01) were significant. Axis 1 is better explained by the Landscape Characteristics, suitable habitat amount within the 100m buffer ring (HA100); numbers of land-cover within the 100m ring (Num_LC) and edge length within the 100m buffer ring (EL100). The first one had opposite sign to the other two (Table 4). Axis 2 is better explained by Fruit Resources Distribution, this means the variables related with key resources offer (*Ficus, Cecropia* and *Miconia*). Abundance of *Cecropia* (Abu_Cecr) had opposite behavior to the other variables: key fruiting trees total species richness (Treerich); key fruiting trees total abundance (Treeabun); Abundance of *Ficus* (Abu_Ficu) and Abundance of *Miconia* (Abu_Mico) (Table 4).

The majority of the Otún's sites and some characteristic forest species (i.e., *Aratinga wagleri, Hemispingus frontalis, Penelope perspicax, Pharomachrus auriceps, Pionus tumultuosus, Pyroderus scutatus, Sericossypha albocristata, Masius chrysopterus, Pipreola riefferii*) are positively correlated with HA100 and negatively correlated with Num_LC and EL100. *Tangara vitriolina* and *Turdus serranus* are positively correlated with Num_LC and EL100. The rest of Otún and the Filandia's sites are positively correlated not only with HA100 but also with Treerich and Treeabun. Species such as *Aburria aburri, Chlorochrysa nitidissima, Aulacorhynchus prasinus, Chlorospingus ophthalmicus, Mionectes olivaceus, Piranga leucoptera, Anisognathus flavinucha, Euphonia xanthogaster, Habia cristata* have the same behavior (Fig. 4).

The Chambery's sites and species such as *Columba fasciata, Saltator atripennis, Tangara heinei, Tangara vitriolina, Turdus fuscater, Turdus ignobilis* are positively correlated with Treerich; Treeabun; Abu_Ficu and Abu_Mico. The majority of Nima's sites and species like a *Buthraupis Montana, Chlorospingus canigularis, Hemispingus superciliaris, Ortalis motmot, Saltator albicollis* are negatively correlated with these variables and are positively correlated with Abu_Cecr. In both cases, the distribution of these species and sites of Chambery and Nima are influenced by Num_LC and EL100 (Fig. 4).

At intermediate scale (312.5 ha) and for abundance data of frugivorous bird species the three first axes accounted for 59% of the variance in the species data (axis 1 28.3%; axis 2 18.4% and axis 3 12.2%) and 97% of the extracted variance in the species – explanatory variables relationship. The Monte Carlo test of relationships showed that both the first CCA axis ($p<0.01$) and the overall analysis ($p<0.01$) were significant. Axis 1 was better explained again by Landscape Characteristics, especially by Suit_Am_Habit (native forest) and Num_LC. However, Suit_Am_Habit had a contrary behavior respect Num_LC, EL and Num_Patch (Table 13 and Fig. 5). Axiss 2 and 3 were explained by Fruit Resources Availability. For the Axis 2, Treerich and Abu_Ficu had opposite behavior to the other variables Treeabun, Abu_Cecr and Abu_Mico (Table 5).

Otun's quadrants and some typical forest species (i.e. *Aburria aburri, Penelope perspicax, Piranga leucoptera, Pyroderus scutatus*) are mainly correlated with Suit_Am_Habit. The distribution of *Chlorochrysa nitidissima* and *Pipreola riefferii* are positively correlated with Suit_Am_Habit, but Num_Patch influenced on the final location in the biplot. The Filandia's quadrants are also positively
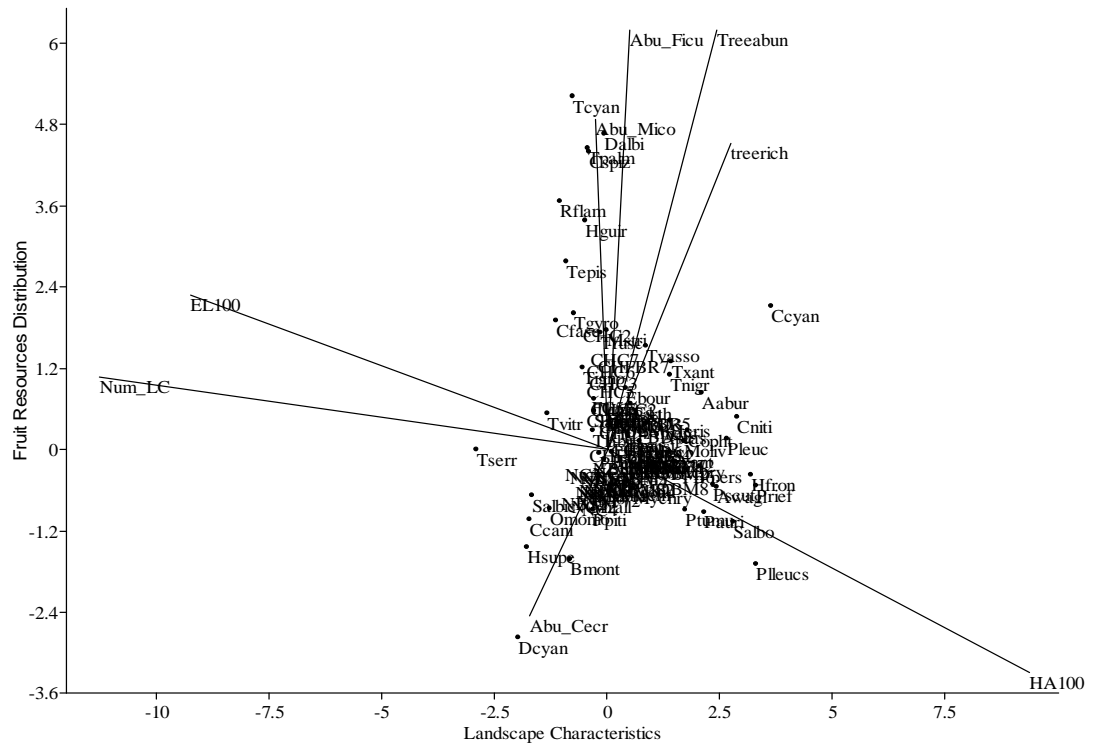
Fig. 4: Ordination bi-plot depicting the first two axes of the CCA of 76 sites (local scale) with 58 frugivorous bird species of the Central Andes of Colombia. 9 vector representing equal number of variables. Labels with dot are bird species. Full bird names are in Table 2. Site's labels (in capital letters) starts with CH are from Chambery; F from Filandia; O from Otún and N from Nima.

Table 4: Intra-set correlations between landscape / resource variables and CCA axes 1, 2 and 3 at local scale for the four studied landscapes in the Central Andes of Colombia. Complete name of the variables are in Table 2.

Abbreviation	Axis 1	Axis 2	Axis 3
Num_LC	0.911	-0.051	0.105
HA100	-0.723	0.303	0.413
EL100	0.683	-0.284	-0.291
Treerich	-0.230	-0.452	0.391
Treeabun	-0.153	-0.639	0.396
Abu_Ficu	-0.128	-0.609	0.378
Abu_Cecr	0.162	0.265	0.757
Abu_Mico	0.069	-0.543	-0.057

correlated with Suit_Am_Habit and Abu_Mico, but their distribution is highly influenced by Num_Patch and EL and in lower level by Treerich and Abu_Ficu (Fig.5). Species such as *Diglossopis cyanea, Mionectes striaticollis, Myadestes ralloides, Saltator atripennis, Thraupis episcopus, Turdus ignobilis* are present in Filandia and almost all are characteristic of edge and open areas (Fig. 5).

The quadrants of Nima and Chambey are negatively correlated with Suit_Am_Habit and are characterized by species from edge and open areas (i.e. *Hemithraupis guira, Ortalis motmot, Tangara vitriolina*). Mainly, the Chambery's quadrants are positively correlated with EL, Num_Patch, Num_LC and Treeabund, and negatively correlated with Treerich and Abu_Ficu. Species like *Tangara gyrola, Chlorophanes spiza, Tangara heinei, Tangara xanthocephala* are positively correlated with EL, Num_Patch and Treeabun (Fig. 5). The majority of Nima's quadrants are positively correlated with Treerich, Abu_Ficu and Abu_Cecr. Forest species like a *Amazona mercenaria, Aulacorhynchus haematopygus, Chlorospingus canigularis, Chlorospingus ophthalmicus* and *Hemispingus superciliaris* are also positive correlated with Treerich, Abu_Ficu and Abu_Cecr (Fig. 5).

Fig. 5: Ordination bi-plot depicting the first two axes of the CCA of 32 quadrants (312 ha) with 58 frugivorous bird species of the Central Andes of Colombia. 9 vector representing equal number of variables. Labels with dot are bird species. Full bird names are in Table 2. Site's labels (in capital letters) starts with CH are from Chambery; F from Filandia; O from Otún and N from Nima.

At landscape scale (2500 ha) I did not find significant results after the Monte Carlo test mainly because I had not enough replicates.

Table 5: Intra-set correlations between landscape / resource variables and CCA axes 1, 2 and 3, at intermediate scale, for the four studied landscapes in the Central Andes of Colombia. Complete name of the variables are in Table 2.

Abbreviation	Axis 1	Axis 2	Axis 3
Suit_Am_Habit	0.881	-0.055	-0.141
Num_LC	-0.839	-0.240	-0.330
Num_Patch	-0.341	-0.394	0.385
EL	-0.371	-0.325	0.657
Treerich	0.131	0.398	0.148
Treeabun	-0.265	-0.049	-0.197
Abu_Ficu	0.218	0.215	-0.577
Abu_Cecr	-0.110	-0.037	0.200
Abu_Mico	-0.083	-0.011	-0.003

At local scale, 14 species showed significant relationships with the explanatory variables. Ten out the fourteen forest species selected as negatively affected by habitat transformation had a highly significant relationships with one or more explanatory variables. For the forest – edge species, only four species showed highly significant relationships (Table 6). Patch area, number of land cover (Num_LC) and edge length (EL100) were the variables which most of the selected species showed strong relationships. In almost all cases Num_LC and EL100 had negative relationships with the presence of the species. Only two species (*Euphonia musica* and *Hemispingus superciliaris*) had significant relationships with fruit resources (Table 6).

Table 6: Results of the stepwise logistic regression models of the species presence related to explanatory variables at local scale (n = 76). Probability, $**p \leq 0.01$; $***p \leq 0.001$. Marginally significant values are shown in brackets ($p \leq 0.02$). 10 forest species in bold and 4 forest – edge species. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

Abbreviation	Single specific variable	β_1
Ahaem	HA100	5.943**
Apras	Num_LC	-7.806**
	Patch_Area	1.277**
Exant	Patch_Area	1.515**
	Num_LC	-13.177***
	EL100	-0.972***
Hsupe	Treerich	-5.850**
	Treeabun	-3.293**
	Num_LC	7.782 (0.014)
Mychry	Patch_Area	1.829**
	HA100	9.180**
Moliv	Patch_Area	2.371**
	EL100	-0.773 (0.014)
Mrall	HA100	5.970 (0.011)
	EL100	-3.109 (0.019)
Ppers	Patch_Area	3.388***
	Num_LC	-11.811***
	EL100	-1.028***

	HA100	36.944 (0.014)
Pauri	Num_LC	-12.229**
	EL100	-1.052**
	Patch_Area	1.584 (0.019)
Pscut	Patch_Area	4.369***
	Num_LC	-15.054***
	EL100	-1.323***
	HA100	65.776 (0.016)
Aflav	Patch_Area	2.367***
	HA100	7.982 (0.011)
Awagl	Patch_Area	2.047**
	EL100	-0.649 (0.014)
Emusi	Abu_Mico	5.084**
Pchal	Patch_Area	2.308***
	Num_LC	-7.586**
	EL100	-0.833**
	HA100	16.297 (0.02)

At intermediate scale, seven species had a significant relationship with the explanatory variables. Five of these species showed a positive relationship with forest cover variable (Suit_Am_Habit) (Table 7). *Euphonia xanthogaster* which showed positive relationship with the forest cover variable was negatively correlated to landscape configuration variables –Num_LC- (Table 7). Similarly to local scale, only one species showed significant relationship with fruit resources (*Aulacorhynchus haematopygus*). Five out of the 14 species which had a significant response at local scale, showed a congruent response at intermediate scale, this means responded significantly to forest cover variables. *A. haematopygus* showed response to a different variable at local and intermediate scales, and only one species showed response only at intermediate scale (*Tangara gyrola*) (Table 7). For landscape scale, no significant relationships were found.

The correlation between patch area and total abundance of fruiting tree species *Ficus, Cecropia* and *Miconia*, was positive and significant (Spearman Correlation; r = 0.375; p = 0.003). This means that increasing patch area more presence of individuals of those key fruit resources are expected.

Table 7: Results of the stepwise logistic regression models of the species presence related to explanatory variables at local scale (n = 32) at intermediate scale. Probability, **p≤0.01; ***p≤0.001. Marginally significant values are shown in brackets (p≤0.02). Five forest species in bold and 2 forest – edge species. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

Abbreviation	Single specific variable	β_1
Ahaem	Abu_Ficu	6.929 (0.015)
Exant	Suit_Am_Habit	9.594**
	Num_LC	-24.045***
Moliv	Suit_Am_Habit	5.179 (0.014)
Ppers	Suit_Am_Habit	6.373**
Pscut	Suit_Am_Habit	5.781**
Pchal	Suit_Am_Habit	4.808 (0.018)
Tgyro	Num_LC	11.294**

Ecological Thresholds

After the ROC analysis, and to determine thresholds in species response at local scale to the explanatory variables (Table 2), only significant AUC values were used. This procedure discards eight relationships for further analysis. No relationships were discarded at intermediate scale.

The AUC values for all species (14) at local scale were positively and highly significant correlated with Nagelkerke's R^2 (Spearman Correlation; r = 0.82, p < 0.001). Thus, AUC and R^2 provide similar assessment of model fit (Guénette & Villard 2005). At intermediate scale, the relationship was not significant because there were too few points for the correlation analysis.

At local scale the species which exhibiting the highest discrimination between presence and absence based on forest cover variables (Patch_Area and HA100) were *Mionectes olivaceus* (AUC = 0.865), *Penelope perspicax* (AUC = 0.898) and *Pyroderus scutatus* (AUC = 0.927) for Patch_Area (Fig. 6) and *Penelope perspicax* (AUC = 0.859) and *Pyroderus scutatus* (AUC = 0.902) for HA100. On the other hand, based on landscape configuration variables (Num_LC; EL100) the highest values were again *Penelope perspicax* (AUC = 0.841), *Pyroderus scutatus* (AUC = 0.901), *Pharomachrus auriceps* (AUC = 0.863) (Fig. 6) and *Pyroderus scutatus* (AUC =0.852), *Pharomachrus auriceps* (AUC = 0.815), *Penelope perspicax* (AUC = 0.805) respectively (Table 8). At intermediate scale the species exhibiting the highest discrimination between presence and absence based on Suit_Am_Habit were *Euphonia xanthogaster* (AUC = 0.91), *Penelope perspicax* (AUC = 0.854), *Pyroderus scutatus* (AUC = 0.85) (Table 9; Fig. 7).

In general, the threshold values validation showed that at local and intermediate scales the number of true positives was higher than the number of false positives (Tables 10 and 11). In only one case the number of true

positives was lower than the number of false positives (*Aulacorhynchus haematopygus*) (Table 10). This could be explained because the lower accuracy in the threshold identification by the AUC value (0.69, Table 8).

Table 8: Threshold values (cut-off value c, established with maximum accuracy) at local scale in the occurrence of 14 species (10 forest species in bold and 4 forest – edge species) with strong relationship with single landscape and key resources explanatory variables. The sign of relationship was established based on logistic regression results, Table 6. Probability, **p≤0.01; ***p≤0.001. Marginally significant values are shown in brackets. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

| Single specific variable	Abbreviation	AUC	Threshold value (c)	Units	Sign of relationship between species and variables
HA100	**Ahaem**	0.695**	2.99	Hectares (ha)	+
	Mychry	0.728***	2.77	ha	+
	Mrall	0.742**	2.10	ha	+
	Ppers	0.859***	2.79	ha	+
	Pscut	0.902***	2.88	ha	+
	Aflav	0.673 (0.017)	2.16	ha	+
	Pchal	0.803***	2.79	ha	+
Num_LC	**Apras**	0.722***	1.5	Land covers	-
	Exant	0.801***	2.5	Land covers	-
	Ppers	0.805***	1.5	Land covers	-
	Pauri	0.815**	1.5	Land covers	-
	Pscut	0.852***	1.5	Land covers	-
Patch_Area	**Mychry**	0.753***	7.88	ha	+
	Moliv	0.865**	97.83	ha	+
	Ppers	0.898***	97.83	ha	+
	Pscut	0.927***	57.28	ha	+
	Aflav	0.83***	7.88	ha	+
	Awagl	0.79**	97.83	ha	+
	Pchal	0.769 (0.015)	57.28	ha	+
EL100	**Exant**	0.714**	187.25	Meters (m)	-
	Ppers	0.841***	180.68	m	-
	Pauri	0.863***	127.55	m	-
	Pscut	0.901***	127.55	m	-
	Mrall	0.803***	452.99	m	-
	Pchal	0.813***	127.55	m	-
	Awagl	0.753**	399.12	m	-
Treerich	**Hsupe**	0.728**	2.5	Species	-
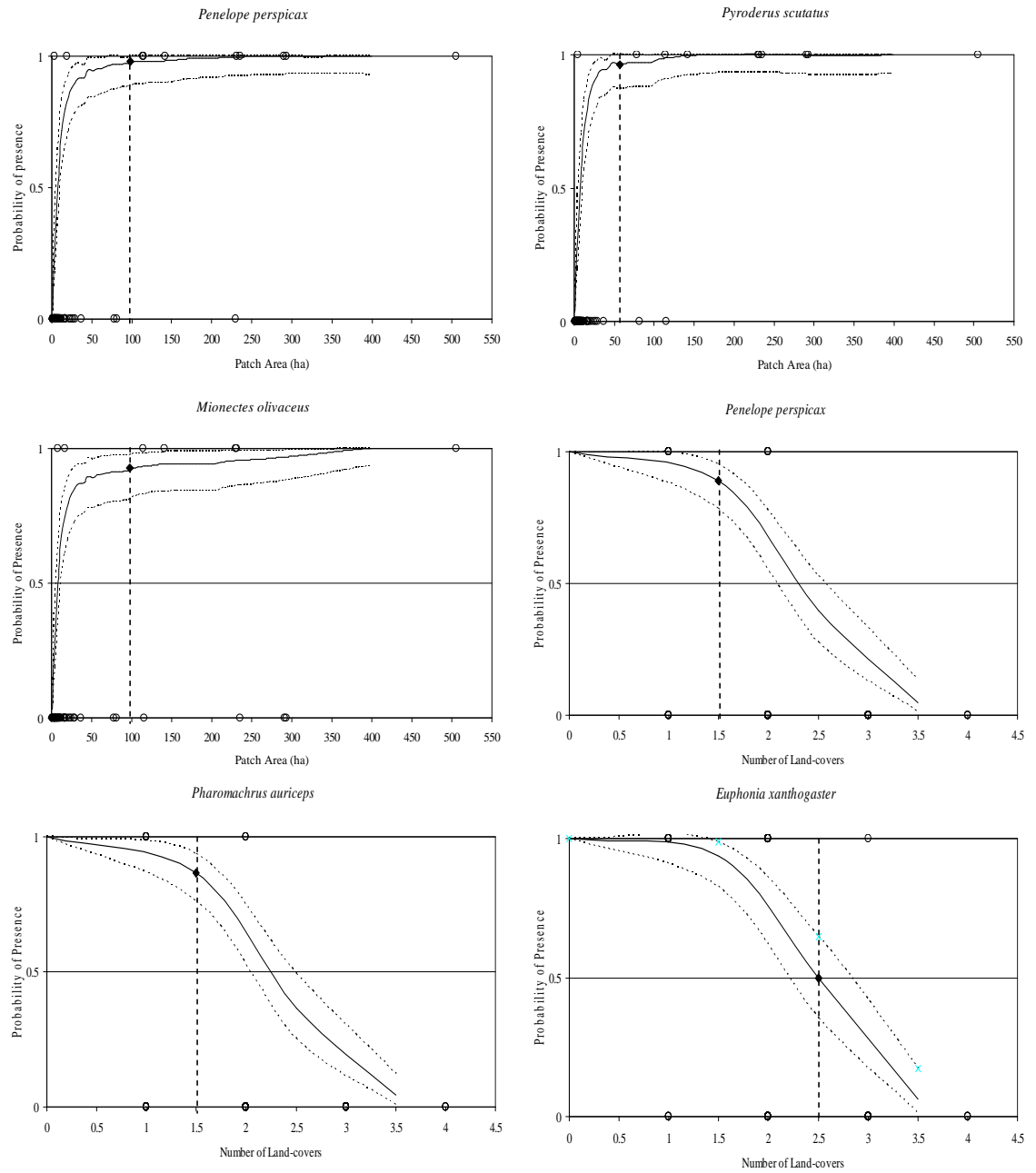
Fig. 6: Probability of presence of species which exhibiting the highest discrimination between presence and absence based on forest cover variable (Patch_Area) and landscape configuration (Num_LC) at local scale. Dashed lines represent 95% confidence intervals. Vertical dashed line indicates thresholds determined using ROC analysis. Curves were smoothed using a local smoothing technique with tricube weighting and polynomial regression.

Table 9: Threshold values (cut-off value c, established with maximum accuracy) at intermediate scale in the occurrence of 8 species (6 forest species in bold and 2 forest – edge species) with strong relationship with single landscape and key resources explanatory variables. The sign of relationship was established based on logistic regression results, Table 7. Probability, **p≤0.01; ***p≤0.001. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

Single specific variable	Abbreviation	AUC	Threshold value (c)	Units	Sign of relationship between species and variables
Suit_am_habit	**Exant**	0.91***	83.74	Hectares (ha)	+
	Ppers	0.854**	121.74	ha	+
	Pscut	0.85**	206.62	ha	+
	Moliv	0.802(0.012)	121.74	ha	+
	Pchal	0.818**	83.74	ha	+
Num_LC	**Exant**	0.804**	3.5	Land covers	-
	Tgyro	0.794**	4.5	Land covers	+
Abu_Ficu	**Ahaem**	0.843**	2.25	Individuals	+
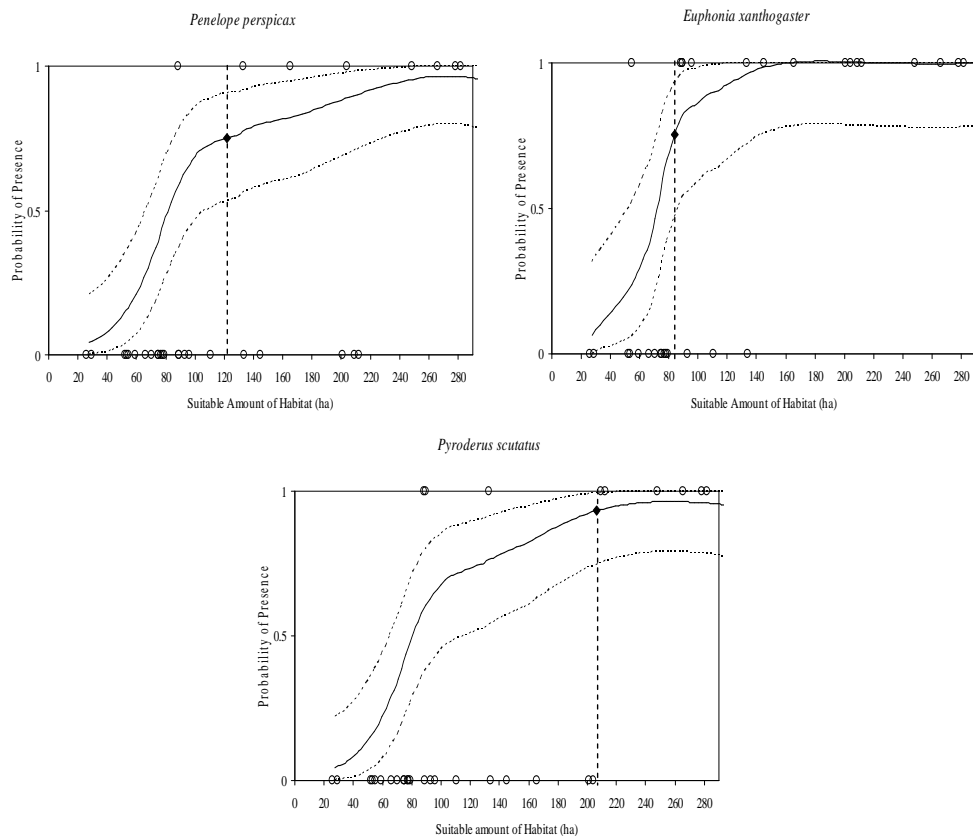
Fig. 7: Probability of presence of species which exhibiting the highest discrimination between presence and absence based on forest cover variable (Suit_Am_Habit) at intermediate scale. Dashed lines represent 95% confidence intervals. Vertical dashed line indicates thresholds determined using ROC analysis. Curves were smoothed using a local smoothing technique with tricube weighting and polynomial regression.

Table 10: Threshold validation at local scale based on the number of true positives and true negatives versus the false positives and false negatives. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

Single specific variable	Abbreviation	Threshold value (c)	True Positives	False Positives
HA100	Ahaem	2.99	17	23
	Mychry	2.77	21	11
	Mrall	2.10	44	16
	Ppers	2.79	12	1
	Pscut	2.88	12	0
	Aflav	2.16	20	3
	Pchal	2.79	12	1
Num_LC	Apras	2.5	25	2
	Exant	2.5	27	1
	Ppers	1.5	7	6
	Pauri	1.5	5	3
	Pscut	1.5	8	4
Patch_Area	Mychry	7.88	20	4
	Moliv	97.83	5	2
	Ppers	97.83	8	2
	Pscut	57.28	9	1
	Aflav	7.88	18	3
	Awagl	97.83	5	3
	Pchal	57.28	6	2
EL100	Exant	187.25	20	8
	Ppers	180.68	12	1
	Pauri	127.55	7	1
	Pscut	127.55	11	1
	Mrall	452.99	44	16
	Pchal	127.55	10	3
	Awagl	399.12	12	1
Treerich	Hsupe	2.5	9	8

Table 11: Threshold validation at intermediate scale based on the number of true positives and true negatives versus the false positives and false negatives. Complete name of the frugivorous bird species and explanatory variables are in Tables 1 and 2 respectively.

Single specific variable	Abbreviation	Threshold value (c)	True Positives	False Positives
Suit_am_habit	Exant	83.74	16	1
	Ppers	121.74	7	1
	Pscut	206.62	6	3
	Moliv	121.74	7	1
	Pchal	83.74	8	0
Num_LC	Exant	3.5	16	1
	Tgyro	4.5	10	2
Abu_Ficu	Ahaem	2.25	19	3

Discussion

In general my results indicate that, the distribution of frugivorous bird species in the Central Andes of Colombia is better explained at local and intermediate scales by landscape characteristics, especially forest cover, than fruit resources distribution. At local scale (3 ha) I established 27 species-specific occurrence thresholds for four landscape characteristic variables (forest cover and landscape configuration) and one fruit resources variable, for 14 forest frugivorous bird species. While, at intermediate scale (312 ha) I set eight occurrence thresholds in two landscape characteristic variables and one fruit resource distribution variable for seven bird species.

My results about thresholds values are novel for Neotropical landscapes and this is one of the first empirical studies conducted at different scales. Other studies presenting empirical threshold values come mainly from temperate and sub-tropical regions, and are most often related with changes in habitat amount. Several taxa have been investigated, e.g. birds (Vance et al. 2003; Bennet & Radford 2004; Radford et al. 2005; Guénete & Villard 2005; Suorsa et al. 2005), lizards (Lindenmayer et al. 2005); frogs, fungi, plants (Drinnan 2005; Bascompte & Rodriguez 2001), squirrels (Rodriguez & Andrén 1999) and butterflies (Schultz & Crone 2005).

Recently Guénette & Villard (2004, 2005) set species-specific ecological thresholds using ROC curves. They argued that using single variables rarely succeeds in capturing complex changes. Instead they used synthetic variables (multivariate axes in a Principal Component Analysis) to set their threshold values. Furthermore, they proposed that this method could be useful to examine thresholds in bird response to specific habitat variables. My results support empirically this last affirmation and I consider that single variables approach is meaningful and easier to interpret, especially if the results will go directly to decision makers. Threshold values obtained in multivariate axes always require further investigations of single variables for interpretation. I also agree with these authors that the selection of appropriate variables is a key issue and variables reflecting the relative fitness of the individual will be better than merely presence/absence or abundance (Guénette & Villard 2004).

My results show that most species are positively responding to forest cover variables (Patch Area, HA100 and Suit_Am_Habit) at local and intermediate scales. In all cases species which are negatively affected by habitat loss are positively related to these variables (e.g. *Aulacorhynchus haematopygus, Aulacorhynchus prasinus, Mionectes olivaceus, Penelope perspicax, Pharomachrus auriceps, Pyroderus scutatus, Myiodynastes chrysocephalus*). Many other works report similar results concerning the importance of habitat amount on the maintenance of bird species richness and abundance (Martínez-Morales 2005; Westphal et al. 2003; Trzcinski et al. 1999; Mazerolle and Villard 1999; Villard et al. 1999;

McIntyre 1996; Bellamy et al. 1996; Wilson et al. 1994; McGarical and McComb 1995), and it appears as if this is the reason why habitat loss is the primary cause of the threshold response of species to habitat change (Dykstra 2004). In my case and in other studies as well, many of those species, which are considered as a highly vulnerable group to habitat loss and fragmentation, are large-bodied frugivorous (i.e. *Aulacorhynchus haematopygus, A. prasinus, Penelope perspicax, Pharomachrus auriceps, Pionus chalcopterus, Pyroderus scutatus*; Kattan 1992; Kattan et al. 1994). For instance, according to my results, *Penelope perspicax*, which is an endemic and endangered species of Colombia (geographical range ≤ 50 000 Km2; Renjifo 2001; 2002), need patches with at least 98 ha to ensure their presence in fragmented landscapes of the Central Andes of Colombia. Almost all species negatively related to forest cover variables are small frugivores, which are considered to be generalists, with more tolerance to habitat disturbances (Kattan 1992). The landscape heterogeneity seems to increase mobility of many species as a common strategy for survival (Block & Brennan 1993). Then, the more heterogeneous the habitat mosaic is, the higher expected proportion of multi-habitat or generalist species is (Kozakiewicz 1995).

My results show low response of fruit eating birds to fruit resource distribution, even though I found significant correlations among landscapes between frugivorous richness / abundance and fruiting tree richness / abundance. Though *Ficus, Cecropia* and *Miconia* are important elements in frugivores diets (Ríos 2005; Luck & Daily 2003; Poulin et al. 1999; Loiselle & Blake 1999; Loiselle & Blake 1990; Estrada et al. 1984; Hilty 1980) at local and intermediate scales, they are not enough to be a good predictor of frugivores birds. The explanation might be that most frugivorous bird species need a broader set of resources to ensure their presence. For instance, almost all species that I chose for my study include in their diets other resources besides fruits such as, insects, leaves, nectar, and seeds, and in some cases, eggs and chicks (Hilty and Brown 1986; Muñoz & Kattan 2007). My results showed that increasing patch area means increasing number of individuals of key fruiting trees (*Ficus, Cecropia* and *Miconia*), but the relationship between birds and these specific genera is too diffuse and difficult to be tracked at species-specific level. Perhaps, to perceive a clear threshold response in species presence related to food resources the exploration should be during fruit scarcity periods, because during these periods majority of species will be depending on few keystone species. I found only three species related with fruit resources distribution. At intermediate scale *Aulacorhynchus haematopygus* is positively related with abundance of *Ficus*. The threshold for high probability of occurrence was found to be at least 2.25 individuals of *Ficus* within 3 ha of forest. Figs species are mainly adapted to intermediate succession phase of the vegetation, and some species are common elements within other kind of land-covers such as forestry plantations and as isolated trees in grasslands in the sub Andean landscapes (Vargas 2002). Renjifo (2001) reports that *A. haematopygus* is able to

use other kind of land-covers as forestry plantations and grasslands. At local scale, *Hemispingus superciliaris* seems to be present in sites with less than 2.5 species of *Ficus, Cecropia* or *Miconia*, this could be indicating that this bird species avoid competition by using other fruit resources and visit sites with low richness of these by other frugivores highly consumed resources. *Euphonia musica* was positively related to the abundance of *Miconia*, even though a threshold response not was found. It is a small frugivore mainly foraging in the intermediate strata of the forest (Hilty and Brown 1986). *Miconia* is a very common genus in forest understory and edge habitats with small and fleshy-fruits with high water and carbohydrate concentrations, suitable for small bodied animals (Kattan 1992; Vargas 2002). However, these results were found at specific scales, and from my results it is not possible to find out if this response also is present at broader scales.

From my results I can say that for Sub-Andean landscapes in all places where we want to ensure presence of species negatively affected by habitat transformation such as *Penelope perspicax, Pyroderus scutatus, Pionus chalcopterus, Pharomachrus auriceps, Mionectes olivaceus,* and *Aratinga wagleri*, patch arrangements at intermediate scales with no less than 206 ha of suitable habitat (forest) with at least one big patch no smaller than 98 ha, and a good connectivity among patches to enhance species movements looking for other resources and mates will be required. Those resources may be complementary or supplementary to each species (Dunning et al. 1992; Taylor et al. 1993). It is also important that at local scale, within the 98 ha patch, the heterogeneity should be restricted to the forest itself (less than 1.5 kinds of land-covers) and has the smaller amount of edges with a highly contrasting matrix as it is possible (less than 128 m). For instance, for *Penelope perspicax* the current resident populations are only in few natural preserve areas or big forest patches in the Colombian Andes, and in all cases with extension not lower than 98 ha (Kattan & Valderrama 2006). Based on results from this study I could think that *P. perspicax, P. scutatus* and *M. olivaceus* might be considered as umbrella species, because these species showed a positive relation with forest cover, both at local and intermediate scales and they need high amount of forest to be present. Probably, the proposed landscape configuration, suitable for *P. perspicax, P. scutatus* and *M. olivaceus*, also is suitable for other species with poor dispersal ability such as *Chlorochrysa nitidissima, Aburria aburri* and *Habia cristata* (Renjifo et al. 2002). However, further studies in nestedness patterns of species diversity are required to identify if those species could be considered as umbrella species.

Though I found significant relationship between landscape characteristics, fruit resource distribution and some frugivorous bird species at local and intermediate scale, many frugivorous species did not show any response to those variables. The reasons for this might be low abundances which excluded some species from the analysis and restrict the statistical significance (Manel et al. 2001). Some species may be perceiving fragmentation or habitat loss at

broader scales than the scales I considered, and other species find that the landscape connectivity is good enough to ensure their movements searching for complementary and supplementary resources (Dunning et al. 1992; Taylor et al. 1993), which means that the selected explanatory variables are not influencing their strictly presence on forest patches.

My study highlights the importance of habitat amount, local habitat configuration and the landscape arrangement at intermediate scales for species conservation. Though for some species big forest patches (e.g. patch size > 98ha) in the landscape seem to be compulsory to ensure their presence, small forest patches could be enough for other species (e.g. *Anisognathus flavinucha* or *Myiodynastes chrysocephalus*, 7.8 ha). How these patches are arranged (landscape configuration) is one primary aspect to consider in landscape planning and conservation strategies to ensure presence of a broad spectrum of frugivorous bird species (Taylor et al. 2003; Turner 2005).

It is an implicit assumption in logistic regression models, wherever species occurs it is a suitable place for breeding and not a sink habitat (Westphal et al. 2003) or an ecological trap (Kristan III 2003). For conservation purposes this means that even though this study provides information about variables which explain the species distribution and occurrence thresholds are not enough to ensure species conservation in transformed landscapes. In this sense, my results are related with the patterns but more information about processes which generated these patterns is still missing. To improve the conservation strategies in my studied landscapes of the Central Andes of Colombia it is also necessary to understand the frugivorous bird dynamic related to habitat quality, demography, resources availability upon time and intra and inter patch movement capacity.

To make general conclusions from critical threshold values (i.e. fragmentation thresholds) across landscapes or regions is difficult, because they are not reflecting the high variability in transformed landscapes (Lindenmayer & Luck 2005), and are reflecting the requirements of common and widespread species but not the requirements of the most sensible species (Mönkkönen & Reunanen 1999). However, species-specific threshold values for focal species, such as species negatively affected by habitat transformation, are useful tools as surrogates within a conservation strategy. Focal species might indicate minimum requirements for presence of other species, and help in conservation prioritize, without the need for detailed auto-ecological information on those species (Hugget 2005). Nevertheless, better results will be obtained from threshold values supporting management decisions if a combination of different species responses to different variables and scales is considered. Now, even tough ecological thresholds can assist conservation strategies they are not the strategy by themselves. A threshold theory mis-interpretation in decision-making processes could lead to major negative implications for conservation

(Lindenmayer & Luck 2005). An effective conservation does not means fit with the minimum requirement in some ecological variables (threshold values) to ensure species presence, they are another piece in "the conservation puzzle", and for effective species conservation in the long run more aspects must be preserved such as habitat quality, population and metapopulation dynamics, landscape connectivity, prevent invasions, maintenance of natural disturbance regimes, and prevent negative impacts in structure and composition of biotic communities by human inhabitants from the surroundings.

Acknowledgments

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Appendix 1 Species of *Cecropia, Ficus* and *Miconia* and their total abundance recorded in the study areas of the Central Andes of Colombia.

Abbreviation	Scientific Name	Total Abundance
Cangu	*Cecropia angustifolia* Trecul	66
Ctele	*Cecropia telealba* Cuatrecasas	110
Fand	*Ficus andicola* Standley	23
Fcuat	*Ficus cuatrecasana* Dugand	19
Fglab	*Ficus glabrata* Kunth	32
Fhart	*Ficus hartwegii* (Miq.) Miq.	2
Fkill	*Ficus killipii* Standl.	12
Fmuti	*Ficus mutisii* Dugand	10
Fsp1	*Ficus* sp.1	1
Fsp3	*Ficus* sp.3	4
Ftond	*Ficus tonduzii* Standley	19
Fvellu	*Ficus velutina* Willd.	1
Fyopo	*Ficus yoponensis* Desv.	1
Macum	*Miconia acuminifera* Tr.	95
Mcaud	*Miconia caudata* (Bonpl.) de Candolle	54
Mcoro	*Miconia coronata* (Bonp.) de Candolle	33
Mlehm	*Miconia lehmannii* Cogn.	97
Mnota	*Miconia notabilis* Triana	110
Mores	*Miconia orescia* Uribe	1
Mresi	*Miconia resima* Naud.	1
Msmara	*Miconia smaragdina* Naud.	4
Msp1	*Miconia* sp.1	4
Msp7	*Miconia* sp.7	7
Msp11	*Miconia* sp.11	1
Msp12	*Miconia* sp.12	1
Msp13	*Miconia* sp.13	2
Msp14	*Miconia* sp.14	1
Msp16	*Miconia* sp.16	6
Msp20	*Miconia* sp.20	9
Msp21	*Miconia* sp.21	9
Msp22	*Miconia* sp.22	1
Mthea	*Miconia theaezans* (Bonpl.) Cogniaux	22
Mwurd	*Miconia wurdackii* Uribe	4