The value of secondary forest for understory birds in a shifting cultivation landscape in the Colombian Amazon

Verdien av sekundærskog for fuglefaunaen i eit svijordbruksområde i det vestlege Amazonas, Colombia

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Preface

This thesis marks the end of my studies in Tropical Ecology and Natural Resource Management at the Department of Ecology and Natural Resource Management (INA), and five wonderful years as a student at the Norwegian University of Life Sciences (UMB). It has been a great journey and I want to thank everybody sharing it with me.

I want to thank my supervisor, Torbjørn Haugaasen, for his support and comments on my thesis, and for giving me the opportunity to spend two and a half months studying birds in the Amazon rainforest. My co-supervisor, Gustavo Alarcón-Nieto, deserves a great deal of thanks for all the help and support during the field work. This study would not have been possible without him. I further want to thank my field assistants Romulo Miraña and Hernán Miraña and all the members of the Madroño community for their assistance and hospitality. A special thanks to Celina Miraña for all her assistance. I would like to thank Professor Ørjan Totland for help with CANOCO and Astrid Haavik for proof-reading my thesis.

The project was funded by the Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences (UMB). Conservation International in Colombia provided assistance through housing and equipment, and I want to thank the people working and staying at their station in La Pedrera for their support and many good times during my fieldwork. Lastly I want to thank my friends and family for their support during the long months before everything was ready to start the fieldwork.

Ås, May 14th 2010

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Abstract

The Amazon rainforest is highly threatened by deforestation, and vast areas of secondary forest are appearing on abandoned land. The potential of this forest for conserving biodiversity is increasingly recognized, yet little is known about its actual role as habitat for the tropical forest fauna. The current study used mistnets to sample the understory bird communities in primary forest and abandoned slash-and-burn agricultural patches of varying ages in the Lower Caquetá River, Colombian Amazonia. Species richness was similar in primary and young secondary forest, while older secondary forest had lower species richness. Bird abundance did not differ significantly between habitats. Composition and structure of the bird communities differed between habitats, with the largest difference in composition found between primary and young secondary forest. The highest similarity was found within primary forest. Dead-leaf gleaning insectivores were exclusively captured in primary forest. Ant-following insectivores had significantly higher richness in primary forest, while arboreal nectarivores and omnivores had highest richness in young secondary forest. External bark-searching insectivores had highest abundance in primary forest. Arboreal gleaning and sallying insectivores had lowest abundance in old secondary forest. Forest structure also varied between habitats, and bird community composition was found to be related to the understory density and canopy cover of the forest. Species and guilds related to high understory density and low canopy cover were typically found in young secondary forest, while those related to high canopy cover and low understory density were typical of primary forest. The results suggest that the fallow period of slash-and-burn agriculture in many cases is not long enough to restore both the structural features and the bird community typical of primary forest. I therefore conclude that slash-and-burn agriculture can only be considered sustainable as long as small agricultural patches with long fallow cycles are embedded in large areas of primary forest.

Samandrag

Regnskogen i Amazonas er alvorleg trua av avskoging, og enorme områder av sekundærskog veks opp på forlatne landareal. Det er aukande fokus på verdien av denne skogen for vern av biologisk mangfald, men kor viktig den er som habitat for tropisk skogsfauna er usikkert. I dette studiet blei fuglar fanga i nett i primærskog og forlatne svijordbruksareal av varierande alder ved nedre del av elva Caquetá i Colombiansk Amazonas. Artsrikdommen var relativt lik i primær- og ung sekundærskog, men lågare i gammal sekundærskog. Talet på individ var ikkje signifikant forskjellig mellom habitata. Det var derimot forskjell i samansettinga av fuglesamfunn mellom skogtypane, med størst forskjell mellom primærskog og ung sekundærskog. Likskapen mellom fuglesamfunn var størst innan primærskog. Insektetande fuglar som leitar etter mat blant dødt lauv vart utelukkande fanga i primærskog. Maurfølgjande insektetarar hadde signifikant større rikdom i primærskog, medan det var større rikdom av trelevande nektarivorar og omnivorar i ung sekundærskog. Flest eksterne barkleitande insektetarar vart funne i primærskog. Færrast ”sallying” og ”gleaning” trelevande insektetarar vart funne i gammal sekundærskog. Skogstrukturen varierte også mellom habitata, og samansettinga av fuglesamfunnet var relatert til vegetasjonstettleik i busksjiktet og kronedekket i skogen. Artar og laug relatert til eit tett busksjikt og eit relativt opent kronedekke var karakteristiske for ung sekundærskog, medan artar og laug relatert til eit tett kronedekke og eit relativt opent busksjikt var karakteristiske for primærskog. Resultata tilseier at brakkperioden i svijordbruk i mange tilfeller er for kort til at skogen rekk å utvikle ein struktur og eit fuglesamfunn likt det ein finn i primærskog. Eg konkluderar med at svijordbruk berre er berekraftig so lenge små områder i eit landskap dominert av primærskog blir dyrka i ein syklus med lange brakkperiodar.

Contents

Introduction

Tropical rainforests are the most species-rich terrestrial ecosystems on earth. By the year 2000, more than 1.75 million species were described in this ecosystem, but the actual number could be as high as 60 million (Myers 2000). The Amazon basin contains the world's largest intact tropical rainforest, but this forest is increasingly threatened by deforestation and human-induced degradation (Myers 2000). During the period 2000-2005, 0.5% of forested area disappeared every year in South-America. This deforestation rate is almost three times as high as the global deforestation rate (FAO 2009). One of the main causes of deforestation is conversion of forest to agricultural lands and plantations (FAO 2009; Myers 2000). The land is often abandoned after use, and the forest allowed to re-grow, leading to large expanses of secondary forest throughout the Amazon (Borges & Stouffer 1999).

In recent years, the rapidly expanding area of secondary forest has lead to increased research as to the role of this habitat in protecting biodiversity. For example, a multi-taxonomic study was recently completed where the biodiversity value of plantations, secondary forest and primary forest was investigated in Jari, eastern Amazonia (Barlow et al. 2007a). Additionally, three reviews have recently compared biodiversity in tropical primary and secondary forest across four continents (Chazdon et al. 2009; Dent & Wright 2009; Dunn 2004). Chazdon et al. (2009) looked at the proportion of old-growth species present in secondary forest, Dent and Wright (2009) studied similarity of species composition, and Dunn (2004) compared species richness between primary and secondary forest. The forest type supporting the highest species richness varied between studies, but many have reported the richness to increase parallel to forest recovery (e.g. Bowman et al. 1990; Dent & Wright 2009; Raman et al. 1998). Initially, the species composition of secondary forest can be very different from that of primary forest (Barlow et al. 2007b; Klanderud et al. 2010; Loiselle & Blake 1994), but the proportion of old-growth species have also been found to increase over time if the forest regeneration is left uninterrupted (Chazdon et al. 2009). However, it is currently unclear how long it takes for primary forest species to return, and for the forest ecosystem to fully recover (Dunn 2004). While Andrade and Rubio-Torgler (1994) reported almost complete recovery of the bird community after 10 years in Colombia, Raman et al. (1998) found the recovery of the bird community in India to take 100 years. It is uncertain what creates this inconsistency between studies, but several factors have been found to affect the recovery rate of tropical fauna after disturbances. These factors include the structure and species composition of the vegetation

(Borges & Stouffer 1999; Karr & Freemark 1983; Laurance 2004; Terborgh 1985), distance to primary forest (Chazdon 2003; Dent & Wright 2009; Stouffer & Bierregaard 1995b) and intensity of previous disturbances (Barlow & Peres 2004; Borges & Stouffer 1999; Dent & Wright 2009; Klanderud et al. 2010; Letcher & Chazdon 2009).

Slash-and-burn agriculture is normal practice in many tropical forest regions (Lawrence et al. 2010; Myers 1991; Schmidt-Vogt et al. 2009). An area of forest is cut, burned and cultivated for two-three years, before it is abandoned and left to re-grow. This practice is considered a low intensity disturbance compared to permanent agriculture (FAO 2009), and has been used since 7000 BP (Piperno 2006). Still, it has been estimated that slash-and-burn agriculture is responsible for 60% of deforestation worldwide (Myers 1991). In South America the intensification and expansion of shifting agriculture constituted 6% of the total change in forest cover between 1990 and 2000 (FAO 2009). Slash-and-burn agriculture can also be interrelated with other disturbance factors. Most importantly the expansion of slash-and-burn agriculture represents sources of ignition for forest fires (Barlow et al. 2002), but the cultivation of small patches also leads to increased fragmentation of the forest (Metzger 2002). The sustainability of slash-and-burn agriculture is therefore debated (Lawrence et al. 2010). Some studies have found it to be a sustainable use of the rainforest (e.g. Andrade & Rubio-Torgler 1994), while others have been more critical (e.g. Metzger 2002; Raman 2001). The question of its sustainability is increasingly important as a growing human population has resulted in intensification and shortening of fallow cycles in several areas (Metzger 2002; Schmidt-Vogt et al. 2009; Styger et al. 2007).

Habitat modification has been found to affect different species and taxonomic groups differently (Barlow et al. 2007a; Lawton et al. 1998; Schulze et al. 2004). However, Barlow et al. (2007a) found similar community response to land-use change in such different taxonomic groups as trees, birds, large mammals, fruit-feeding butterflies, lizards, dung beetles and epigeic arachnids. As it is rarely within the scope of a study to focus on more than one or a few groups, several studies have tried to identify indicator species or taxa (e.g. Barlow et al. 2007a; Lawton et al. 1998; Schulze et al. 2004). In the current study I have chosen to focus on birds. Birds are relatively easy to study, and have been identified as one of the better indicator taxa (Barlow et al. 2007a). Particularly small and inconspicuous understory birds have been found to be greatly affected by human disturbances (Aleixo 1999; Barlow et al. 2002; Haugaasen et al. 2003; Johns 1991).

Although many studies have investigated the value of secondary forest for both birds and other taxonomic groups (for review see Chazdon et al. 2009; Dent & Wright 2009; Dunn 2004), many of these studies have been focused around a few well studied areas. Within the Amazon, this is particularly true for certain areas in Brazil (Barlow et al. 2007b; Hawes et al. 2008; Johns 1991). To my knowledge, only one study comparing bird communities in primary and secondary forest has been conducted in the neighboring country of Colombia (Andrade & Rubio-Torgler 1994).

In this study, understory bird communities were sampled in a landscape mosaic of primary and secondary forest in the Lower Caquetá River in the Colombian Amazon. Bird communities sampled in primary forest were compared with those of two different age classes of second growth, developing after the abandonment of slash-and-burn agricultural patches. I addressed the question of how species richness and abundance, as well as structure and composition of the understory bird community, was affected by small-scale slash-and-burn agriculture, and if the composition of the bird community could be related to the structure of the forest. I tested the hypotheses that (1) species richness increase with forest age, (2) primary forest, old secondary forest and young secondary forest contain distinct bird communities, with the largest difference found between primary and young secondary forests, (3) different guilds respond differently to habitat modification, and (4) composition of the bird community is related to the structure of the forest.

Methods

Study area

The study was carried out in the Lower Caquetá River in southeastern Colombia. Colombia is among the ten countries with the highest biodiversity in the world (FAO 2009). In total, 58.5 percent of the land is covered by forest (FAO 2009), of which 87 percent is regarded as primary forest (FAO 2006). Only one percent of the forested area is protected, compared to 11.3 percent in South-America (FAO 2006). The decline in forested area in Colombia is lower than for South-America as a whole, but it has been noted that this may partly be because of secondary forest re-growing on abandoned land (FAO 2009).

The Caquetá River is a white-water river of Andean origin, and one of the major tributaries of the Amazon (Duivenvoorden & Lips 1995). The area is part of the humid lowlands of Amazonia. The main vegetation is primary terra firme forest, located above the floodplains of rivers and lakes. Temperature is fairly constant throughout the year, with a mean annual temperature of 25.7ºC. The climate is tropical with a mean annual rainfall of 3060 mm (Duivenvoorden & Lips 1995). Rainfall shows a bimodal pattern with the driest season from December to February, and a less pronounced dry season in August (Duivenvoorden & Lips 1995). Even in the "dry" seasons, precipitation averages more than 100 mm per month. The wettest months are April to June and September to November. In May, the wettest month, it rains an average of 409 mm (Duivenvoorden & Lips 1995).

The human population density in the area is low, consisting mostly of indigenous people living in small communities along the river. The people mostly practice shifting cultivation, hunting, fishing and gathering of forest products for subsistence. Shifting cultivation relies on the clearing of forest patches of approximately 1 ha, which are left to dry before the cut trees are burned and the patch subsequently planted with various crops for 3-5 years (Fig. 1). The main cultivated crop is yucca (Fig. 1). After cultivation, the patches are abandoned and the forest allowed to regenerate. This creates a mosaic of different aged secondary forest in an otherwise relatively undisturbed primary terra firme forest setting.

Figure 1. Four steps in the production of yucca through slash-and-burn agriculture in the Lower Caquetá River, Colombia. One ha of forest is a) cut and b) burned before yucca is c) planted and d) harvested (Photos: Jorunn Ospedal Vallestad).

The study sites were located on the land of the Madroño community, close to the village La Pedrera (1°19'S, 69°35'W; Fig 2). Three study sites were located in each of primary forest (PF) and two stages of second growth, defined as young secondary forest (YSF, approximately 4-6 years after abandonment) and old secondary forest (OSF, approximately 9-15 years after abandonment). The primary forest was somewhat affected by anthropogenic disturbances, particularly hunting, but this is believed to have limited impact on the understory bird fauna. The nine study areas were located approximately 50 - 100 m above sea level.

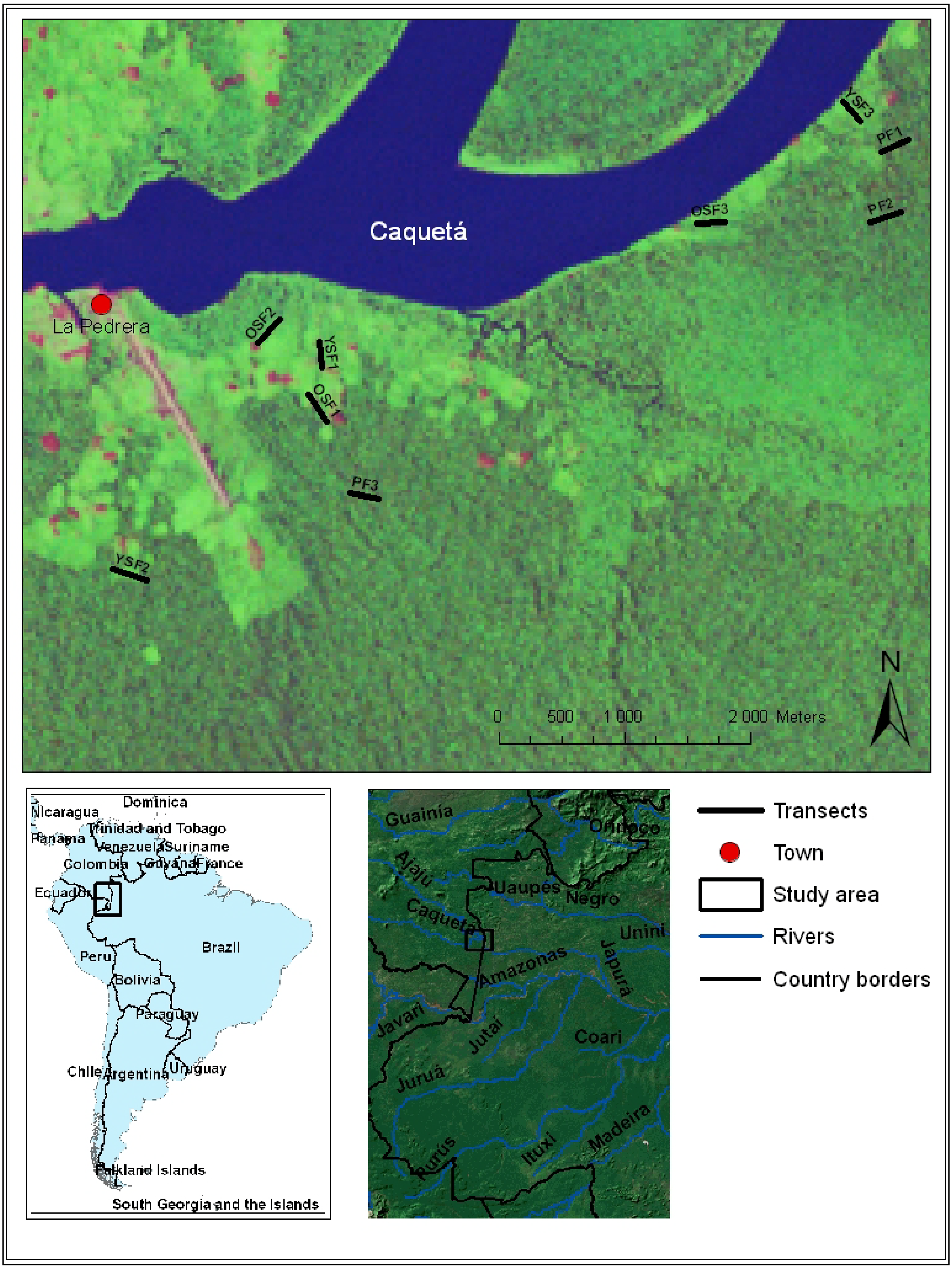

Figure 2. Map of the study area in the Lower Caquetá River, Colombia, showing the location of the transects used for sampling birds in primary (PF) old secondary (OSF) and young secondary (YSF) forest.

Forest structure

Canopy cover (CC), understory density (UD) and ground cover (GC) was measured every 20 m on both sides of a 200 m transect, totaling 22 points in each of the nine sites (three per forest type). Canopy cover was measured with a concave spherical densiometer (Lemmon 1957). Readings were taken in each of the four compass directions at points located 15 m from the transect line, and then averaged to get one value for canopy cover (Loiselle & Blake 1994). This value was multiplied by 1.04 and subtracted from 100 to get the percent canopy cover (Lemmon 1957). Ground cover was defined as the percentage of ground covered by green vegetation lower than one and a half meter. This was measured visually within 2.5 x 2.5 m squares located 5 m to both sides of the transect. Understory density was estimated using a 2.5 m pole divided into 25 orange and white 10-cm segments. The pole was held vertically by one observer at the transect, while another counted the number of visible segments with binoculars from 15 m away (Barlow et al. 2002). The number of observed segments was subtracted from the total number of segments, multiplied by 100 and divided by the total number of segments to get an estimation of percent understory density.

Within a 200 x 5 m transect, the diameter at breast height (DBH) of all trees with a diameter≥ 10 cm was measured. This was converted into tree basal area (TBA), averaged for each transect and multiplied with ten to find basal area per hectare. Tree height (TH) was estimated visually for all trees with a diameter≥ 10 cm, and averaged to get an estimate of the mean tree height of the forest.

Avifaunal sampling

The understory avifauna was sampled using mistnets (Fig. 3). Mistnetting is a much used and effective tool for capturing small understory birds, flying in a height of 2-3 m above ground (Remsen & Good 1996). The nets capture nonvocal and secretive understory birds that are often overlooked using other sampling methods (Karr 1981; Rappole et al. 1998; Terborgh et al. 1990). These birds are also found to be the ones most affected by human disturbance (Johns 1991). Because the sampling technique is highly standardized, the results are easily comparable within studies, and can also to some extent be used for between-study comparisons. Mistnetting is similarly free of many of the observer biases experienced with point counts and transect walks (Alldredge et al. 2007; Rappole et al. 1998), and requires less identifying skills (Terborgh et al. 1990). A potential bias with mistnets is that they may capture a larger portion of the bird community in secondary than in primary forest (Blake & Loiselle 2001; Rappole et al. 1998). However, the same problem has been noted during point counts and transect walks, since a lower and more open canopy makes species easier to detect in young second growth (Borges 2007; Bowman et al. 1990; Johns 1991). A detailed description of the advantages and disadvantages of using mistnets can be found in Karr (1981).

Figure 3. a) Mistnets used for capturing birds during the study in the Lower Caquetá River, Colombia. b) *Thraupis episcopus* being extracted from the mistnet at one of the young secondary forest (YSF1) netlines (Photos: Jorunn Ospedal Vallestad).

Transects measuring approximately one meter wide and 240 meters long were cut through the understory, and twenty mistnets with mesh size 36 mm set in a straight line. Each netline was open from dawn to midday on two consecutive days, and then re-sampled three weeks later for another two days, totaling 480 mistnet hours per site. All netlines in the same type of forest were located at least 500 m apart, to make sure they were spatially independent (Barlow et al. 2002). Sites were sampled randomly to minimize potential seasonal effects, although all sampling was concluded within two months and such effects were thus likely to be negligible. Four of the secondary forest patches were not long enough to fit 20 nets, and we therefore had to adjust the number of nets and use only 18 or 19 nets in those plots. This was always compensated for by opening the nets longer, making sure the total effort in an area was always 480 net hours. The nets were checked hourly and closed during periods of heavy rain. These hours were compensated for in the afternoon. Sampling was aborted on days with persistent heavy rain. All birds captured were extracted from the nets, identified to species, weighed and measured. Whenever possible the individuals were sexed and aged. All new captures, except hummingbirds, were marked with numbered aluminium bands. For hummingbirds, a cut was made in the first primary tail feather to allow recognition. Recaptures were excluded from the analyses. The birds were released in the capture area as soon as all measurements had been taken.

Data Analysis

Forest structure variables

The five variables describing forest structure were tested for normal distribution using the Anderson-Darling test. Thereafter, Kruskal-Wallis and Mann-Whitney U tests were used to test for differences between habitats. Non-significant variables were excluded from further analyses. Pearson correlation coefficients were calculated for each pair of forest variables to study the degree of correlation between the variables. These tests were carried out in the statistical package Minitab.

Bird abundance and species richness

Species richness and data on bird abundance was tested for normal distribution using the Anderson-Darling test and for homogeneity of variance with the Levene's test. Thereafter, one-way ANOVA with Tukey's post hoc test was used to compare species abundance and richness between habitats. These tests were carried out using the statistical package Minitab.

The statistical program EstimateSWin820 was used to compute Sample-based species rarefaction curves based on species abundances (Colwell 2004). This allows a comparison of bird species richness, standardized by sampling effort, between habitats (Colwell 2004). Sample-based curves were chosen over individual-based curves to account for natural patchiness in the data (Gotelli & Colwell 2001). The x-axis was rescaled by individuals, to account for differences in bird abundance between samples (Colwell et al. 2004; Gotelli & Colwell 2001). Differences in rarefied species richness were tested by visually comparing 95% confidence intervals at the point of the highest common number of sampled individuals. Richness was considered significantly different if less than half the length of one arm of the confidence intervals overlapped (Cumming 2009).

Expected species richness was compared using eight non-parametric species estimators implemented in the statistical package EstimateS; ACE, ICE, CHAO1, CHAO2, Jack1, Jack2, MMMean and MMRuns. These were also used to calculate the efficiency of the survey.

Community structure and composition

The statistical package Primer v5 was used to conduct non-metric multidimensional scaling (NMDS), analysis of similarity (ANOSIM), and similarity percentage analysis (SIMPER) (Clarke & Gorley 2001). Bray Curtis similarity index was used to analyze between samples. All tests were carried out using untransformed species data, and since the sampling effort was equal in all areas, I did not standardize the data. NMDS was used to visualize the difference in community composition within and between habitats. ANOSIM was used to test for a significant difference in the community composition in each habitat. SIMPER was used to compare similarities within and between the three different habitat types, and to identify the species contributing most to the dissimilarity.

Bird species were grouped into guilds following Terborgh et al. (1990), with additional information from the literature (Barlow et al. 2007b; Hawes et al. 2008; Hilty & Brown 1986; Ridgely & Tudor 1994; Schulenberg et al. 2007). The abundance and richness of guilds were tested for normal distribution using the Anderson-Darling test. Within each guild, differences in species richness and abundance between forest types were tested using one-way ANOVA with Tukey's post hoc test. Only guilds containing seven individuals or more were included in guild analyses.

Relating bird communities to forest structure

Multivariate analyses were carried out using the statistical package CANOCO for Windows v4.5 (Lepš & Šmilauer 2003). These were used to study the relationship between forest structure and bird community composition. First a Detrended correspondence analysis (DCA) was carried out to estimate the heterogeneity of the community composition. As the result showed that the data was relatively homogenous, with ordination axes shorter than 3 S.D, redundancy analyses (RDA) were chosen to study the contribution of forest structure in explaining the variation in bird community composition. RDA is a constrained linear ordination method where the ordination axes are weighted sums of environmental variables. The principal axes explain the highest variation in both environmental and species data simultaneously. It is common that species show unimodal response curves with regards to environmental gradients (Jongmann et al. 1995), but the low heterogeneity in the data indicated that only parts of the underlying gradient had been sampled (Lepš & Šmilauer 2003). It is therefore reasonable to expect a linear function to constitute the best approximation. I used untransformed bird species data, centered by species and with species scores divided by standard deviation to facilitate comparison. Forward selection of forest structure data with Monte-Carlo permutation tests was used to identify the variables best explaining the bird species data, and to choose which structural variables to include in the analysis.

Results

Forest structure

There was a significant difference between forest types in understory density (PF-OSF: W=3772, P=0.0049; PF-YSF: W=2623, P<0.001; OSF-YSF: W=2919.5, P<0.001) and canopy cover (PF-OSF: W=5618, P<0.001; PF-YSF: W=6167.5, P<0.001; OSF-YSF: W=5593.5, P<0.001; Table 1). Tree basal area and average tree height were significantly different in young secondary forest compared to old secondary forest (W=46167.5, P<.001 and W=47499, P<0.001, respectively) and primary forest (W=30939, P<0.001 and W=31940.5, P<0.001, respectively). No difference was found for tree basal area and tree height between primary forest and old secondary forest (W=39019.5, P=0.9903 and W=38567.5, P=0.8940 respectively). Ground cover did not differ significantly between habitats (H_2=1.80, P=0.407), and was excluded from further analyses.

Table 1. Forest structure variables for primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Habitats not sharing the same letter differ significantly (Kruskal-Wallis and Mann-Whitney U, P<0.05).

	Understory density (%)		Canopy cover (%)		Ground cover (%)		Tree basal area (m^2/ha)		Average tree height (m)	
	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
PF	61.5^a	2.16	98.1^a	0.26	18.4^a	1.58	28.7^a	3.80	13.2^a	0.35
OSF	70.4^b	2.01	95.5^b	0.57	19.6^a	1.79	24.6^a	2.73	13.2^a	0.29
YSF	90.1^c	1.52	88.5^c	1.19	18.5^a	2.17	7.5^b	2.63	9.9^b	0.40

Primary forest sites were characterized by a relatively closed canopy, high basal area, high average tree height and open understory, while young secondary forest tended to have a relatively closed understory, open canopy, low basal area and low average tree height (Table 1). Old secondary forests had values intermediate between the two other forest types.

Canopy cover, understory density, average tree height and tree basal area were highly correlated (Table 2). Particularly high was the correlation between canopy cover and understory density (-0.964), and between average tree height and tree basal area (0.953).

Table 2. Pearson Correlation coefficients for pairs of four measured forest variables in the Lower Caquetá River, Colombia.

Variable	Variable	Correlation	P-value
Av tree height	Canopy cover	0.714	0.031
Av tree height	Tree basal area	0.953	<0.001
Av tree height	Understory density	-0.818	0.007
Canopy cover	tree basal area	0.819	0.007
Canopy cover	Understory density	-0.964	<0.001
Tree basal area	Understory density	-0.898	0.001

Bird abundance and species richness

A total effort of 4320 net hours yielded 848 captures of 710 individuals, giving a capture rate of 0.196 per net hour. In total, 97 species from 25 families were captured (Appendix 2). The highest number of species was found in young secondary forest, closely followed by primary forest. Fewer species were found in old secondary forest (Table 3). Species richness differed significantly between habitats ($F_{2,8}$=13.3, P=0.006), with lower species richness in old secondary forest than in the two other forest types (Fig. 7a). The highest number of individuals was captured in primary forest and the lowest in old secondary forest. However, there was no significant difference in total abundance across forest types ($F_{2,8}$=0.98, P=0.428).

Table 3. Summary of bird capture data in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia.

	PF	OSF	YSF	Total
Number of species	60	40	62	97
Number of individuals	273	199	238	710
Number of unique species	25	3	26	54
Number of "rare" species*	16	2	23	41

*represented by one or two individuals in the total sample

Estimated species richness was higher than the observed species richness in all habitats (Table 4). Estimated species richness was highest in young secondary forest (91-117 species) and lowest in old secondary forest (45-65 species). In primary forest the estimated species richness was 76-94 species. The sampling was more complete in old secondary forest (average 78%) than in primary forest (average 70.5%) and young secondary forest (average 61.4%; Table 4).

Table 4. Estimated bird species richness and the proportion of birds captured in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia.

	PF		OSF		YSF	
	Estimated species richness	Proportion of birds captured	Estimated species richness	Proportion of birds captured	Estimated species richness	Proportion of birds captured
ICE	93.2	0.64	51.6	0.76	117.2	0.53
ACE	79.9	0.75	45.6	0.88	101.0	0.61
CHAO1	75.8	0.79	45.1	0.89	91.1	0.68
CHAO2	82.9	0.72	45.5	0.88	97.0	0.64
Jack 1	83.8	0.72	51.0	0.78	91.3	0.68
Jack 2	96.4	0.62	53.4	0.75	108.9	0.57
MMRuns	84.5	0.71	64.5	0.62	105.4	0.59
MMMean	84.2	0.71	53.7	0.75	96.2	0.65
Average	85.1	0.71	51.3	0.78	101.0	0.61

The slope of the sample-based rarefaction curve declined in all forest types with increasing sampling effort, but did not reach an asymptote (Fig. 5). However, the curve for old secondary forest is starting to level out earlier than the curves representing the two other forest types, and relatively few species would have been added to the old secondary forest sample had more than 200 individuals been captured.

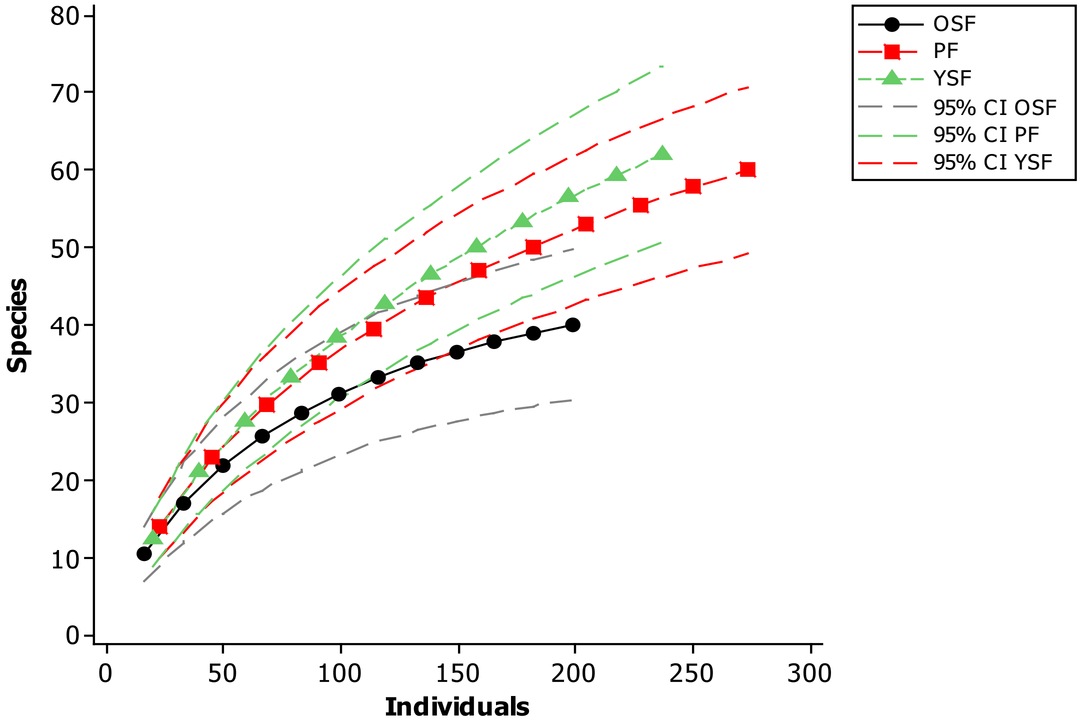

Figure 5. Sample-based species rarefaction curve for data from primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. X-axis is re-scaled to show individuals.

Rarefied species richness is significantly lower in old secondary forest compared to young secondary forest (Fig. 5). There is no significant difference between primary forest and old secondary forest, or between primary and young secondary forest. However, the difference between primary and old secondary forest is close to being significant (Fig. 5).

Community structure and composition

The number of unique species was similar for young secondary and primary forest. Only three species were exclusively captured in old secondary forest (Table 3). *Thamnomanes caesius*, *Myrmotherula haematonota* and *Automolus infuscatus* were found in all three primary forest sites, but in none of the secondary forest sampling sites. The number of rare species was highest in young secondary forest (Table 3). None of the species exclusively captured in young secondary forest were found in all three sampling sites.

There was a significant difference between the community composition in the three forest types (Global R= 0.449, P=0.007; Table 2). Pairwise comparisons showed primary forest to be very different from young secondary forest (R=0.852). This is illustrated in the non-metric multidimentional scaling ordination plot (Fig. 6). The three sampling plots in primary forest form a distinct cluster at the opposite end of the diagram to the plots in young secondary forest (Fig. 6). The species contributing most to this difference were *Glyphorynchus spirurus* and *Gymnopithys leucaspis,* which were much more common in primary forest, and *Thryothorus coraya*, which was more abundant in young secondary forest. The composition of the bird communities in old secondary forest was intermediate between the two other forest types (Fig. 6). There was an intermediate separation between primary and old secondary forest (R=0.407). Some of this separation was due to higher abundance of *G. leucaspis* and *Lepidothrix coronata* in primary forest, and the absence of *Thamnomanes caesius* in old secondary forest. There was only a low degree of separation between old and young secondary forest (R=0.185). The existing separation is also here due to the absence of *T. caesius* in old secondary forest. There is also higher abundance of *L. coronata*, *Pipra erythrocephla* and *Mionectes oleaginea* in young secondary forest. In the pairwise comparisons, only 10 permutations could be carried out, and significant results were therefore not achieved (Table 5).

Table 5. Analysis of similarity (ANOSIM) between bird communities in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. The R-value gives an absolute measure of how different the bird communities are on a scale of 0-1.

	R statistic	Significance level	All possible permutations
Global	0.449	0.007	280
PF-OSF	0.407	0.1	10
PF-YSF	0.852	0.1	10
OSF-YSF	0.185	0.2	10

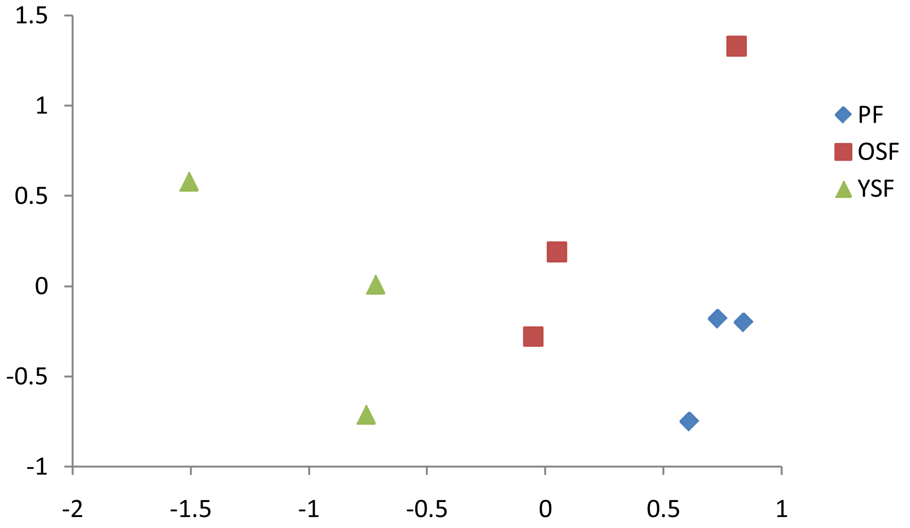

Figure 6. Non-metric multi-dimensional scaling ordination of the avifauna in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. The distance between points corresponds to the difference in bird community composition.

The similarity between the three sampling sites within each forest type was highest in primary forest and lowest in old secondary forest (Table 6). The similarities between habitats were consistent with the results found in the analysis of similarity (Table 5), but differed in that the highest similarity was found between primary and old secondary forests (Table 6).

Table 6. Similarity percentages (SIMPER) of bird communities within and between the habitats primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia.

Within forest types		Between forest types	
Habitat	Similarity (%)	Habitat	Similarity (%)
PF	53.7	PF-OSF	40.7
OSF	38.7	PF-YSF	32.0
YSF	43.7	OSF-YSF	37.3

The most common species in all forest types was *L. coronata*, with a total capture of 90 individuals - 12.7% of the total number of captures. Other species common to all three habitats were *M. oleaginea* and *Phaethornis malaris* (Table 7). *G. spirirus*, which was the second most common bird in both primary and old secondary forest, was only found in low numbers in young secondary forest. The ten most common species in each forest type contributed to almost 60% of the total number of captures in each habitat (Table 7).

Table 7. Abundance of the ten most common species and their contribution to the total catch in each of primary, old secondary and young secondary forest in the Lower Caquetá River, Colombia.

Primary forest			Old secondary forest			Young secondary forest		
Species	Mean no. of inds.	Contribution (%)	Species	Mean no. of inds.	Contribution (%)	Species	Mean no. of inds.	Contribution (%)
Lepidothrix coronata	11.7	12.82	*Lepidothrix coronata*	8.7	13.07	*Lepidothrix coronata*	9.7	12.18
Glyphorynchus spirurus	8.7	9.52	*Glyphorynchus spirurus*	5.7	8.54	*Mionectes oleaginea*	9.0	11.34
Gymnopithys leucaspis	6.0	6.59	*Mionectes oleaginea*	5.3	8.04	*Pipra erythrocephala*	5.7	7.14
Mionectes oleaginea	4.7	5.13	*Phaethornis malaris*	4.0	6.03	*Thryothorus coraya*	5.0	6.30
Thamnomanes caesius	4.3	4.76	*Pipra erythrocephala*	3.3	5.03	*Percnostola rufifrons*	3.3	4.20
Hylophylax poecilonota	4.0	4.40	*Phaethornis bourcieri*	3.0	4.52	*Glaucis hirsuta*	3.3	4.20
Phaethornis malaris	3.7	4.03	*Pipra filicauda*	2.7	4.02	*Phaethornis malaris*	2.7	3.36
Pithys albifrons	3.3	3.66	*Phaethornis hispidus*	2.7	4.02	*Phaethornis hispidus*	2.7	3.36
Myrmotherula haematonota	3.0	3.30	*Gymnopithys leucaspis*	2.3	3.52	*Catharus ustulatus*	2.3	2.94
Hylophylax naevia	2.7	2.93	*Thalurania furcata*	2.0	3.02	*Myrmotherula axillaris*	2.0	2.52
Sum		57.14			59.80			57.56

Birds from 17 different guilds were captured (Appendix 1). The most numerous guilds were arboreal frugivores and arboreal nectarivores, while the most species rich guild was arboreal sallying insectivores, represented by 20 species. One-way ANOVA showed that species richness differed between forest types for ant-following insectivores ($F_{2,8}$=12.40, P=0.007), arboreal gleaning insectivores ($F_{2,8}$=6.79, P=0.029), arboreal nectarivores ($F_{2,8}$=9.50, P=0.014), arboreal omnivores ($F_{2,8}$=7.64, P=0.022) and dead-leaf gleaning insectivores ($F_{2,8}$=64, P<0.001). No significant differences were found for the other guilds. Terrestrial granivores, raptors, aerial feeding insectivores, internal bark-searching insectivores and terrestrial sallying insectivores were all represented by no more than three species, and were therefore not included in the analysis. Species richness of ant-following insectivores was significantly higher in primary forest than in secondary forest (Fig. 7b). Significantly fewer species of arboreal gleaning insectivores were found in young secondary forest than in old secondary forest (Fig. 7c). The species richness of arboreal nectarivores and omnivores were significantly lower in primary forest than in young secondary forest (Fig. 7d, e). Dead-leaf gleaning insectivores were exclusively captured in primary forest (Fig. 7f).

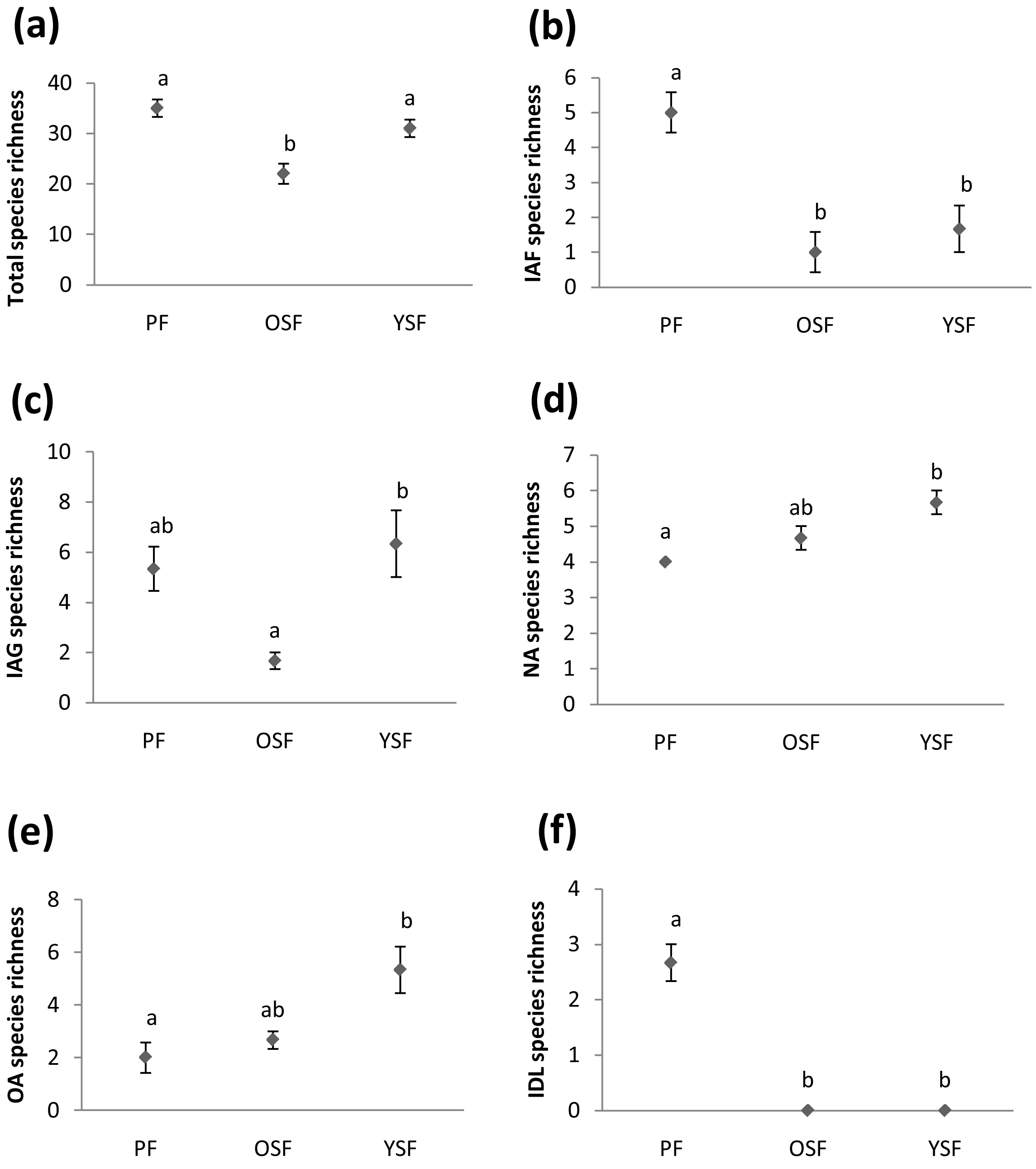

Figure 7. Average species richness of a) all birds, b) ant-following insectivores (IAF), c) arboreal gleaning insectivores (IAG), d) arboreal nectarivores (NA), e) arboreal omnivores (OA) and f) dead-leaf gleaning insectivores (IDL) in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá river, Colombia. Different letters indicate significance as distinguished by Tukey's post-hoc comparsions (P<0.05). Error bars represent standard error.

Species abundance differed between forest types for arboreal gleaning insectivores ($F_{2,8}$=6.91, P=0.028), arboreal omnivores ($F_{2,8}$=9.55, P=0.014), arboreal sallying insectivores ($F_{2,8}$=6.86, P=0.028), external bark-searching insectivores ($F_{2,8}$=6.30, P=0.034) and dead-leaf gleaning insectivores ($F_{2,8}$=18.75, P=0.003). Arboreal gleaning insectivores had a significantly lower abundance in old secondary forest than in primary forest and young second growth (Fig. 8a). There were significantly more individuals of arboreal omnivores in young secondary forest than in the two other forest types (Fig. 8b). Arboreal sallying insectivores were more abundant in primary forest than in old secondary forest (Fig. 8c). External bark-searching insectivores were more abundant in primary forest than in young secondary forest (Fig. 8d). All individuals of dead-leaf gleaning insectivores were captured in primary forest (Fig. 8e).

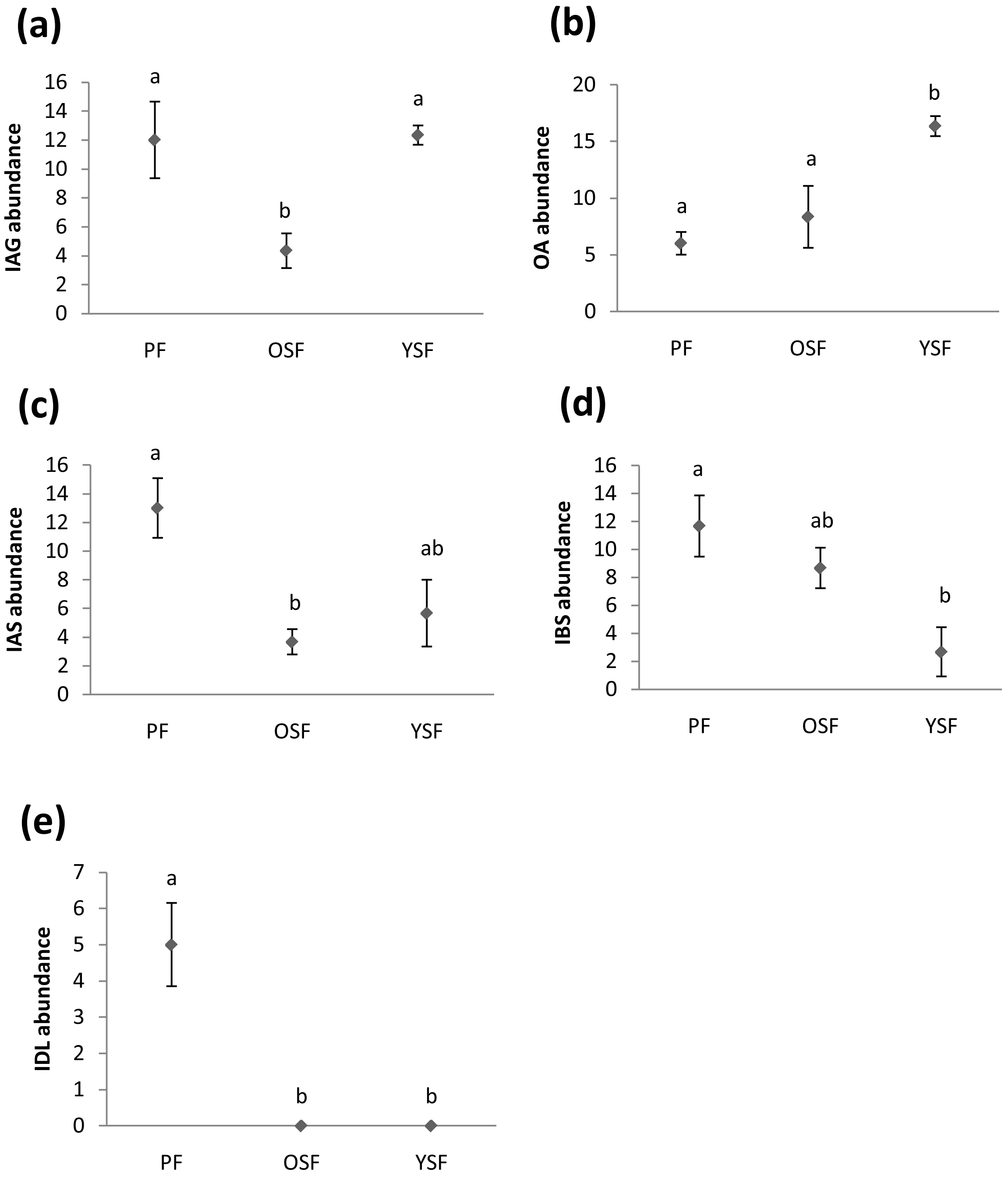

Figure 8. Average species abundance of a) arboreal gleaning insectivores (IAG), b) arboreal omnivores (OA), c) arboreal sallying insectivores (IAS), d) external bark-searching insectivores (IBS), and e) dead-leaf gleaning insectivores (IDL) in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Different letters indicate significance as distinguished by Tukey's post-hoc comparsions (P<0.05). Error bars represent standard error.

Relating bird communities to forest structure

Redundancy analysis showed that bird communities of young secondary forest were correlated with high understory density, while bird communities of primary forest and, to a lesser degree, old secondary forest, were correlated with high canopy cover, tree basal area and tree height (Fig. 9).

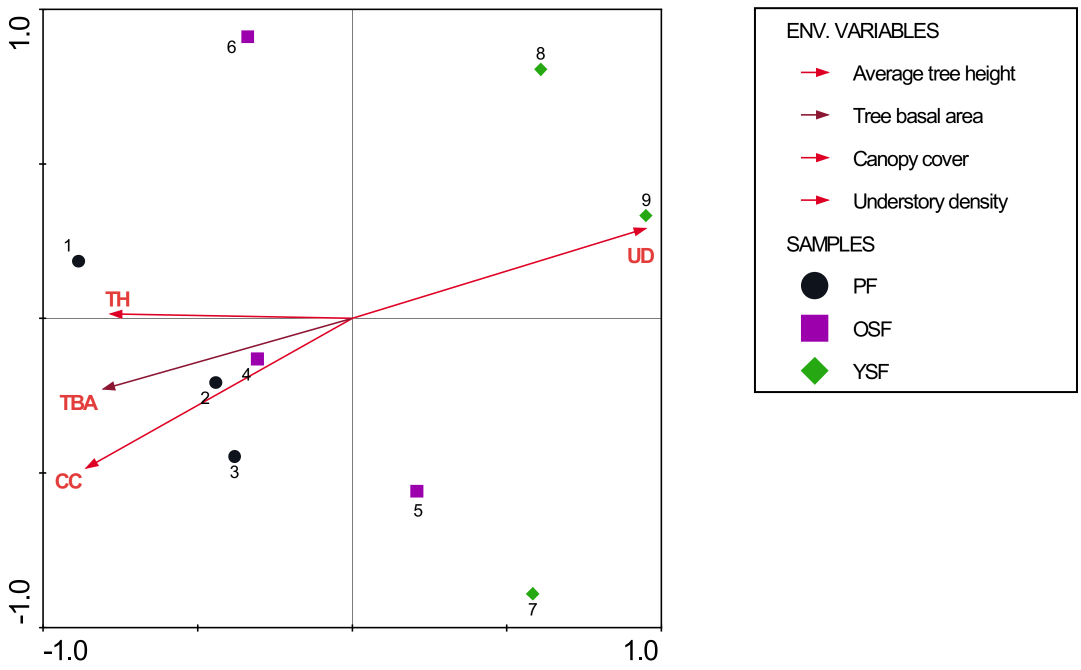

Figure 9. Redundancy analysis (RDA) biplot of forest structure variables and sampling sites in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia Forest structure variables are represented by red arrows pointing in the direction of increasing values for that variable. Study sites are placed in the ordination diagram according to their bird community composition, and their correlation with the forest variables.

Forward selection of environmental variables with Monte-Carlo permutation tests identified understory density as the variable most related to the composition of the bird communities (F= 2.13, P=0.016), closely followed by canopy cover (F=1.97, P=0.018). Understory density explained 23% of the observed bird community variation. The correlation of bird communities with tree basal area and tree height were not significant (TBA: F=1.66, P=0.068; TH: F=1.57, P=0.088). Due to this lack of significance and the high correlation between understory density and canopy cover (R=-0.964, P<0.001), only understory density was included in subsequent models (Figs. 10 & 11).

Of the 20 bird species showing the strongest correlations to understory density, four were negatively correlated, while 16 were positively correlated (Fig. 10). The four species negatively correlated were all found primarily in primary forest. *Schistocichla schistacea, Automolus infoscatus* and *Myrmotherula haematonota* were not found in young secondary forest, while *Glyphorynchus spirurus* was only found in low abundances. The 16 species positively correlated with a dense understory were only found in secondary forests.

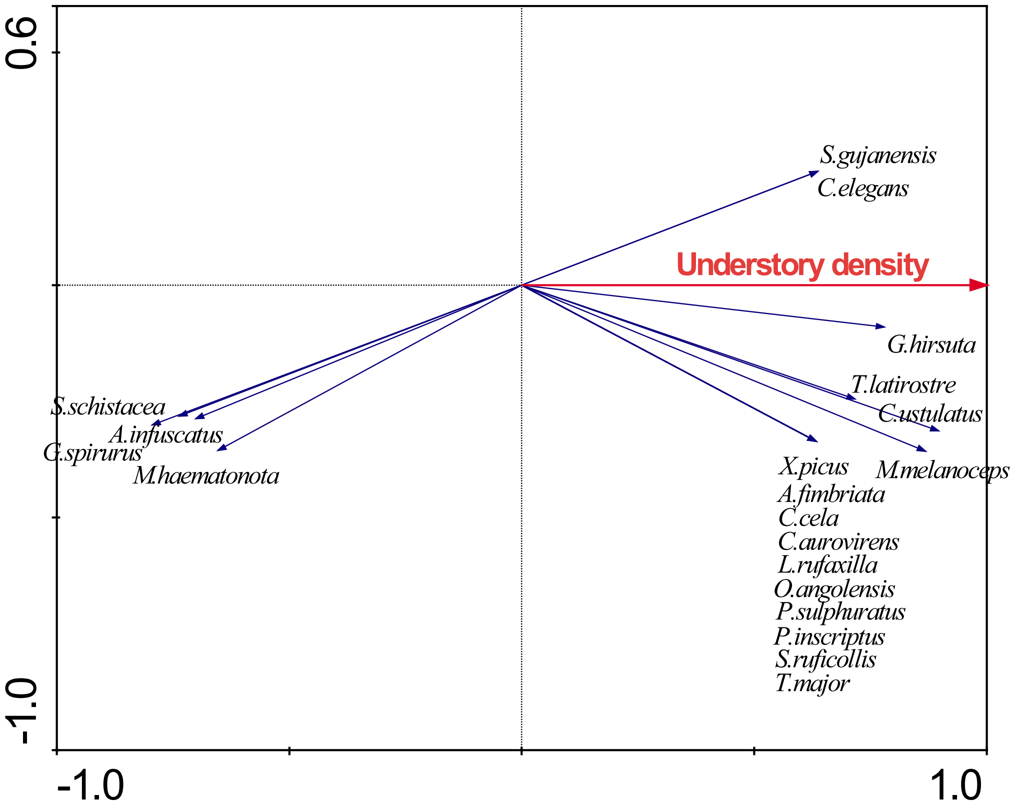

Figure 10. Redundancy analysis (RDA) biplot of the composition of understory birds and forest structure variables (selected through forward selection with Monte-Carlo permutation tests) in the Lower Caquetá River, Colombia. Species are represented by blue arrows pointing in the direction of increased species abundance. The length of the arrows is a function of how well the values of individual species are approximated by the ordination diagram. Understory density is represented by the red arrow pointing in the direction of an increasing value along the first canonical axis. Only the 20 bird species best fitted to this axis were included.

Understory density was also the best explanatory variable for the species richness of guilds (F=2.183, P=0.08). High species richness of nectarivores (NA) and arboreal omnivores (OA) were strongly correlated with high understory density (Fig. 11). High richness of terrestrial gleaning insectivores (ITG), external bark-searching insectivores (IBS), dead-leaf gleaning insectivores (IDL) and ant-following insectivores (IAF) were correlated with low understory density (Fig. 11).

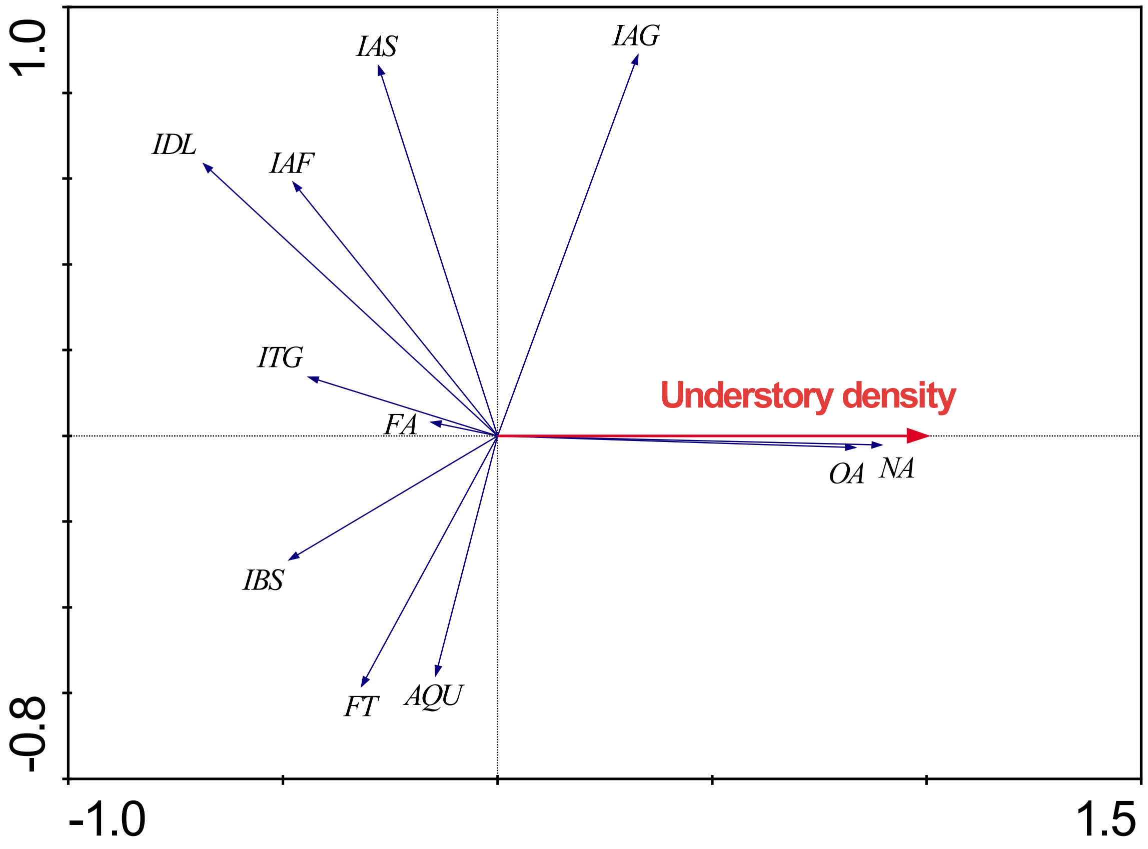

Figure 11. Redundancy analysis (RDA) biplot of guild species richness and forest structure variables (selected through forward selection with Monte-Carlo permutation tests) in the Lower Caquetá River, Colombia. Guilds are represented by blue arrows pointing in the direction of increased species richness. The length of the arrow is a function of how well the values of individual guilds are approximated by the ordination diagram. Understory density is represented by the red arrow pointing in the direction of an increasing value along the first canonical axis. Only guilds containing seven individuals or more were included in the model. Guild abbreviations are explained in Appendix 1.

Discussion

Forest structure

The clearing of a forest area for slash-and-burn agriculture results in a complete breakdown of the area's structural features. Nevertheless, when conditions are right, regeneration after disturbance in tropical forests can be very rapid (Loiselle & Blake 1994) and species richness and structural complexity of the forest increases with fallow age (van Breugel et al. 2006). Raman et al. (1998) found canopy cover to reach high levels after only five years of re-growth in India. Similarly, van Breugel et al. (2006) found basal area in one of their study plots in Mexico to reach the level of primary forest after only 6 years. The basal area in this study was similar in 9-15 year old secondary forest and primary forest, indicating rapid forest recovery. Average tree height was also similar between primary and old secondary forest in the current study. However, because the height was estimated visually from the ground, the height of tall trees may have been underestimated. Several other studies have found canopy height of old secondary forest to be lower than in primary forest (e.g. Borges 2007; Bowman et al. 1990; van Breugel et al. 2006).

In the current study, understory density and canopy cover had not reached the same level as that in primary forest after 9-15 years of re-growth. Bowman et al. (1990) found similar results in their 26 year old secondary forest in Papua New Guinea, indicating that more time is needed to attain the structural complexity of primary forest. In addition, the rate of increase in structural variables, biomass and species richness has been shown to slow down over time (Gehring et al. 2005; van Breugel et al. 2006). Gehring et al. (2005) found biomass after 25 years of re-growth following slash-and-burn agriculture to be 50% of that of primary forest in central Amazonia, but estimated that it would take 175 years for biomass to reach 75% of the primary forest level. Therefore, it seems unclear how long it takes for the structural features to reach the level of undisturbed forest, and even though the structural function is similar, it may take centuries for second growth to regain the biotic diversity of the pre-existing undisturbed forest (DaSilva et al. 1996; Guariguata & Ostertag 2001).

Forest recovery has also been shown to depend on the intensity and duration of disturbance prior to abandonment (Gehring et al. 2005; Guariguata & Ostertag 2001; Letcher & Chazdon

2009; Loiselle & Blake 1994; Uhl et al. 1988). For example, Klanderud et al. (2010) found the establishment of tree seedlings to depend on the number of slash-and-burn cycles, and Lawrence et al. (2010) showed that the rate of biomass accumulation declined by an average 9.3 percent per cycle. The decline was also found to be somewhat greater at sites with shorter fallow periods (Lawrence et al. 2010). The same authors observed that cultivation of nitrogen demanding maize led to N-limitation over time, indicating that crop type can also affect the recovery of subsequent re-growth. The size of agricultural plots and their distance from primary forest may also affect the rate of re-growth (Guariguata & Ostertag 2001; Steininger 2000). All secondary forest plots studied in the Lower Caquetá River were small (approx. 1ha) and located adjacent to relatively undisturbed primary forest. This may have facilitated faster regeneration of secondary forest than what may be found in many other disturbed areas. However, it is important to note that the soil seed bank may be just as important for tropical forest regeneration as seed rain from nearby primary forests (Guariguata & Ostertag 2001; Klanderud et al. 2010).

S*pecies richness*

Trends in bird species richness across forest types vary widely in the literature. While some studies have reported a higher species richness in primary forest (e.g. Barlow et al. 2007a; Barlow et al. 2007b; Bowman et al. 1990; Raman et al. 1998; Terborgh & Weske 1969), others have found highest richness in secondary forest (e.g. Blake & Loiselle 2001; Estrada et al. 1997; Johns 1991). Yet others have found no significant difference between habitats (e.g. Andrade & Rubio-Torgler 1994; Borges 2007; Sodhi et al. 2005; Waltert et al. 2004) Equally high variation has also been recorded in areas affected by logging (Aleixo 1999; Johns 1991; Wunderle et al. 2006), forest fires (Barlow et al. 2002; Barlow & Peres 2004), fragmentation (Barlow et al. 2006; Stouffer et al. 2009) and other disturbances (Maas et al. 2009). However, common across all studies is that species richness decreases dramatically after forest clearing or disturbance (Dunn 2004), before re-colonization subsequently leads to increased richness. How fast the increase in richness happens, and if it follows a linear gradient towards the richness observed in primary forest, is unclear. As the age classes sampled vary widely between studies, it is generally difficult to compare patterns of species richness during secondary succession.

In the current study, the species richness was similar between primary and young secondary forest, while the richness in old secondary forest was significantly lower. Comparing richness between forest types at the point of maximum number of captured individuals in old second growth, the difference between primary and old secondary forest was not significant. Expected species richness was in fact highest in young secondary forest. The current study therefore indicates that species richness does not follow a linear gradient in relation to forest age, as suggested by some other studies (e.g. Blankespoor 1991; Raman et al. 1998), and the first hypothesis, that species richness increase with forest age, must therefore be rejected.

The high species richness observed in young secondary forest can be explained by many factors. Elevated species richness in secondary forest has, for example, been attributed to high spatial heterogeneity in and around these habitats (Aleixo 1999; Blake & Loiselle 2001; Johns 1991). Secondary forest is often located on the borders between undisturbed forest and human-dominated landscapes. In addition to species coming from undisturbed primary forest, they may therefore harbor many birds entering from open agricultural areas, as well as from other forest types (Borges 2007). In fact, Terborgh et al. (1990) found that the largest number of rare species in their study consisted of birds more commonly found in other habitats.

High species richness in second growth could perhaps be expected in this study due to the proximity of primary forest, where the source habitat for many species is located (Blake & Loiselle 2001; Marsden et al. 2006; Stouffer & Bierregaard 1995b). This is supported by Dent and Wright (2009) who found a higher proportion of primary forest species in secondary forest adjacent to primary forest, than in isolated patches of second growth. Although this pattern is not observed in all studies (e.g. Antongiovanni & Metzger 2005; Klanderud et al. 2010), it appears that high species richness in second growth in many cases is related to the proximity of species rich old growth forests (Chazdon 2003).

Young secondary forest is also more commonly used by latitudinal migrants than primary forest (Karr 1990). This is supported in the current study where the only latitudinal migrants in the sample (*Empidonax traillii*, *Catharus minimus* and *Catharus ustulatus*) were almost exclusively captured in young secondary forest.

High temporal habitat heterogeneity can also explain the high species richness recorded in secondary forest. Borges (2007) found higher species richness in secondary than in primary forest when they pooled different aged secondary forest in one category, but not when they considered them separately. Similarly, Blake and Loiselle (2001) noted that the high species richness in young second growth in their study may partly have been a result of changing species composition over the ten year study period. The short time-span of the current study makes this an unlikely bias. However, the study sites in young secondary forest ranged from four to six years in age, and the sites in old secondary forest from nine to fifteen years. Differences in species composition within the same forest type may therefore be due to differing forest ages, and may partly explain the relatively high richness observed in young secondary forest.

A number of studies may be overestimating the species richness and the value of secondary forest as habitat for forest bird species in other ways. Firstly, many birds may have been recorded in second growth as they travel between areas of primary forest (Johns 1991). Secondly, even though a number of species may be able to forage in second growth, primary forest areas may still be the principal nest and lek sites (Stouffer & Bierregaard 1995a). Thirdly, it has been noted that it is easier to sample a larger portion of the bird community in secondary than in primary forest, leading to elevated species numbers in this habitat (Becker et al. 2008; Blake & Loiselle 2001; Borges 2007; Bowman et al. 1990). One of the reasons for this may be that canopy birds more regularly come down to feed on flowers and fruits in the understory of secondary forest (Becker et al. 2008). An example from the current study is the capture of four individuals of the canopy-dwelling *Pteroglossus inscriptus* at one of the young secondary forest sites. Additionally, many canopy species may come down to the understory during the midday heat to find shade. This may be more common in secondary than in primary forest, as a more open canopy leads to higher heat intensity (T. Haugaasen, pers. comm.). The current study may suffer from one or more of the above problems and thereby give a skewed estimate of secondary forest species richness. It is, however, currently unclear how to best deal with these biases.

Bird Abundance

The abundance of birds found in different forest types is also highly variable among studies. Some studies have reported abundances to be higher in second growth (e.g. Blake & Loiselle 2001) and some in primary forest (e.g. Raman et al. 1998; Renner et al. 2006; Waltert et al. 2004). Others have, like the current study, found no significant difference (e.g. Andrade &

Rubio-Torgler 1994; Borges 2007). One explanation for similar abundances in primary and secondary forest may be that the high productivity of second growth (Blake & Loiselle 2001) outweighs the structural complexity of primary forests (Bowman et al. 1990). In the current study, the high abundance of omnivores in young secondary forest and high abundance of resource specialists in primary forest may be an indication of this. In addition, many forest bird species are unable to utilize anthropogenically altered areas (Barlow et al. 2002). The forest species that are able to utilize these areas may therefore experience reduced competition or predation from those unable to utilize second growth (Laurance et al. 2002).

Community structure and composition

Tropical forest bird communities are notoriously difficult to sample due to a rich community with many rare species (Dent & Wright 2009). Of the species captured in this study, 42% were represented by two individuals or less. Similar high proportions of rare birds have also been recorded in other studies (Pearman 2002). It is, however, important to note that these rare species may not necessarily be intrinsically rare; they may just be rarely captured in a given study (Raman 2001). For example, none of the species in this study are listed on the IUCN Red List of Threatened Species (IUCN 2010), although they may be locally rare.

The observed rarity may also be related to patchy distribution of species, low sampling effort or biased sampling methodology (Dent & Wright 2009; Laurance et al. 2002; Terborgh et al. 1990). Species rarely captured in mistnets will, for example, be reported as rare in the current study, although they may be common above the nets. Small, common species in the Amazon are known to have territories ten times larger than their equivalents in temperate zones, making the scale of most sampling projects too small to capture more than a few individuals (Robinson 1990; Terborgh et al. 1990; Terborgh 1985). Similarly, the patchy distribution often portrayed by rare species makes them harder to sample (Karr 1990; Queheillalt et al. 2002; Terborgh et al. 1990). Due to these difficulties, similarity between areas has been known to increase with the number of individuals in the sample, and is often underestimated in studies with small sample sizes (Dent & Wright 2009). With more intensive sampling, the number of rare species in this study would thus have been expected to decline. Nevertheless, new species would also have been added to the sample, and it is practically impossible to sample all bird species in an area of tropical rainforest (Terborgh 1985).

Many studies have shown that rare species are restricted to undisturbed primary forest, while secondary forests are dominated by common generalist species (e.g. Barlow et al. 2007b; Blake & Loiselle 2001; Maas et al. 2009; Raman 2001; Terborgh & Weske 1969). The current study does not follow this pattern. Instead I found a relatively high number of rare species in young secondary forest, and the number of unique species was high in both primary and young secondary forest (Table 3). This is an indication that many species specialized to live in primary forest is not able to utilize second growth and vice versa. This is consistent with the results of Barlow et al (2007b), who found the difference in bird communities between primary and secondary forest to be much higher than previously reported.

For old secondary forest the picture is quite different. Few species were found to be restricted to this habitat, and although the species composition was intermediate between young secondary and primary forest, the species richness was lower. Similar results have been found in other studies (e.g. Marsden et al. 2006; Raman 2001; Terborgh 1985), demonstrating that the most distinctive bird communities are found at either end of the successional gradient (Terborgh 1985). Generally there was a much higher variability in avifaunal communities in secondary than in primary forests, consistent with previous studies in Mexico (Estrada et al. 1997) and in fragmented forest in Brazil (Stouffer & Bierregaard 1995b). This may be linked to the fact that secondary forest is a constantly changing habitat, which therefore does not facilitate evolution of specialized birds (Raman 2001).

The similarity between sampled sites in primary forest is low, but is still higher than the similarity between primary forest and second growth; both young and old (Table 6). The analysis of similarity further showed that the avifaunal community differed between forest types, with the largest difference between young secondary and primary forest (Table 5). However, the results of the pairwise comparisons within ANOSIM lacked statistical significance (Table 5). This may be a result of relatively few replicates within each habitat, allowing few possible permutations. With only 10 permutations, the significance level cannot be lower than 10% (Clarke & Gorley 2001). More replicate samples within each forest type would therefore be necessary to test for significant differences in the overall community composition between forest types. Yet, trends observed here indicate that the bird community in primary forest differs profoundly from that of young secondary forest and, to a lesser extent, from that of old second growth. I therefore conclude that the second hypothesis; that primary, old secondary and young secondary forests contain distinct bird communities, with the largest difference found between primary and young secondary forests, is confirmed.

The differences observed between the avifaunal communities in primary and secondary forests in the current study suggest that they had not recovered 9-15 years after abandonment of agricultural patches. This contrasts significantly with the study by Andrade and Rubio-Torgler (1994) where they noted that most of the captured birds in re-growth older than ten years were typical of the primary forest interior. Loiselle and Blake (1994), on the other hand, found only a minority of forest species to be present in their 10 year old study plot, and the current study support their conclusion that a longer time-scale is needed to fully regain the composition and structure of the bird community in primary forest. However, the specific time-frame required to achieve this remains unclear. While Sodhi et al. (2005) observed that 40 year old secondary forest had a very similar bird species composition to primary forest in Indonesia, the bird community was found to be almost identical to that of undisturbed forest only after 100 years of regeneration in India (Raman et al. 1998; Sodhi et al. 2005). Few long-term studies, which include data from before and after disturbance, have been carried out, and more research is needed to fully understand recovery rates in secondary forests (Dunn 2004).

Guild responses

Ant-following insectivores

Many studies have reported ant-following insectivores as highly sensitive to disturbances, and almost exclusively found in primary forest (e.g. Andrade & Rubio-Torgler 1994; Barlow & Peres 2004; Barlow et al. 2006; Barlow et al. 2007b; Blake & Loiselle 2001; Borges 2007; Hawes et al. 2008). This is supported by the current study, as the abundance of ant-followers was higher in primary forest than in both young and old second growth. However, the number of species did not differ significantly, indicating that most ant-following insectivores were able to utilize secondary forest - though in lower numbers. This may be due to the relatively small areas of second growth at Madroño, and the close proximity of primary forest. These results contrast with a similar study by Andrade and Rubio-Torgler (1994), where *Gymnopithys leucaspis* was the only ant-follower registered in young second growth. Dunn (2004) estimated that 39 years of regeneration was necessary for the complete recovery of ant species richness. This may partly explain the slow recovery of ant-following birds in second growth areas. However, Barlow and Peres (2004) observed that only a single species of obligate ant-followers was able to utilize ant-swarms which had re-colonized burned forest, and Johns (1991) found this guild to be more affected by the type and density of insects flushed by ants, than by the presence of ant-swarms. It has also been suggested that either the ant-following insectivores themselves or the ants that they follow may be restricted by high temperatures in second growth, due to a more open canopy (Johns 1991; Pearman 2002).

Dead-leaf gleaning insectivores

Dead-leaf gleaning insectivores were only captured in primary forest, consistent with other studies showing no (e.g. Barlow et al. 2007b) or a reduced number (e.g. Haugaasen et al. 2003; Hawes et al. 2008; Johns 1991; Pearman 2002) of dead-leaf gleaners in disturbed habitats. An explanation for this could be the larger leaves found in secondary forest, especially in forests dominated by *Cecropia* spp (Stouffer & Bierregaard 1995b). Leaves from *Cecropia* may simply be too large to handle for many dead-leaf gleaners (Stouffer & Bierregaard 1995b).

Arboreal nectarivores

The higher species richness of arboreal nectarivores in young secondary forest than in primary forest is consistent with several previous studies (e.g. Barlow et al. 2006; Borges 2007). Stouffer and Bierregaard (1995a) observed that understory hummingbirds were able to live in a matrix of fragmented primary forest and second growth in central Amazonia, a landscape similar to the current study area. However, results vary widely in the literature. Other studies have found no difference (e.g. Andrade & Rubio-Torgler 1994; Loiselle & Blake 1994; Pearman 2002) and higher species richness was found in primary forest in India (Raman et al. 1998). This disagreement between studies may be because the availability of food resources is more important in determining the distribution of nectarivores than the type and structure of the forest (Borges 2007; Pearman 2002; Terborgh 1985). While some nectarivores are specialists, and have been found to be related to the diversity of particular plant families (Raman et al. 1998), Loiselle and Blake (1994) found capture rates of nectarivores to parallel the number of flowering plants, indicating more generalist species. All but two nectarivorous species captured in primary forest in this study were also captured in secondary forest, indicating a high proportion of opportunistic species. The higher abundance of nectarivores in young secondary forest may therefore be a result of higher fruit and flower production in this forest type compared to more mature forests – a result of lower canopy cover and higher light intensity (Blake & Loiselle 2001). Generalist feeders will move to this area of greater resource availability and where less energy is required for foraging (DaSilva et al. 1996).

Arboreal frugivores

Arboreal frugivores show a similar pattern to that of the nectarivores. Frugivores that feed opportunistically can be successful in disturbed areas (Johns 1991), while those adapted to specific plants may depend on primary forest (Raman et al. 1998). Depending on the study, they have been reported to be most common in primary forest (e.g. Bowman et al. 1990; Hawes et al. 2008; Raman et al. 1998) or second growth (e.g. Andrade & Rubio-Torgler 1994; Barlow et al. 2007b; Blake & Loiselle 2001). In this study, there was no significant difference between forest types. The large variation across studies regarding the habitat preferences of both nectarivores and frugivores may be a result of the movement of generalist species tracking resource availability (Martin & Karr 1986).

Arboreal omnivores

While arboreal omnivores were most abundant in secondary forest in Brazil (Barlow et al. 2007b), they were more abundant in primary forest in the cloud forests of Guatemala (Renner et al. 2006). In the current study, this guild is significantly more abundant and species rich in young secondary forest than in primary forest. Since omnivores have a varied diet, they are able to dominate disturbed landscapes, including areas experiencing continuous disturbance (e.g. new plots being burned and cultivated; Johns 1991). Like opportunistic nectarivores and frugivores, they are also able to utilize resources with a patchy distribution in space and time, and may be able to dominate in secondary forest due to high plant productivity.

Arboreal sallying insectivores

Arboreal sallying insectivores were found to be more abundant in primary forest than in burned forest by Haugaasen et al. (2003) and Barlow et al. (2002). These results are similar to those presented here, where this guild is more abundant in primary than in secondary forest. The secondary forest in this study and the burned forest in the study by Barlow et al. (2002) both had higher understory density than primary forest in the same area. This may indicate that arboreal sallying insectivores depend on a more open understory for foraging.

Arboreal gleaning insectivores

Gleaning insectivores were also found to be more abundant in primary forest than in burned forest (Barlow et al. 2002). However, other studies have reported this guild to be more common in disturbed habitats (e.g. Barlow & Peres 2004; Barlow et al. 2006). In the current study, arboreal gleaning insectivores were common in both primary forest and young second growth, but less common in old secondary forest. However, it was generally not the same species that occurred in both forest types, indicating that many aerial gleaning insectivores are specialized to live in either primary or young secondary forest. This may also explain the inconsistent results found in earlier studies.

External bark-searching insectivores

External bark-searching insectivores had the highest abundance in primary forest and a significantly lower abundance in young second growth. This is in agreement with previous studies (e.g. Blake & Loiselle 2001; Johns 1991; Raman et al. 1998). The lower abundance of this guild in secondary vegetation is likely explained by a reduced abundance of dead trees and large living trees in young forests, leading to a reduced foraging substrate (Barlow & Peres 2004; Johns 1991; Raman et al. 1998). Different results were reported from another study in the Colombian Amazon, where significantly more bark-searching insectivores were found in both young and old second growth than in primary forest (Andrade & Rubio-Torgler 1994). These authors attributed the differences to the sampling limitations of only using mistnets at ground level. The contrasting results obtained in the current study, which used an identical sampling method, suggest that there may be other explanatory factors involved.

Overall guild responses

Studies show that the guilds that are negatively affected by slash-and-burn agriculture, are also negatively affected by other disturbances, such as fire (Barlow et al. 2002; Barlow & Peres 2004), fragmentation (Stouffer & Bierregaard 1995b) and logging (Johns 1991). The birds most negatively affected by such anthropogenic disturbances are usually understory insectivores (Barlow et al. 2002; Becker et al. 2008; Johns 1991; Marsden et al. 2006; Stratford & Stouffer 1999). This is consistent with results in the current study, where both ant-following insectivores, dead-leaf gleaning insectivores, arboreal sallying insectivores and external bark-searching insectivores were found to be less abundant or species rich in secondary forest (Figs. 7 & 8). Many of them are resource specialists (Barlow et al. 2002; Stratford & Stouffer 1999), and they are often used as “disturbance indicator species” (Aleixo 1999). The nectarivore, frugivore and omnivore guilds are known to contain more generalist species, which are often better able to utilize second growth (Barlow et al. 2007b; Johns 1991; Loiselle & Blake 1994). This is consistent with the current study where these guilds were found in equal or higher numbers in secondary forest.

The third hypothesis, that different guilds respond differently to habitat modification, is clearly accepted. Although the relatively low number of replicates in the current study increases the risk of obtaining spuriously significant results, the consistency with results of other studies indicates a high degree of reliability. However, it is important to note that not all species within a guild show the same response to disturbances. For example, Antongiovanni and Metzger (2005) found two of their seven understory insectivores to be positively affected by second growth.

Species specific responses

Only three species were found in all nine sampling sites; the arboreal frugivore *Lepidothrix coronata,* the arboreal omnivore *Mionectes oleaginea* and the nectarivore *Phaethornis malaris.* They are all among the most abundant species in the study and are therefore good examples of widespread generalist species (Blake & Loiselle 2009; Pearman 2002). Another common bird is the external bark-searching insectivore *Glyphorynchus spirirus.* The abundance of this species increased with forest age, probably due to increasing foraging substrate. *Thryothorus coraya*, one of the most common species in young secondary forest, was almost exclusively captured in this forest type. It is an arboreal gleaning insectivore and a prime example of an edge/gap species specialized for living in secondary forest (Borges 2007; Laurance 2004).

Three of the species captured in this study was found in all three primary forest sites while occurring in none of the sites in secondary forest. These species, showing the highest consistency in avoiding secondary habitats, were *Thamnomanes caesius, Myrmotherula haematonota* and *Automolus infuscatu*s. *T. caesius* and *M. haematonota* were among the top ten most abundant species in primary forest. *T. caesius* is an arboreal sallying insectivore, known to be fairly common to common in terra firme and mature secondary forest. *M. haematonota* and *A. infuscatus* are dead-leaf gleaning insectivores, showing a strong correlation with low understory density. Common for these three species is that they are normally found in mixed species flocks, often guided by *T. caesius* (Antongiovanni & Metzger 2005; Hilty & Brown 1986). Their absence from secondary forest is an indication that these understory mixed-species flocks avoid this habitat. Mixed-species flocks have previously been found to avoid edges and to disintegrate or go extinct following isolation in small forest fragments (Develey & Stouffer 2001; Laurance 2004; Stouffer & Bierregaard

1995b; Van Houtan et al. 2007). While they can avoid the small gaps in primary forest created by slash-and-burn agriculture in the current study area, they may be highly threatened in areas with more intensive anthropogenic disturbances.

Relating bird communities to forest structure

Vegetation structure has been considered one of the main factors in shaping bird communities along successional gradients (Karr & Freemark 1983). The diversity of birds has, for example, been found to increase parallel to vegetation recovery after disturbances (Raman et al. 1998), and many bird species are unable to live in disturbed areas due to their dependency on the structure and resources of mature forests (Stouffer & Bierregaard 1995b). Although no linear gradient of increasing species richness or abundance of birds was seen to parallel forest recovery in the current study, a significant correlation was still found between forest structure and the composition of the bird communities.

Canopy cover and understory density were significantly correlated with the bird communities. These variables have also previously been shown to be related to the composition of bird communities (e.g. Barlow & Peres 2004; Laurance 2004). I found these two structural variables to be highly correlated. This is logical, as an open canopy allows more light to reach the ground, consequently leading to a higher rate of re-growth and, in turn, a denser understory. However, due to the high correlation, it was impossible to identify their individual effect in determining the composition of the bird communities (Hawes et al. 2009)

The importance of forest structure varied between foraging guilds. Nectarivores and omnivores were the guilds strongest correlated with high understory density. A dense understory is a result of high productivity, and often results in high abundances of flowers and fruits. As previously discussed, omnivores and generalist nectarivores are able to utilize these resources, and are therefore often found in large abundances in these areas. Terborgh (1985) suggested that structural features may be more important for insectivores than for other birds. In the current study, all insectivorous guilds (with the exception of arboreal gleaning insectivores), were correlated with low understory density - a structural feature typical of primary forest. Since primary forest show a higher structural complexity than secondary, particularly young secondary, forest (Bowman et al. 1990), correlation with low understory density may reflect a dependency on other structural features of primary forest.

In light of the results above, I am inclined to accept the fourth hypothesis, that the bird community composition is related to the structure of the forest. Nevertheless, forest structure alone is unlikely to determine the distribution of bird species (Terborgh 1985). In this study, understory density was able to explain 23 percent of the variation in avifaunal community composition. Although the explanatory power of forest structure increased by adding other structural variables, this was not significant, and unknown factors are likely to play an important role in structuring the bird communities.

Other factors affecting bird community composition

Terborgh (1985) identified the presence or absence of food resources as the most obvious explanatory factor for bird community composition. Micro-climatic conditions may also be important for certain birds. As previously mentioned, this may be the case for certain ant-following insectivores, which appear to be restricted to primary forest due to elevated temperatures in second growth (Pearman 2002). In addition, the species composition of the vegetation is important in determining the distribution of birds, particularly for resource specialists (Antongiovanni & Metzger 2005; Borges & Stouffer 1999; Stouffer & Bierregaard 1995b; Terborgh 1985). Long distances to primary forest may also affect the rate of re-growth through reduced seed rain, and represent a barrier for many bird species (Chazdon 2003; Dent & Wright 2009; Develey & Stouffer 2001). However, simple actions like leaving a few remnant trees in agricultural fallows could help speed up the recovery of the forest, as it provides perching sites for forest birds bringing seeds from surrounding forest areas (Carriere et al. 2002; DaSilva et al. 1996; Duncan & Chapman 1999).

The intensity of disturbance is another important factor affecting the bird communities. Dent and Wright (2009) observed a much higher proportion of primary forest species in secondary forest regenerating after slash-and-burn agriculture, than in secondary forest growing on areas previously used as pastures, or where intensive agriculture had been practiced. This may be due to greater soil disturbance in intensively managed areas, leading to an increased destruction of the soil seed-bank and slower re-growth (Guariguata & Ostertag 2001).

Borges (2007) found lower bird species richness in sites of second growth that had been repeatedly cultivated, compared to sites of the same age that had only been cultivated once. Similar results were obtained by Barlow and Peres (2004) comparing the richness of understory birds in twice-burned forest with that in forest that had only burned once. The twice-burned forest had burned twice in living memory with an interval of approximately 15 years (Barlow & Peres 2004), longer than many fallow periods for slash-and-burn agriculture (Lawrence et al. 2010; Metzger 2002). They also found that it was the most abundant understory species that dominated in twice-burned forests (Barlow & Peres 2004). If these results are transferable to the practice of slash-and-burn agriculture, it implies that the understory bird community may become more depleted as areas are re-cultivated several times, and that it is the most common, and thereby the least threatened, birds that survive.

Shorter fallow periods before an area is re-cultivated also negatively affects both woody plants and bird communities (Raman et al. 1998). Metzger (2002) found slash-and-burn systems to be sustainable only if agricultural patches are left fallow for 11 years for each cropping year. Raman et al. (1998) argues that the slash-and-burn cycle in India needs to be at least 50 years to hinder substantial changes in the community structure of woody plants, while 25 years is enough for the avifauna (Raman et al. 1998). The current study suggests that a fallow period of 9-15 years is not enough to regain the structural features and the avifaunal assemblages typical of primary forests. Due to agricultural intensification following growing human populations, fallow periods have in some areas been reduced to 3-4 years (Blankespoor 1991; Metzger 2002), leading to a system in a non-equilibrium state, where forest cover is being lost and agricultural area is increasing over time (Metzger 2002).

What complicates the matter is that the sustainability of slash-and-burn agriculture has been found to differ between areas, depending, amongst other factors, on the local ecological knowledge of the farmers and whether the focus has been on subsistence or cash crops (Lawrence et al. 2010). While the shifting agriculture for subsistence carried out by locals in West Kalimantan for centuries was found to be sustainable, slash-and-burn agriculture based on cash-crops among farmers that moved to Southern Yucatan 30-60 years ago, showed an 18% decline in biomass recovery following each slash-and-burn cycle (Lawrence et al. 2010). In the Lower Caquetá River, slash-and-burn agriculture is mainly carried out for subsistence, but this may change over time due to increasing population and growing commercial markets.

Conclusions and conservation implications

Species richness and abundance did not show a linear increase following forest regeneration. Rather, abundance was similar in all forest types, and species richness was high in both young second growth and primary forest. However, community composition and structure was different, and the current study therefore suggests that overall species richness or abundance is not the best indicator for the conservation value of secondary forest. As agricultural land and human dominated landscape increases, and the area of primary forest decreases, it is the bird species dependent on primary forest that become threatened, and in need of special attention. The focus should therefore be on the presence of mixed species flocks and the abundance and richness of disturbance-sensitive guilds, particularly dead-leaf gleaning insectivores, ant-following insectivores, external bark-searching insectivores and arboreal sallying insectivores. Even within these guilds, some species are more negatively affected by human disturbances than others, and subsequent studies should more clearly identify these.

As the area of primary forest is reduced, secondary forest or areas under slash-and-burn cultivation may play important roles as additional habitat for many species (Chazdon et al. 2009; Dent & Wright 2009). When located in close proximity to undisturbed forest, secondary forests have the potential of successfully recovering the avifauna of primary forest (Sodhi et al. 2005). However, this study indicates that this recovery may take longer than the fallow period of many slash-and-burn areas. Secondary forests are therefore often burned and cultivated again before the bird communities have had time to recover.

The factors affecting the rate of bird community recovery are many and inter-correlated (Lawrence et al. 2010). While the composition of the bird communities was correlated with structural features of the forest - particularly understory density and canopy cover - previous land-use, and the presence of primary forest in the landscape, may be just as important in shaping the bird community in regenerating vegetation (Borges 2007; Dent & Wright 2009). Good management practices are therefore necessary for slash-and-burn agricultural systems to be considered sustainable in the long-term.

References

Aleixo, A. (1999). Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor*, 101 (3): 537-548.

Alldredge, M. W., Simons, T. R. & Pollock, K. H. (2007). Factors affecting aural detections of songbirds. *Ecological Applications*, 17 (3): 948-955.

Andrade, G. I. & Rubio-Torgler, H. (1994). Sustainable use of the tropical rain forest: Evidence from the avifauna in a shifting-cultivation habitat mosaic in the Colombian Amazon. *Conservation Biology*, 8 (2): 545-554.

Antongiovanni, M. & Metzger, J. P. (2005). Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*, 122 (3): 441-451.

Barlow, J., Haugaasen, T. & Peres, C. A. (2002). Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biological Conservation*, 105 (2): 157-169.

Barlow, J. & Peres, C. A. (2004). Avifaunal responses to single and recurrent wildfires in Amazonian forests. *Ecological Applications*, 14 (5): 1358-1373.

Barlow, J., Peres, C. A., Henriques, L. M. P., Stouffer, P. C. & Wunderle, J. M. (2006). The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis. *Biological Conservation*, 128 (2): 182-192.

Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. M., et al. (2007a). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, 104 (47): 18555-18560.

Barlow, J., Mestre, L. A. M., Gardner, T. A. & Peres, C. A. (2007b). The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation*, 136 (2): 212-231.

Becker, C. D., Loughin, T. M. & Santander, T. (2008). Identifying forest-obligate birds in tropical moist cloud forest of Andean Ecuador. *Journal of Field Ornithology*, 79 (3): 229-244.

Blake, J. G. & Loiselle, B. A. (2001). Bird assemblages in second-growth and old-growth forests, Costa Rica: Perspectives from mist nets and point counts. *Auk*, 118 (2): 304-326.

Blake, J. G. & Loiselle, B. A. (2009). Species composition of Neotropical understory bird communities: Local versus regional perspectives based on capture data. *Biotropica*, 41 (1): 85-94.

Blankespoor, G. W. (1991). Slash-and-burn shifting agriculture and bird communities in Liberia, West Africa. *Biological Conservation*, 57 (1): 41-71.

Borges, S. H. & Stouffer, P. C. (1999). Bird communities in two types of anthropogenic successional vegetation in central Amazonia. *Condor*, 101 (3): 529-536.

Borges, S. H. (2007). Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon. *Journal of Tropical Ecology*, 23: 469-477.

Bowman, D., Woinarski, J. C. Z., Sands, D. P. A., Wells, A. & McShane, V. J. (1990). Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea: Response of birds, butterflies and reptiles. *Journal of Biogeography*, 17 (3): 227-239.

Carriere, S. M., Andre, M., Letourmy, P., Olivier, I. & McKey, D. B. (2002). Seed rain beneath remnant trees in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology*, 18: 353-374.

Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6 (1-2): 51-71.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E. & Miller, S. E. (2009). The potential for species conservation in tropical secondary forests. *Conservation Biology*, 23 (6): 1406-1417.

Clarke, K. R. & Gorley, R. N. (2001). *PRIMER v5: User manual/tutorial*. Plymoth: PRIMER-E Ltd.

Colwell, R. K. (2004). *EstimateS: Statistical estimation of species richness and shared species from samples*. 7 ed.

Colwell, R. K., Mao, C. X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85 (10): 2717-2727.

Cumming, G. (2009). Inference by eye: Reading the overlap of independent confidence intervals. *Statistics in Medicine*, 28 (2): 205-220.

DaSilva, J. M. C., Uhl, C. & Murray, G. (1996). Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology*, 10 (2): 491-503.

Dent, D. H. & Wright, S. J. (2009). The future of tropical species in secondary forests: A quantitative review. *Biological Conservation*, 142 (12): 2833-2843.

Develey, P. F. & Stouffer, P. C. (2001). Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology*, 15 (5): 1416-1422.

Duivenvoorden, J. F. & Lips, J. M. (1995). *A land-ecological study of soils, vegetation, and plant diversity in Colombian Amazonia*. Tropenbos Series, vol. 12. Wageningen: The Tropenbos Foundation. 428 pp.

Duncan, R. S. & Chapman, C. A. (1999). Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9 (3): 998-1008.

Dunn, R. R. (2004). Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, 18 (2): 302-309.

Estrada, A., CoatesEstrada, R. & Meritt, D. A. (1997). Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodiversity and Conservation*, 6 (1): 19-43.

FAO. (2006). Global forest resources assessment 2005: Progress toward sustainable forest management. *FAO Forestry Paper*. Rome: Food and Agricultural Organization of the United Nations.

FAO. (2009). State of the world's forests 2009. Rome: Food and Agricultural Organization of the United Nations.

Gehring, C., Denich, M. & Vlek, P. L. G. (2005). Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. *Journal of Tropical Ecology*, 21: 519-527.

Gotelli, N. J. & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4 (4): 379-391.

Guariguata, M. R. & Ostertag, R. (2001). Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management*, 148 (1-3): 185-206.

Haugaasen, T., Barlow, J. & Peres, C. A. (2003). Effects of surface fires on understorey insectivorous birds and terrestrial arthropods in central Brazilian Amazonia. *Animal Conservation*, 6: 299-306.

Hawes, J., Barlow, J., Gardner, T. A. & Peres, C. A. (2008). The value of forest strips for understorey birds in an Amazonian plantation landscape. *Biological Conservation*, 141 (9): 2262-2278.

Hawes, J., Motta, C. D., Overal, W. L., Barlow, J., Gardner, T. A. & Peres, C. A. (2009). Diversity and composition of Amazonian moths in primary, secondary and plantation forests. *Journal of Tropical Ecology*, 25: 281-300.

Hilty, S. L. & Brown, W. L. (1986). *A guide to the birds of Colombia*. Princeton: Princeton University Press.

IUCN. (2010). *IUCN Red List of Threatened Species. Version 2010.1.* Available at: http://www.iucnredlist.org (accessed: 29 April).

Johns, A. D. (1991). Responses of Amazonian rain-forest birds to habitat modification. *Journal of Tropical Ecology*, 7: 417-437.

Jongmann, R. H. G., Ter Braak, C. J. F. & Van Tongeren, O. F. R. (1995). *Data analysis in community and landscape ecology*. Cambridge: Cambridge University Press. 299 pp.

Karr, J. R. (1981). Surveying birds in the tropics. *Studies in Avian Biology*, 6: 548-553.

Karr, J. R. & Freemark, K. E. (1983). Habitat selection and environmental gradients: Dynamics in the "stable" tropics. *Ecology*, 64 (6): 1481-1494.

Karr, J. R. (1990). Birds of tropical rainforests: Comparative biogeography and ecology. In Keast, A. (ed.) *Biogeography and ecology of forest bird communities*, pp. 215-228. Den Haag: SPB Academic publishing.

Klanderud, K., Mbolatiana, H. Z. H., Vololomboahangy, M. N., Radimbison, M. A., Roger, E., Totland, Ø. & Rajeriarison, C. (2010). Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. *Biodiversity and Conservation*, 19 (1): 187-204.

Laurance, S. G. W. (2004). Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications*, 14 (5): 1344-1357.

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, 16 (3): 605-618.

Lawrence, D., Radel, C., Tully, K., Schmook, B. & Schneider, L. (2010). Untangling a decline in tropical forest resilience: Constraints on the sustainability of shifting cultivation across the globe. *Biotropica*, 42 (1): 21-30.

Lawton, J. H., Bignell, D. E., Bolton, B., Bloemers, G. F., Eggleton, P., Hammond, P. M., Hodda, M., Holt, R. D., Larsen, T. B., Mawdsley, N. A., et al. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, 391 (6662): 72-76.

Lemmon, P. E. (1957). A new instrument for measuring forest understory density. *Journal of Forestry*, 55.

Lepš, J. & Šmilauer, P. (2003). *Multivariate analysis of ecological data using CANOCO*. Cambridge: Cambridge University Press. 269 pp.

Letcher, S. G. & Chazdon, R. L. (2009). Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica*, 41 (5): 608-617.

Loiselle, B. A. & Blake, J. G. (1994). Annual variation in birds and plants of a tropical second-growth woodland. *Condor*, 96 (2): 368-380.

Maas, B., Putra, D. D., Waltert, M., Clough, Y., Tscharntke, T. & Schulze, C. H. (2009). Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. *Biological Conservation*, 142 (11): 2665-2671.

Marsden, S. J., Symes, C. T. & Mack, A. L. (2006). The response of a New Guinean avifauna to conversion of forest to small-scale agriculture. *Ibis*, 148 (4): 629-640.

Martin, T. E. & Karr, J. R. (1986). Temporal dynamics of Neotropical birds with special reference to frugivores in 2nd-growth woods. *Wilson Bulletin*, 98 (1): 38-60.

Metzger, J. P. (2002). Landscape dynamics and equilibrium in areas of slash-and-burn agriculture with short and long fallow period (Bragantina region, NE Brazilian Amazon). *Landscape Ecology*, 17 (5): 419-431.

Myers, N. (1991). Tropical forests: Present status and future outlook. *Climatic Change*, 19 (1-2): 3-32.

Myers, N. (2000). Tropical rain forests and biodiversity. In Osborne, P. L. (ed.) *Tropical ecosystems and ecological concepts*, pp. 238-279. Cambridge: Cambridge University Press.

Pearman, P. B. (2002). The scale of community structure: Habitat variation and avian guilds in tropical forest understory. *Ecological Monographs*, 72 (1): 19-39.

Piperno, D. R. (2006). Quaternary environmental history and agricultural impact on vegetation in central America. *Annals of the Missouri Botanical Garden*, 93 (2): 274-296.

Queheillalt, D. M., Cain, J. W., Taylor, D. E., Morrison, M. L., Hoover, S. L., Tuatoo-Bartley, N., Rugge, L., Christopherson, K., Hulst, M. D., Harris, M. R., et al. (2002). The exclusion of rare species from community-level analyses. *Wildlife Society Bulletin*, 30 (3): 756-759.

Raman, T. R. S., Rawat, G. S. & Johnsingh, A. J. T. (1998). Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology*, 35 (2): 214-231.

Raman, T. R. S. (2001). Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. *Conservation Biology*, 15 (3): 685-698.

Rappole, J. H., Winker, K. & Powell, G. V. N. (1998). Migratory bird habitat use in southern Mexico: Mist nets versus point counts. *Journal of Field Ornithology*, 69 (4): 635-643.

Remsen, J. V. & Good, D. A. (1996). Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk*, 113 (2): 381-398.

Renner, S. C., Waltert, M. & Muhlenberg, M. (2006). Comparison of bird communities in primary vs. young secondary tropical montane cloud forest in Guatemala. *Biodiversity and Conservation*, 15 (4): 1545-1575.

Ridgely, R. S. & Tudor, G. (1994). *The birds of South America volume 2: The suboscine passerines*. Austin: University of Texas Press. 940 pp.

Robinson, S. K. (1990). Lowland tropical forest bird communities of a site in western Amazonia. In Keast, A. (ed.) *Biogeography and ecology of forest bird communities*. Den Haag: SPB Academic publishing.

Schmidt-Vogt, D., Leisz, S. J., Mertz, O., Heinimann, A., Thiha, T., Messerli, P., Epprecht, M., Cu, P. V., Chi, V. K., Hardiono, M., et al. (2009). An assessment of trends in the extent of swidden in southeast Asia. *Human Ecology*, 37 (3): 269-280.

Schulenberg, T. S., Stotz, D. F., Lane, D. F., O'Neill, J. P. & Parker, T. A. (2007). *Birds of Peru*. Princeton field guides. Princeton: Princeton University Press. 656 pp.

Schulze, C. H., Waltert, M., Kessler, P. J. A., Pitopang, R., Shahabuddin, Veddeler, D., Muhlenberg, M., Gradstein, S. R., Leuschner, C., Steffan-Dewenter, I., et al. (2004). Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications*, 14 (5): 1321-1333.

Sodhi, N. S., Koh, L. P., Prawiradilaga, D. M., Tinulele, I., Putra, D. D. & Tan, T. H. T. (2005). Land use and conservation value for forest birds in central Sulawesi (Indonesia). *Biological Conservation*, 122 (4): 547-558.

Steininger, M. K. (2000). Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology*, 16: 689-708.

Stouffer, P. C. & Bierregaard, R. O. (1995a). Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology*, 9 (5): 1085-1094.

Stouffer, P. C. & Bierregaard, R. O. (1995b). Use of Amazonian forest fragments by understory insectivorous birds. *Ecology*, 76 (8): 2429-2445.

Stouffer, P. C., Strong, C. & Naka, L. N. (2009). Twenty years of understorey bird extinctions from Amazonian rain forest fragments: Consistent trends and landscape-mediated dynamics. *Diversity and Distributions*, 15 (1): 88-97.

Stratford, J. A. & Stouffer, P. C. (1999). Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology*, 13 (6): 1416-1423.

Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M. & Bates, D. M. (2007). Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture Ecosystems & Environment*, 119 (3-4): 257-269.

Terborgh, J. & Weske, J., S. (1969). Colonization of secondary habitats by Peruvian birds. *Ecology*, 50 (5).

Terborgh, J., Robinson, S. K., Parker, T. A., Munn, C. A. & Pierpont, N. (1990). Structure and organization of an Amazonian forest bird community. *Ecological Monographs*, 60 (2): 213-238.

Terborgh, J. W. (1985). Habitat selection in Amazonian birds. In Cody, M. L. (ed.) Physiological ecology, *Habitat selection in birds*, pp. 311-340. Orlando: Academic press.

Uhl, C., Buschbacher, R. & Serrao, E. A. S. (1988). Abandoned pastures in eastern Amazonia. 1. Patterns of plant succession. *Journal of Ecology*, 76 (3): 663-681.

van Breugel, M., Martinez-Ramos, M. & Bongers, F. (2006). Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, 22: 663-674.

Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard, R. O. & Lovejoy, T. E. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*, 10 (3): 219-229.

Waltert, M., Mardiastuti, A. & Muhlenberg, M. (2004). Effects of land use on bird species richness in Sulawesi, Indonesia. *Conservation Biology*, 18 (5): 1339-1346.

Wunderle, J. M., Henriques, L. M. P. & Willig, M. R. (2006). Short-term responses of birds to reduced-impact logging in a lowland Amazon forest: Can reduced-impact methods help to retain avian biodiversity in tropical timber production forests? *Journal of Ornithology*, 147 (5): 114-115.

Appendix 1. Species richness and abundance within different foraging guilds in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia.

Code	Guilds	PF		OSF		YSF	
		No. of species	No. of inds.	No. of species	No. of inds.	No. of species	No. of inds.
IA	Aerial feeding insectivore	0	0	0	0	1	1
IAF	Ant-following insectivore	7	43	3	14	4	11
AQU	Aquatic	1	1	2	4	2	2
FA	Arboreal frugivore	4	47	3	44	3	50
IAG	Arboreal gleaning insectivore	8	36	3	13	11	37
NA	Arboreal nectarivore	6	26	8	46	9	41
OA	Arboreal omnivore	3	18	5	25	11	49
IAS	Arboreal sallying insectivore	14	39	6	11	10	17
IBS	Bark-searching insectivore (external)	5	35	5	26	3	8
IBI	Bark-searching insectivore (internal)	1	1	0	0	1	2
IDL	Dead-leaf gleaning insectivore	3	15	0	0	0	0
RAD	Diurnal raptor	1	1	0	0	0	0
RNA	Nocturnal raptor	0	0	0	0	1	1
FT	Terrestrial frugivore	1	1	1	5	1	4
ITG	Terrestrial gleaning insectivore	5	9	3	9	2	12
GT	Terrestrial granivore	0	0	0	0	3	3
ITS	Terrestrial sallying insectivore	1	1	1	2	0	0

Appendix 2. Species list and abundance of birds captured in mistnets in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Species are listed by family and foraging guilds.

Latin name	English name	Guild	PF	OSF	YSF	Total
Accipitridae						
Accipiter superciliosus	Tiny Hawk	RAD	1	0	0	1
Columbidae						
Leptotila rufaxilla	Grey-fronted Dove	GT	0	0	1	1
Geotrygon montana	Ruddy Quail-dove	FT	1	5	4	10
Strigidae						
Glaucidium brasilianum	Ferruginous Pygmy-owl	RNA	0	0	1	1
Trochilidae						
Glaucis hirsuta	Rufous-breasted Hermit	NA	0	1	10	11
Threnetes leucurus	Pale-tailed Barbthroat	NA	2	5	2	9
Phaethornis malaris	Great-billed Hermit	NA	11	12	8	31
Phaethornis hispidus	White-bearded Hermit	NA	0	8	8	16
Phaethornis bourcieri	Straight-billed Hermit	NA	5	9	4	18
Phaethornis ruber	Reddish Hermit	NA	0	3	1	4
Florisuga mellivora	White-necked Jacobin	NA	1	0	0	1
Chlorestes notatus	Blue-chinned Sapphire	NA	0	2	1	3
Thalurania furcata	Fork-tailed Woodnymph	NA	5	6	3	14
Amazilia fimbriata	Glittering-throated Emerald	NA	0	0	4	4
Heliodoxa aurescens	Gould’s Jewelfront	NA	2	0	0	2
Alcedinidae						
Chloroceryle inda	Green-and-rufous Kingfisher	AQU	0	2	1	3
Chloroceryle aenea	American Pygmy Kingfisher	AQU	1	2	1	4
Galbulidae						
Galbula albirostris	Yellow-billed Jacamar	IAS	2	0	0	2
Bucconidae						
Malacoptila fusca	White-chested Puffbird	IAS	2	0	0	2
Nonnula rubecula	Rusty-breasted Nunlet	IAS	0	0	2	2
Capitonidae						
Capito aurovirens	Scarlet-crowned Barbet	OA	0	0	1	1
Ramphastidae						
Pteroglossus inscriptus	Lettered Aracari	FA	0	0	4	4
Picidae						
Celeus elegans	Chestnut Woodpecker	IBI	0	0	2	2
Dendrocolaptidae						
Dendrocincla fuliginosa	Plain-brown Woodcreeper	IAS	1	3	2	6
Dendrocincla merula	White-chinned Woodcreeper	IAF	7	0	1	8

Appendix 2. Species list and abundance of birds captured in mistnets in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Species are listed by family and foraging guilds.

Latin name	English name	Guild	PF	OSF	YSF	Total
Deconychura longicauda	Long-tailed Woodcreeper	IAS	1	0	0	1
Deconychura stictolaema	Spot-throated Woodcreeper	IAS	1	2	0	3
Glyphorynchus spirurus	Wedge-billed Woodcreeper	IBS	26	17	5	48
Dendrocolaptes certhia	Amazonian Barred Woodcreeper	IAS	1	1	2	4
Xiphorhynchus picus	Straight-billed Woodcreeper	IBS	0	0	1	1
Xiphorhynchus ocellatus	Occelated Woodcreeper	IBS	4	0	0	4
Xiphorhynchus spixii	Spix's Woodcreeper	IBS	0	1	0	1
Xiphorhynchus elegans	Elegant Woodcreeper	IBS	1	4	0	5
Xiphorhynchus guttatus	Buff-throated Woodcreeper	IBS	1	3	2	6
Campylorhamphus procurvoides	Curve-billed Scythebill	IBI	1	0	0	1
Furnariidae						
Synallaxis gujanensis	Plain-crowned Spinetail	ITG	0	0	2	2
Philydor pyrrhodes	Cinnamon-rumped Foliage-gleaner	IDL	3	0	0	3
Automolus infuscatus	Olive-backed Foliage-gleaner	IDL	3	0	0	3
Xenops minutus	Plain Xenops	IBS	3	1	0	4
Sclerurus mexicanus	Tawny-throated Leaftosser	ITG	1	0	0	1
Sclerurus rufigularis	Short-billed Leaftosser	ITG	1	0	0	1
Thamnophilidae						
Taraba major	Great Antshrike	IAG	0	0	2	2
Thamnophilus murinus	Mouse-colored Antshrike	IAS	2	1	1	4
Thamnophilus amazonicus	Amazonian Antshrike	IAG	0	0	4	4
Megastictus margaritatus	Pearly Antshrike	IAS	3	1	0	4
Thamnomanes ardesiacus	Dusky-throated Antshrike	IAS	4	0	0	4
Thamnomanes caesius	Cinereous Antshrike	IAS	13	0	0	13
Myrmotherula hauxwelli	Plain-throated Antwren	IAG	2	0	0	2
Myrmotherula haematonota	Stipple-throated Antwren	IDL	9	0	0	9
Myrmotherula axillaris	White-flanked Antwren	IAG	4	6	6	16
Myrmotherula menetriesii	Grey Antwren	IAG	4	0	1	5
Hypocnemis cantator	Guianan Warbling-antbird	IAG	0	0	1	1
Hypocnemis hypoxantha	Yellow-browed Antbird	IAG	3	3	2	8
Percnostola rufifrons	Black-headed Antbird	ITG	1	5	10	16
Schistocichla schistacea	Slate-colored Antbird	ITG	4	3	0	7
Sclateria naevia	Silvered Antbird	ITG	0	1	0	1
Myrmeciza melanoceps	White-shouldered Antbird	IAG	0	0	2	2
Myrmeciza fortis	Sooty Antbird	IAF	3	0	0	3
Pithys albifrons	White-plumed Antbird	IAF	10	5	5	20

Appendix 2. Species list and abundance of birds captured in mistnets in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Species are listed by family and foraging guilds.

Latin name	English name	Guild	PF	OSF	YSF	Total
Gymnopithys leucaspis	Bicolored Antbird	IAF	18	7	3	28
Phlegopsis nigromaculata	Black-spotted Bare-eye	IAF	1	2	2	5
Phlegopsis erythroptera	Reddish-winged Bare-eye	IAF	1	0	0	1
Hylophylax naevia	Spot-backed Antbird	IAG	8	0	1	9
Hylophylax poecilonota	Scale-backed Antbird	IAF	12	4	2	18
Conopophagidae						
Conopophaga aurita	Chestnut-belted Gnateater	ITG	2	0	0	2
Pipridae						
Pipra erythrocephala	Golden-headed Manakin	FA	8	10	17	35
Pipra pipra	White-crowned Manakin	FA	1	0	0	1
Pipra filicauda	Wire-tailed Manakin	FA	3	8	0	11
Lepidothrix coronata	Blue-crowned Manakin	FA	35	26	29	90
Tyrannidae						
Mionectes oleaginea	Ochre-bellied Flycatcher	OA	14	16	27	57
Corythopis torquata	Ringed Antpipit	ITS	1	2	0	3
Hemitriccus zosterops	White-eyed Tody-tyrant	IAS	0	0	1	1
Todirostrum latirostre	Rusty-fronted Tody-flycatcher	IAS	0	0	4	4
Cnipodectes subbrunneus	Brownish Twistwing	IAS	0	0	1	1
Ramphotrigon ruficauda	Rufous-tailed Flatbill	IAS	2	0	2	4
Platyrinchus platyrhynchos	White-crested Spadebill	IAS	2	0	0	2
Terenotriccus erythrurus	Ruddy-tailed Flycatcher	IAS	0	3	1	4
Myiobius barbatus	Bearded Flycatcher	IAS	2	0	0	2
Empidonax traillii	Willow Flycatcher	IAS	0	0	1	1
Attila spadiceus	Bright-rumped Attila	IAS	3	0	0	3
Pitangus sulphuratus	Great Kiskadee	OA	0	0	1	1
Hirundinidae						
Stelgidopteryx ruficollis	Southern Rough-winged Swallow	IA	0	0	1	1
Troglodytidae						
Thryothorus coraya	Coraya Wren	IAG	1	0	15	16
Turdidae						
Catharus minimus	Grey-cheeked Thrush	OA	0	0	1	1
Catharus ustulatus	Swainson's Thrush	OA	0	1	7	8
Turdus albicollis	White-necked Thrush	OA	3	0	1	4
Sylviidae						
Microbates collaris	Collared Gnatwren	IAG	2	0	0	2
Vireonidae						

Appendix 2. Species list and abundance of birds captured in mistnets in primary (PF), old secondary (OSF) and young secondary (YSF) forest in the Lower Caquetá River, Colombia. Species are listed by family and foraging guilds.

Latin name	English name	Guild	PF	OSF	YSF	Total
Vireo olivaceus	Red-eyed Vireo	IAG	0	0	1	1
Hylophilus ochraceiceps	Tawny-crowned Greenlet	IAG	3	0	0	3
Icteridae						
Psarocolius decumanus	Crested Oropendola	OA	0	0	1	1
Cacicus cela	Yellow-rumped Cacique	OA	0	0	1	1
Thraupidae						
Thraupis episcopus	Blue-grey Tanager	OA	0	0	1	1
Ramphocelus carbo	Silver-beaked Tanager	OA	0	1	5	6
Tachyphonus surinamus	Fulvous-crested Tanager	OA	0	4	0	4
Cardinalinae						
Cyanocompsa cyanoides	Blue-black Grosbeak	OA	1	3	3	7
Emberizinae						
Oryzoborus angolensis	Lesser Seed-finch	GT	0	0	1	1
Volatinia jacarina	Blue-black Grassquit	GT	0	0	1	1