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MASTERARBEIT

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„Bird assemblages along a tropical forest succession gradient in the Pacific lowlands of southern Costa Rica: the importance of secondary forests as corridor habitats“

Verfasser

Andrés Felipe Reyes Páez B. Sc.

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Betreuerin / Betreuer: Ass.-Prof. Dr. Christian H. Schulze

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Abstract

Nowadays, human-dominated landscapes in most tropical regions are characterized by a low permeability for forest species, thereby preventing movements between forest remnants. This study quantified the importance of secondary forests in different succession stages as potential stepping stone or corridor habitats for forest birds at the margin of protected forest areas in the Pacific lowlands of southern Costa Rica. Birds were surveyed in pastures with scattered trees and bushes, young secondary forests (actively and passively restored), old secondary forests and old abandoned cacao agroforestry systems (N = 4 replicate sites per habitat type) by point counts (duration: 20 min, 10 counts per site) in November 2010-January 2011. Furthermore, the following habitat variables were measured or estimated: density of large trees, density of small trees, maximal tree height, canopy closure, understory density and herb cover. In total 115 forest bird species were recorded, including 54 forest specialists (restricted to closed forest) and 61 forest generalists. Besides affecting species composition, the density of large trees (dbh > 10 cm) was most strongly related to changes in richness of forest specialists. The species number of forest specialists increased with increasing number of large trees. These results emphasize the importance of large trees as structural component of secondary forests for forest birds. This finding has important management implications for forest restoration programs and calls for evaluating the potential of fast-growing native trees to improve the conservation value of secondary forests for forest birds within shorter time periods.

Keywords: forest specialist birds, forest succession, secondary forests, conservation, forest restoration, biological corridor.

Zusammenfassung

In den meisten tropischen Regionen existieren aktuell nur noch stark fragmentierte Regenwälder, welche in eine vom Menschen stark veränderte Landschaftsmatrix eingebettet sind. Diese weist für Waldarten eine nur geringe Permeabilität auf und schränkt somit räumliche Bewegungen von an Wälder gebundene Organismen stark ein. In dieser Studie wurde die Bedeutung von Sekundärwäldern in verschiedenen Sukzessionsstadien als mögliche Trittstein- oder Korridorhabitate für Waldarten am Rande geschützter Waldgebiete im Pazifischen Tiefland im südlichen Teil Costa Ricas untersucht. Dazu wurden Vögel auf Brachen mit einzelnen Bäumen und Büschen, in jungen Sekundärwäldern (angepflanzt und enstanden durch natürliche Sukzession), in alten Sekundärwäldern und in alten Kakao-Agroforstsystemen (N = 4 räumliche Replikate pro Habitattyp) mittels Punktzählungen (Dauer: 20 min; 10 Wiederholungen pro Standort) zwischen November 2010 und Jänner 2011 erfasst. Zudem wurden folgende Habitatvariablen gemessen oder geschätzt: Dichte großer Bäume, Dichte kleiner Bäume, maximale Baumhöhe, Baumkronenschluss, Unterwuchsdichte und Krautschichtdeckung. Insgesamt wurden 115 Waldvogelarten festgestellt, darunter 54 Waldspezialisten (Vorkommen beschränkt auf geschlossene Waldflächen) und 61 Waldgeneralisten. Neben einer signifikanten Auswirkung auf die Artenzusammensetzung, erwies sich die Dichte großer Bäume (DBH >10 cm) als bester Prädiktor für Veränderungen der Artenzahl an Waldspezialisten. Deren Artenzahl nahm mit zunehmeder Anzahl an großen Bäumen zu. Diese Ergebnisse betonen die Bedeutung großer Bäume als wichtige strukturelle Komponente von Sekundärwäldern für Waldspezialisten. Dies hat wichtige Konsequenzen für Wiederbewaldungsmaßnahmen, welche bevorzugt auf das Potential schnell-wachsender einheimischer Baumarten setzen sollten, um den naturschutzfachlichen Wert von Sekundärwäldern für Waldvögel in möglichst kurzen Zeitspannen effizient zu erhöhen.

Introduction

During the past 20 years deforestation and land use (e.g. agriculture, human settlements) have been the main drivers for reducing the primary forest areas in the world's tropical regions (Wilcox & Murphy 1985, Stotz et al. 1996, Turner 1996, Lamb 1998, Laurance 1999, Debinski & Holt 2000, FAO 2010). The resulting forest fragmentation negatively affects population dynamics of tropical forest species and contributes to the ongoing biodiversity loss (Rosero-Bixby & Palloni 1998, Sala et al. 2000, Sodhi & Smith 2007, Harvey et al. 2008, Sodhi et al. 2008). Some secondary habitats may help to reduce increasing forest fragmentation and the related biodiversity loss (Chazdon et al. 2009, Seaman & Schulze 2010, Fahrig et al. 2011). However, the conservation of tropical primary forests is still the main concern, due to their irreplaceable characteristics and their high value as unique home for many tropical species (Dirzo & Raven 2003), especially those with specific habitat dependencies, restricted geographical ranges and little or no tolerance to habitat fragmentation and landscape change (Stotz et al. 1996, Soh et al. 2006). This has been especially well documented for some tropical bird species (Kofron & Chapman 1995, Estrada et al. 1997, Fjeldså 1999, Blake & Loiselle 2001, Naidoo 2004, Waltert et al. 2004, Sodhi et al. 2005, Arriaga-Weiss 2008, Sodhi et al. 2008, Maas et al. 2009).

Nowadays, it is almost impossible to find pristine, undisturbed forests (Willis et al. 2004). The small proportion that remains is still in the focus of commercial or illegal logging activities (Bawa & Dayanandan 1997, Vitousek et al. 1997, Daily et al. 1998). Thus, in the attempt to compensate this loss, forest restoration and renaturation measures are implemented on degraded land (Lamb 1998, Rey Benayas 2000, Petit & Montagnini 2006). Despite efforts to mitigate the damage to nature, there are many limitations, especially monetary; that is why, most of forest regeneration takes place by passive restoration (natural regeneration) (Rey Benayas 2000) resulting in various types of secondary forests (Aide et al. 2000, Wright 2005, Guerrero & da Rocha 2010). Problems for natural regeneration can be the lack of remaing seed banks or seed dispersal in all its sense (Reid et al. 2008, Reid et al. 2012).

Regenerated secondary forests are classified as suitable to support a certain fraction of biodiversity (Sodhi et al. 2004) with a positive species recovery in time (Grau et al. 2003, Dunn 2004). They maintain more forest-dependent species of higher conservation concern than extensive plantations (Peh et al. 2006, Edwards et al. 2010, 2011). Likewise, some studies suggested that forests with secondary growth are potential reservoirs of biodiversity (Chazdon 1998, 2008, Brook et al. 2006, Wright & Muller-Landau 2006a, 2006b, Barlow et al. 2007a, 2007b), and could serve also as temporal refuges, foraging areas and – most important – as landscape structures connecting remaining forest fragments (Myers 1997, Blake & Loiselle 2001, Chazdon 2003, Fischer et al. 2006, Höbinger et al. 2012). Therefore, even though they differ in structural and floristic composition from primary forests, they can contribute to the creation of biological corridors for forest species. Also, due to their relative high productivity these areas should be incorporated into agroecosystems, which consequently may benefit from indirect services (e.g. pollinization and pest control) provided by forest species interacting with the surrounding human-dominated landscape matrix (Finegan 1992, Chazdon 2008).

Secondary forests are rapidly expanding in the tropics (Wright 2005). They are especially emerging in abandoned areas which are not futher used for agricultural purposes (Thomlinson et al. 1996). Before, such areas dominated by human land-use activities represented effective barriers preventing the connection between remnants of primary forests or other important secondary ecosystems such as, old agroforests (Sánchez-Azofeita et al. 2001, 2003, Steffan-Dewenter et al. 2007, Tscharntke et al. 2008). Agroforests can be of high conservation value as they can slightly resemble old-growth forests (Thiollay 1999, Petit & Petit 2003) and therefore can facilitate the occurrence of forest species (Reitsma et al. 2001).

In this study from the Pacific lowlands of Costa Rica, birds were used to study the capability of different successional stages of naturally regenerated and planted secondary forests as well as old abandoned agroforests at the margin of protected rainforest areas to facilitate forest species. We were particularly interested in the potential of these secondary forests to increase landscape permeability and to act as corridor habitats for forest birds. In particular the following hypotheses were tested: (1) Richness and abundance of forest-dependent species increase with forest succession age; (2) species composition changes with progressing forest succession due to an increase of forest-dependent species. Furthermore, relationships between habitat variables and species richness and composition of forest species were evaluated.

Methods

Study area

The study area is located in the "Golfo Dulce" region of southwestern Costa Rica, between "Piedras Blancas" National Park (including "Esquinas" Forest, Valley "Río Esquinas" and Valley "Río Bonito") and the "Fila Gamba" (Figure 1). The Golfo Dulce region is classified as an important Endemic Bird Area (EBA 021: South Central American Pacific slope) hosting several range-restricted bird species (Stattersfield et al. 1998, Birdlife International 2012) and belonging to one of the most diverse regions in terms of faunistic and floristic richness within the tropical region of Central and South America (Hammel et al. 2004, Lobo Segura & Bolaños 2005). So far, more than 300 bird species (including several range-restricted species and subspecies of high conservation value) (Tebb 2008) have been recorded in our study area in vicinity of the Tropical Research Station La Gamba (N 08°42.063',W 083°12.102').

The study area has an annual precipitation of 6,000 mm with a rainfall peak between August and November and lowest precipitation between January and March; the annual mean temperature is 28.5°C (Weissenhofer & Huber 2008). The natural vegetation is mainly represented by tropical lowland wet forest (Weissenhofer et al. 2008). The surroundings of the village "La Gamba", which is located in the centre of our study area, are characterized by pastures with small and elongated forest patches, strips of gallery forests, few big plantations (e.g. oil palm), old (and mostly abandoned) agroforests (cacao) and annual cultures (e.g. rice) (Seaman & Schulze 2010, Höbinger et al. 2012).

Selection of study sites

Study sites represent five different habitat types: pastures with scattered shrubs and small trees (PST), planted young secondary forests (YSFP), naturally regenerated young secondary forests (YSFN), old cacao agroforestry systems (OAF) and naturally regenerated old secondary forests (OSFN) (Table 1). Four replicate sites were selected per habitat type. Sites are located between N 08°41.112'–N 08°43.308' and W 083°11.828'–W 083°12.277' at altitudes between 67-146 m a.s.l. The size of each surveyed habitat patch was bigger than 1.5 ha with homogeneous vegetation and similar biotic characteristics among the habitat categories. The minimum distance between studied sites was 200 m, which is reported to make survey points to be statistically independent (Gutzwiller 1991, Whitman et al. 1998, Barlow et al. 2007a, 2007b, Edwards et al. 2011).

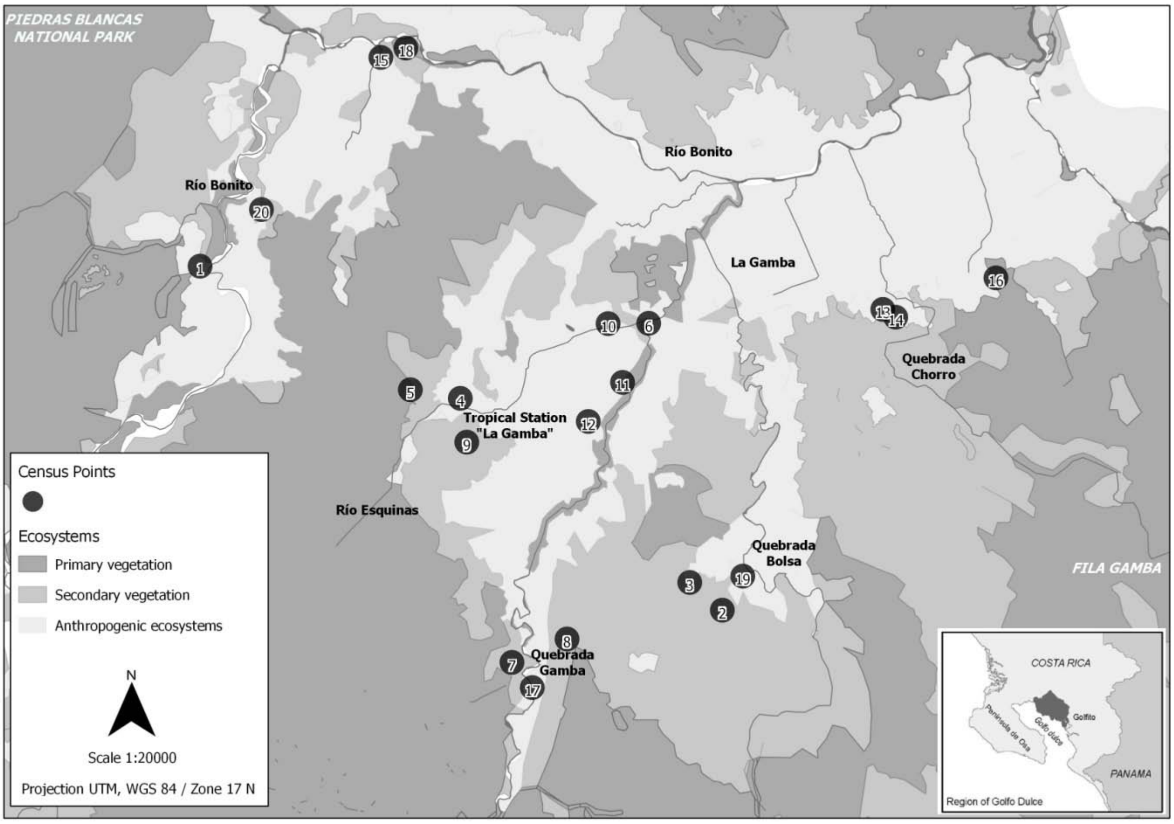


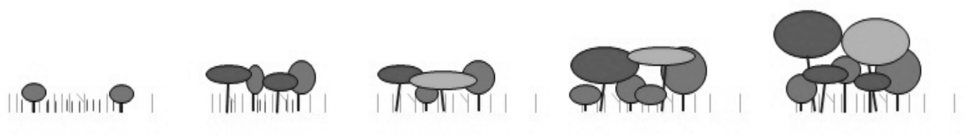
Figure 1. Map of study area indicating census points, and principal ecosystem categories (modified from Weissenhofer et al. 2008). For habitat affiliations of census points compare Table 1.

The census points were all located on private farm areas; some of these areas are part of a forest restoration project developed by the Tropical Research Station "La Gamba" in collaboration with the local community. Other sites were situated on abandoned land once used for agricultural purposes. All sites had a similar distance to areas of old-growth forest (<300 m to forest margin).

Bird survey

The bird survey was conducted between 22 November 2010 and 27 January 2011. Each census point was visited ten times, which should allow for recording a large proportion of the sites' bird species (Ralph et al. 1995). Point counts were conducted for a period of 20 minutes between dawn and 10:00 a.m. The order of surveyed census points was random to avoid sampling bias, that can be caused by a reduction in the bird activity in the course of the day (Blake 1992, Blake & Loiselle 2001). Bird species were recorded visually and acoustically within a radius of 30 m. Unfamiliar bird songs or songs from birds that could not be visually identified (Parker 1991), were recorded by using a Telinga Pro7 Stereo Dat-Microphone and a Foster FR-2 recorder, adjusted to record within the required range. Bird identifications were facilitated using Garrigues & Dean (2007). Recorded bird songs were then identified with the help of Isabell Riedl (University of Vienna), who had two years of experience with bird identification in this region. Additionally the Xeno-canto online-database (http://www.xeno-canto.org/), CD recordings by Ross Jr. & Whitney (1995), Ross Jr. (2000), and Boesman (2006) were used for identification.

Table 1. Habitat classification and detailed description of each habitat type.



Habitat type code	PST	YSFP	YSFN	OAF	OSFN
Habitat classification	Pastures with scattered shrubs and small trees	Young secondary forests: planted	Young secondary forests: natural regeneration	Old agroforestry systems (cacao)	Old secondary forests: natural regeneration
Habitat description	Open land with dense grass cover, ruderal plants and few remnant trees.	Young planted trees with DBH<10 cm, two strata, age: 3-4 years	Young trees with DBH<10 cm, two strata, age: 3-4 years	Closed canopy with complex structure, few tree species.	Closed canopy with complex structure, different tree species.
Census points[1]	4,10,11,17	1,7,13,16	6,12,14,19	2,3,15,20	5,8,9,18

[1] Census point numbers refer to the site codes indicated in Figure 1.

Habitat variables

The vegetation structure was characterized by measuring six variables within a radius of 30 m around census points: density of large trees, density of small trees, maximum tree height, canopy closure, understory density and herb cover. These variables have shown to be important in similar studies (e.g. Thiollay 1999, Barlow et al. 2007b, Abrahamczyk et al. 2008, Reid et al. 2012). Large trees were defined as trees with a diameter at breast height (DBH) bigger than 10 cm. Small trees were defined as trees with a height not larger than 10 m. These two measurements are important to quantify the structural diversity of woody vegetation in secondary forests (Guariguata et al. 1997, Guariguata & Ostertag 2001). Height of the tallest tree was measured with a range finder (Nikon Laser 1200S). To quantify canopy closure a photograph of the canopy was taken directly above the census point. This was then digitalized and processed with a free software photo editor ImageJ 1.44p (Abramoff et al. 2004). The edition started by changing the photos to binary mode in which pixels will have values for black/white colours. Then it is possible to analyze canopy closure in terms of percentage of pixels. Understory density was determined by taking twenty different distance measurements to the nearest tree stem or bush arround the census point above 1.5 m high. The twenty measurements were averaged into a single estimate value; this was done using a laser distance measurement device (Leica DISTO™ D2). Herb cover was estimated as percentage cover, taking into account all herbaceous species, and some low woody plants less than 15 cm tall.

Data analysis

Birds that were observed flying over the census-point, birds without obvious direct habitat affiliation (swifts, swallows), all freshwater birds (ducks, herons, kingfishers, waders etc.), birds with a nocturnal life mode (nightjars, owls) and those bird species associated to open land habitats were not considered in any statistical analysis (Borges & Stouffer 1999, Schulze & Riedl 2008). Nomenclature and taxonomy refer to Gill & Donsker (2012).

Birds were classified according to their habitat affinity as forest specialists (restricted to old-growth forest), forest generalist and open country bird species (Stiles & Skutch 1989, Tebb 2008, Seaman & Schulze 2010, Schulze & Riedl 2008).

Species richness, abundance and species composition of forest specialists and forest generalists was compared between the five habitat types. For each census point, the expected total species richness was calculated using the four most commonly used abundance-based richness estimators: the abundance-based coverage estimator (ACE), Chao1, first-order Jackknife (Jack1) and Michaelis-Menten Mean (MM-Mean). These estimators have been reported to perform well in several studies (e.g. Colwell & Coddington 1994, Chazdon et al. 1998, Gotelli & Colwell 2001, Magurran 2004, Barlow et al. 2007a, 2007b, Arriaga-Weiss et al. 2008, Pejchar et al. 2008, Edwards et al. 2011). All estimates were calculated with EstimateS vers. 8.2 (Colwell 2006) randomizing the order of point counts 100 times. The median of all four estimators was used as a measure for expected total bird species richness. Completeness of inventories was then calculated as the ratio between observed and estimated species. Furthermore species richness and abundance of forest specialists and forest generalists were compared between habitats (e.g. Borges & Stouffer 1999) using analyses of variance (one-way ANOVAs).

Bray-Curtis similarities are found to be a strong and meaningful measure in ecology to determine similarity of species composition between samples (Clarke 1993). We calculated similarity of species composition between census points separately, for forest generalists and forest specialists using square-root transformed abundances. Based on the resulting similarity values, we calculated a non-metric multidimensional scaling (NMDS) ordination visualizing similarity relationships between study sites using the software Primer v. 5.2.9. (Clarke 1993). The NMDS ordinations were accepted as a good representation of the true similarity measures when accompanying stress values were <0.20 (Clarke, 1993). Furthermore analyses of similarities (one-way ANOSIM) with 999 permutations were calculated to test for differences in assemblage composition between habitats (Clarke & Warwick 2001).

To determine how the environmental variables differ between habitat types one-way ANOVAs and subsequent Post-hoc tests (Tukey Honest Significant Difference Tests) were calculated using Statistica for Windows v. 7.1. (StatSoft, Inc. 2005). When variables deviated from a normal distribution, adequate data transformations were applied. To identify relationships between forest generalist as well as, forest specialist birds and the habitat variables; Pearson correlations were calculated. Afterwards, False Discovery Rate (FDR) transformations were applied to correct for bias caused by multiple testing (Pike 2011). FDR procedures provide a mechanism to avoid the rejection of those truly significant comparisons on a data set (Pike 2011).

Results

Species richness of forest birds

The completeness of species inventories did not differ between habitat types (one-way ANOVA: $F_{4,15}$ = 0.40, p = 0.808). Therefore, the absolute species numbers were used instead of richness estimates in all further analyses.

A total of 115 forest bird species were recorded during the point counts, including 61 forest generalist and 54 forest specialist species (for details see Appendix 1). While species richness of forest specialists was affected significantly by habitat type (one-way ANOVA: $F_{4,15}$ = 7.92, p = 0.001), no effects were found for forest generalists ($F_{4,15}$ = 0.63, p = 0.649). Also abundance of forest specialists differed significantly between habitat types (one-way ANOVA: $F_{4,15}$ = 4.69, p = 0.011), while again no difference was detected for forest generalists ($F_{4,15}$ = 0.58, p = 0.643). The mean number of forest specialist bird species was approximately four times higher at OSFN than PST. All other habitat types were characterized by intermediate species richness of forest specialists (Figure 2a). A similar pattern was found for the abundance of forest specialists (Figure 2c). Species richness and abundance of forest generalists did not prominently differ between the five studied habitat types (Figure 2b and 2d, respectively).

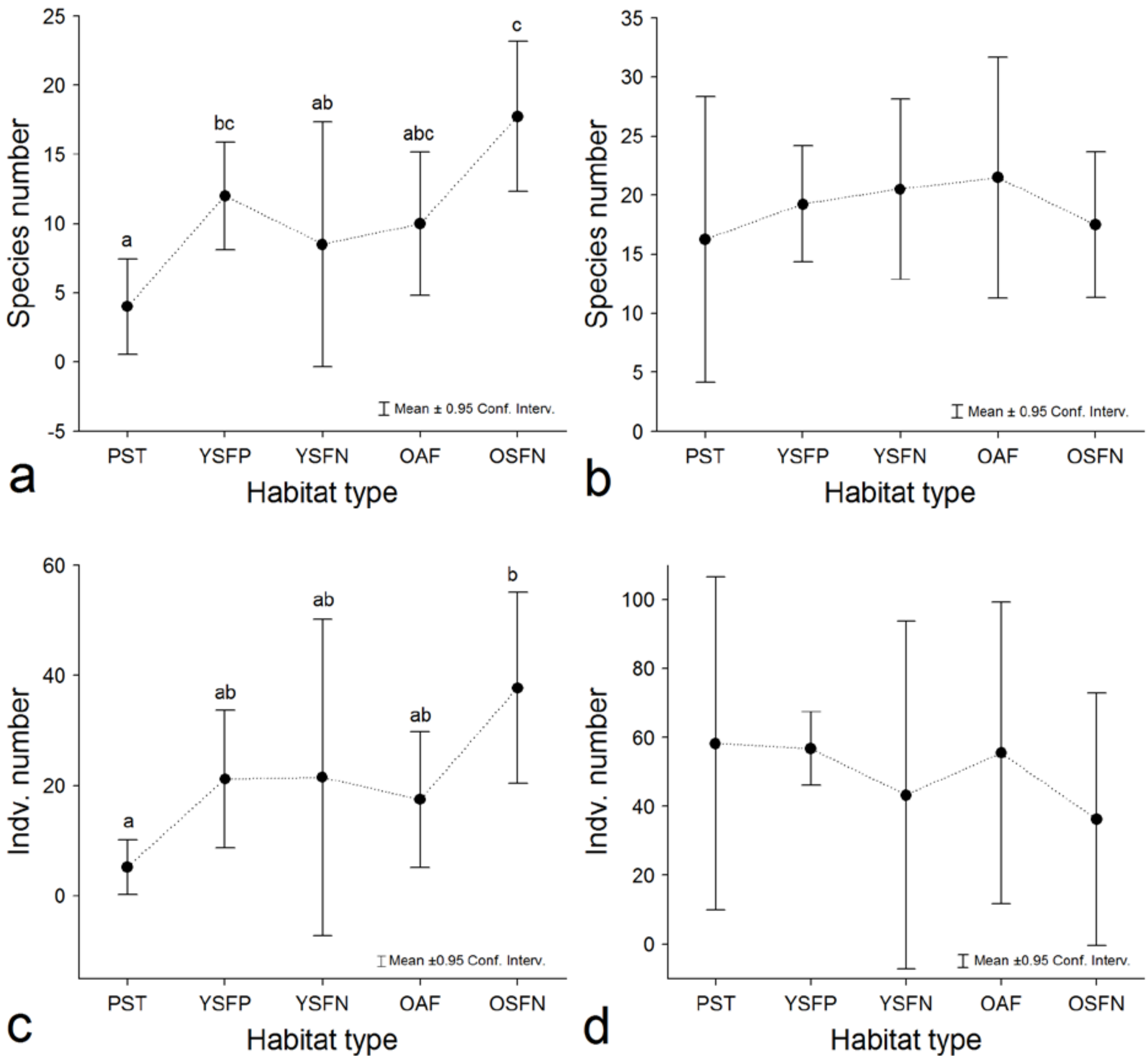


Figure 2. Mean species richness per census point of (a) forest specialist and (b) forest generalist bird species and mean abundance of (c) forest specialist and (d) forest generalist bird species in different habitat types. Habitat types: PST – Pastures with scattered shrubs and small trees, YSFP – planted young secondary forests, YSFN – naturally regenerated young secondary forests, OAF – old agroforestry systems, OSFN – naturally regenerated old secondary forests. Different letters indicate significant differences (p < 0.05; Tukey Honest Significant Difference Test).

Vegetation structure of habitat types

All one-way ANOVAs testing for differences of habitat variables between habitat types still achieved a significant level after FDR corrections (FDR adjusted p<0.05). However, the most prominent differences were found for the density of large trees and the understory density (Table 2). The highest density of large trees was found at OSFN sites, the highest understorey density was estimated at PST sites. The number of small trees was highest at YSFP sites, but only differed significantly between YSFP and PST sites. The maximal tree height and canopy closure were highest at OSFN sites, which, however, only differed significantly from PST sites (Table 2).

Table 2. Means ± SD of herb cover (arcsin√x transformed), max. tree height, number of large trees (DBH >10 cm), understory density (log(x) transformed) and the number of small trees (height <10 m) (log (x+1) transformed) in the five surveyed habitat types (for habitat codes see Table 1) and results of one-way ANOVAs. Different letters following values indicate significant differences between means (Tukeys Honest Significant Difference Test). Habitat variables are printed bold when ANOVA results remained significant after adjusted for False discovery rate.

Habitat variables	*Means ± SD for all habitat types*					*ANOVA results $F_{4,15}$ /P*	*FDR-adjusted P-values*
	PST	*YSFP*	*YSFN*	*OAF*	*OSFN*		
Herb cover	1.45±0.23[a]	1.04±0.24[ab]	1.01±0.30[ab]	0.90±0.27[b]	0.84±0.10[b]	4.10/0.019	**0.029**
Max. tree height	12.75±8.99[a]	21.25±2.5[ab]	22.00±6.16[ab]	25.00±4.08[ab]	26.25±4.35[b]	3.47/0.034	**0.034**
Large trees	2.25±1.71[a]	12.75±2.63[b]	8.75±6.75[ab]	9.50±1.91[ab]	20.75±6.85[bc]	8.58/<0.001	**0.002**
Understory density	3.09±0.10[a]	1.44±0.28[b]	1.59±0.68[b]	1.75±0.28[b]	1.41±0.36[b]	13.02/<0.001	**0.001**
Small trees	1.46±1.24[a]	3.47±0.76[b]	2.45±0.29[ab]	2.69±0.53[ab]	2.56±0.63[ab]	3.60/0.030	**0.034**
Canopy closure	0.17±0.23[a]	1.03±0.34[b]	0.62±0.38[ab]	0.73±0.26[ab]	0.92±0.30[b]	4.66/0.012	**0.024**

Effect of habitat variables on richness of forest birds

Richness of forest specialists was most strongly related to the number of large trees. The number of specialist species increased significantly with the increasing number of large trees (Figure 3, Appendix 2). Other variables were only weakly (herb cover, maximum tree height, canopy closure, understory density) or not significantly related to the richness of forest specialists after applying FDR correction (Figure 3, Appendix 2). Variance in species numbers of forest generalists was only weakly positively related to the maximum tree height and the density of small trees (Figure 3, Appendix 2).

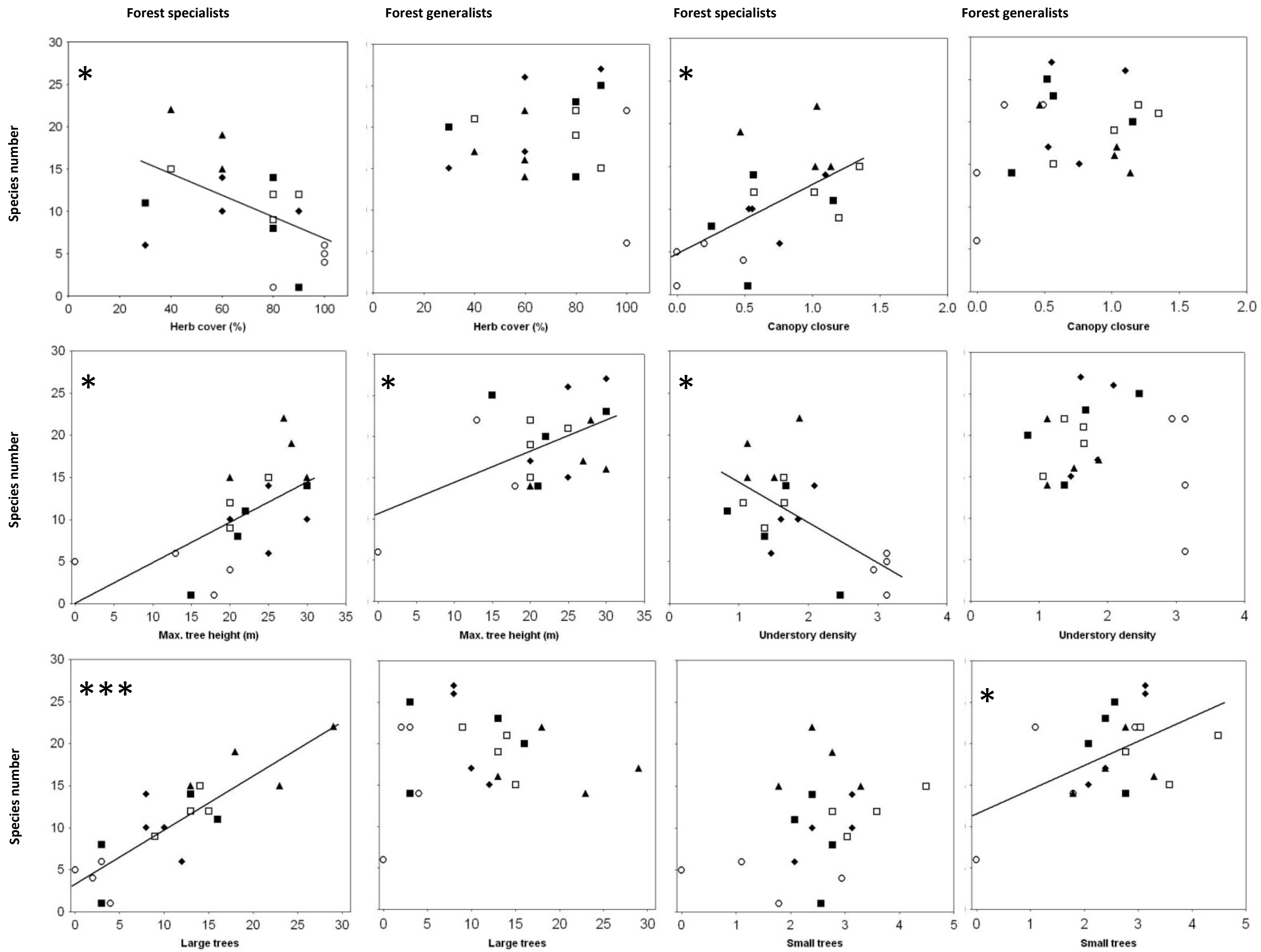


Figure 3. Relationships between species richness of forest specialists and generalists at census points and habitat variables. Different symbols indicate the habitat types: PST – Pastures with scattered shrubs and small trees (empty circles), YSFP – planted young secondary forests (empty squares), YSFN – naturally regenerated young secondary forests (filled squares), OAF – old agroforestry systems (diamonds) and OSFN – naturally regenerated old secondary forests (triangles). Asterisks indicate relationships which remain significant after FDR corrections (* p<0.05, ** p<0.01, *** p<0.001)

Species composition

Species composition differed significantly between habitat types in forest specialists (one-way ANOSIM: global *R* = 0.327, *p* = 0.002), but not in forest generalists (one-way ANOSIM: global *R* = 0.085, *p* = 0.113). Subsequently calculated pairwise tests show that species composition of forest specialists at PST sites differed significantly from all other habitat types. All other pairwise tests did not indicate significante differences except the comparison between OSFN and YSFN sites (Table 3).

Table 3. Results of one-way ANOSIMs testing for differences in species composition of forest specialists between habitat types. Values in bold indicate significant differences.

Pairwise tests	One-way ANOSIM	
	R	***P***
YSFP vs. OAF	0.031	0.457
YSFP vs. PST	**0.698**	**0.029**
YSFP vs. OSFN	0.115	0.229
YSFP vs. YSFN	0.021	0.4
OAF vs. PST	**0.443**	**0.029**
OAF vs. OSFN	0.146	0.286
OAF vs. YSFN	-0.063	0.571
PST vs. OSFN	**1**	**0.029**
PST vs. YSFN	**0.448**	**0.029**
OSFN vs. YSFN	**0.26**	**0.029**

Similar conclusions can be drawn from the NMDS ordinations for forest specialists and forest generalists. While for forest specialists the PST sites and the OSFN sites segregate in the left and right half of the graph, respectively, and all other sites are situated in between (Figure 4a), the NMDS plot for forest generalists shows a high overlap of habitats (Figure 4b). However, in both NMDS ordinations the dimension 1 obviously reflects our gradient of forest sucession. While the dimension 2 values of the NMDS ordinations calculated for forest specialists and forest generalists were not related to any of the measured habitat variables, dimension 1 values of both NMDS ordinations were significantly correlated with all habitat variables except of the number of small trees (Table 4).

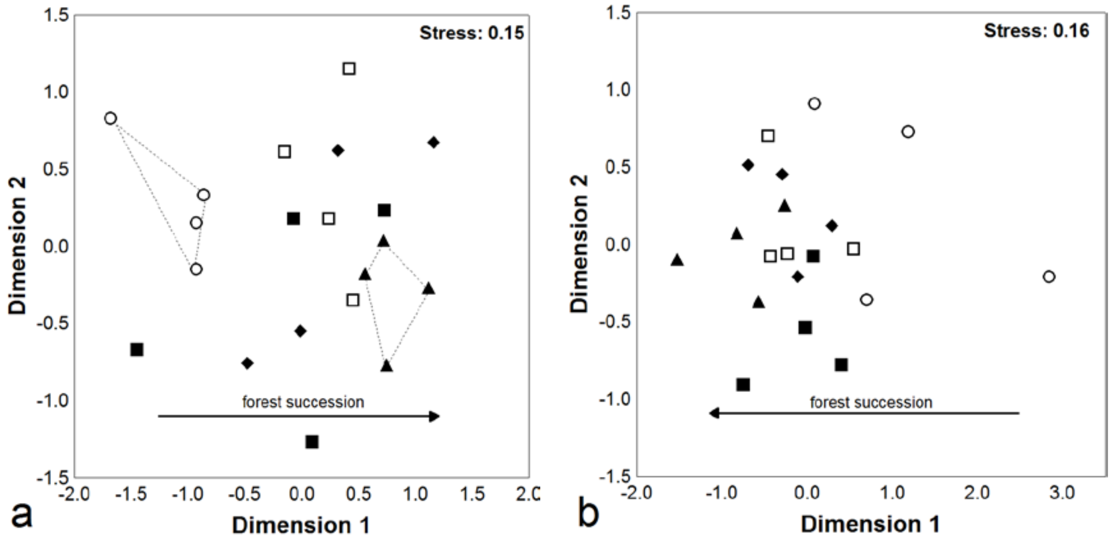


Figure 4. Non-metric multidimensional scaling plots vizualising similarity relationships in species composition of (a) forest specialists and (b) forest generalists surveyed at census points in different habitats. Similarity of species composition was quantified by Bray-Curtis similarities using √x-transformed abundances. Habitat types are indicated by different symbols: circles (PST), empty squares (YSFP), filled squares (YSFN), diamonds (OAF), triangles (OSFN).

Table 4. Shows the results of correlations between Dimension 1 values extracted from the NMDS ordination (Figure 4) and habitat variables.

	Forest specialists		***Forest generalists***	
Habitat variables	***R***	***FDR adjusted P***	***R***	***FDR adjusted P***
Herb cover	**-0.6875**	**0.002**	**0.6749**	**0.002**
Max. tree height (m)	**0.6136**	**0.005**	**-0.6621**	**0.002**
Large trees	**0.6968**	**0.002**	**-0.6388**	**0.002**
Understory density	**-0.7498**	**<0.001**	**0.7109**	**<0.001**
Small trees	0.3258	0.161	-0.4280	0.060
Canopy closure	**0.6392**	**0.003**	**-0.7076**	**<0.001**

Discussion

The importance of forests formed by actively and passive restoration

Specialized birds are recommended as references for the identification of conservation priorities (Stotz et al. 1996). Many tropical forest birds can be classified as habitat specialists with a low capability to adapt to human modified habitats (Turner 1996, Estrada et al. 1997, Brooks et al. 1999, Thiollay 1999, Beier et al. 2002, Watson et al. 2004). At the OSFN sites in total 46% of all forest specialist bird species recorded during our point counts were found. In contrast, only 23%, 26% and

30% of these species were found at YSFN, OAF and YSFP, respectively. The lowest proportion (11 %) of forest specialist species was found at PST sites. That the most striking difference in species richness and abundance of forest specialists was found between the extrems of the successional gradient with most forest specialists observed at OSFN and lowest numbers counted at PST sites was not surprising. Also other studies reported that the least disturbed habitats tend to show the greatest species richness of forest birds (Estrada et al. 1997, Petit & Petit 2003); in our case represented by the OSFN. That no differences in species richness and composition were found between passively and actively restored secondary forests, at least after less than 4 years of succession represents one of the key results of our study. A very similar result was reported by a study conducted at a forest restoration site at Las Cruces Biological Station (Southern Costa Rica) at an altitude of 1,100 m a.s.l. (Reid et al. 2012).

The distance of all census points to old-growth forest was very similar (<300 m) in our study. However, the gaps between surveyed secondary forest patches and the source area for forest birds, the old-growth forest, could have been a significant barrier for several forest specialists. Particularly many tropical understorey birds only rarely cross clearings of more than 250 m width (Laurance & Gomez 2005), some of them even are not capable of crossing road of ca. 30 m in width (Laurance et al. 2009).

Relevant habitat structures for forest birds

While within a homogeneous forest area, plant composition has the strongest effect on bird communities, vegetation structure predominantely influences birds among or between different habitats, e.g. forests sites in a different successional stage (Jayapal et al. 2009, Reid et al. 2012). This is also emphasized by our study, which did not show prominent differences in species richness and composition of forest specialists between OAF, YSFN and YSFP. Although the three highly disturbed forest types are certainly characterized by a different tree species composition, they are characterized by a similar vegetation structure. Only the extremes, PST and OSFN, differed prominently in richness of forest specialists and were characterized by a distinct composition of assemblages of species belonging to this group of forest-dependent birds. Assemblages of forest generalists did not show any clear differences between habitats.

Some studies highlighted canopy closure and structural complexity (i. e. number of vegetation layers) of secondary vegetation as important determinants for the species richness and the composition of tropical forest birds (Blake & Loiselle 2001, George & Zack 2001, Dunn 2004, Barlow 2007b, Borges

2007). The number of large trees contributing to the vertical complexity of secondary forests and the canopy closure seemed to influence the species richness of specialist birds also at our study sites. However, the effect of the number of large trees appeared to have a particularly important role for the occurrence of forest specialist bird species (but not forest generalists). The value of large trees as key structural element for many forest birds in providing breeding niches and food resources has been already emphasized by other studies (Sodhi et al. 2005, Van Bael et al. 2007, Abrahamczyk et al. 2008). The presence of individual large trees in plantations as well as patches or strips (living fenches) of large trees can strongly contribute to the faunal and floral recovery in human-dominated landscapes (Guariguata et al. 1995, Parrotta 1995), as seeds of some primary forest plant species, most likely dispersed by forest birds, have been reported to germinate even in open tree pastures (Harvey & Haber 1998). Despite the presence of large trees, only those birds that require living trees may have a chance to colonize secondary forests, because especially young ones are still lacking standing dead trees or snags (Dewalt et al. 2003). Therefore, the relatively low density of large trees might be one important factor limiting the conservation value of young secondary forest for forest birds. Only secondary forests older than 70 years will have trees large enough (i. e. DBH ≥65cm) for some specialists with sedentary lifestyles and a preference for mature forests (Stratford & Stouffer 1999, DeWalt et al. 2003).

However, although early stages of forest succession may not be appropiate breeding habitats for many forest specialist (Mac Arthur & Mac Arthur 1961, Bowen et al. 2007), at least some of them may infrequently use various resources provided by this forest type, when situated close to the margin of old-growth forest. For example at PST sites, 8 forest specialist species were reported. Most of these being omnivorous (i.e. *Attila spadiceus*, *Cyanocompsa cyanoides*, *Euphonia imitans*, *Ornithion semiflavum* and *Ramphastos swainsonii*), but also including one insectivore (*Pachyramphus aglaiae*), one granivorous (*Leptotila cassini*) and one frugivore species (*Penelope purpurascens*). The presence of such forest specialist bird species at PST sites can be explain by the presence of single larger remnant trees (Guevara et al. 1986). Furthermore, to the dense herbaceous vegetation layer can provide cover to smaller birds feeding on the larger number of arthropods of the dense herb/understory layer (Pejchar et al. 2008). Such scattered large trees are considered to be keystone structures in human-modified areas, offering benefits to forest birds, not only at a landscape level (e.g. connectivity) but also locally (e.g. structural complexity, nesting) (Manning et al. 2006).

Importance of secondary habitats as corridors for the conservation of forest birds

Although supporting predominantly generalists (Brook et al. 2003) and probably acting as reproductive “sinks” for some forest species (Aubrecht & Schulze 2008, Peh et al. 2005, Battin 2004), the total of 115 species of forest-depending birds (with 47 % classified as forest specialists) recorded in the secondary forests of our study area indicates a certain conservation value of these habitat type. Furthermore, the conservation value of secondary forest sites is emphasized by our records of several range-restricted forest species such the Charming Hummingbird (*Amazilia decora)*, Baird’s Trogon (*Trogon bairdii*), Blackhooded Antshrike (*Thamnophilus bridgesi*), Riverside Wren (*Cantorchilus semibadius*), Black-cheeked Ant- Tanager (*Habia atrimaxillaris*) and Spot-crowned Euphonia (*Euphonia imitans*) and the near threatened forest specialist species *Vermivora chrysoptera*. Therefore, we are convinced that secondary forests have a high potential to improve connectivity between remaining areas of old-growth forests in our study area. Furthermore, they may increase the habitat quality for forest birds in the buffer zone adjacent to the margin of primary forest (Fisher et al. 2006). At a regional level, they may even lead to an increase in species richness (Graham & Blake 2001, Hughes et al. 2002).

Conclusions and recommendations

The most important areas to be conserved are the old secondary forests where the highest species richness of forest specialists was observed. Our results also demonstrate that beside old agroforestry systems even young secondary forests created by active and passive forest regeneration are characterized by high species richness of forest specialist birds and therefore may play an important role in the development of biological corridors. Considering the close relationship between the number of large trees and the richness of forest specialists, further research has to evaluate the potential of using fast-growing trees to more rapidly increase the conservation value of actively restored secondary forests for forest birds. Potential candidate trees could be fast-growing native species such as *Terminalia amazonia* (Combretaceae) and *Vitex cooperi* (Verbenaceae) (Lechner et al. 2012).

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Appendix

Appendix 1. Total number of forest bird species recorded during point counts in the five different habitat types: Pastures with scattered shrubs and small trees (PST), planted young secondary forests (YSFP), naturally regenerated young secondary forests (YSFN), old cacao agroforestry systems (OAF) and naturally regenerated old secondary forests (OSFN). Affiliation to forest: forest specialists (1) and forest generalists (2) Guild codes: omnivores (O), granivores (G), frugivores (F), nectarivores (N), insectivores (I), predators (P) or scavengers (S). IUCN (2012) IUCN status code: endangered (EN), near threatened (NT), least concern (LC)

Family	Species Name	PST	YSFP	YSFN	OAF	OSFN	Forest affiliation	Feeding Guild	IUCN Status 2012	Total
Accipitridae	*Leptodon cayanensis*					1	2	N	LC	1
	Spizaetus tyrannus				1		2	N	LC	1
Cardinalidae	*Cyanocompsa cyanoides*	2			1		2	F	LC	3
	Saltator maximus	4	11	5	5	7	2	I	LC	32
	Saltator striatipectus	4	1		1	1	2	O	LC	7
Cathartidae	*Cathartes aura*	19		1			1	O	LC	20
Coerebidae	*Coereba flaveola*	3	6	8	5	12	2	O	LC	34
Columbidae	*Claravis pretiosa*	34	14	12	6	11	1	O	LC	77
	Geotrygon montana			5	6		1	P	LC	11
	Leptotila cassini	5	3	1	3		1	O	LC	12
	Leptotila verreauxi	8	17	27	20	18	2	I	LC	90
	Patagioenas nigrirostris		6	3	14	11	1	I	LC	34
Corvidae	*Cyanocorax morio*			3			2	O	LC	3
Cracidae	*Ortalis cinereiceps*	14	4			1	2	S	LC	19
	Penelope purpurascens	1	1				1	I	LC	2
Cuculidae	*Piaya cayana*		2	4			2	O	LC	6
Emberizidae	*Arremon aurantiirostris*		3	4	1	4	2	O	LC	12
	Arremonops conirostris	6	7	11	7	3	1	O	LC	34
Falconidae	*Herpetotheres cachinnans*	5	4	4	2	4	1	O	LC	19
	Micrastur semitorquatus					1	1	O	LC	1
Formicariidae	*Formicarius analis*				1	5	2	O	LC	6
Fringillidae	*Euphonia elegantissima*				1		2	O	LC	1
	Euphonia imitans	3	5	5	1	2	1	I	NT	16
	Euphonia laniirostris		1		3	1	1	P	LC	5
Furnariidae	*Automolus ochrolaemus*		1			2	2	I	LC	3
	Deconychura longicauda		2	1	3	5	2	I	LC	11
	Dendrocincla anabatina			1	1	1	2	I	LC	3
	Glyphorhynchus spirurus		5	2	1	2	2	O	LC	10
	Xiphorhynchus lachrymosus					1	2	I	LC	1
	Xiphorhynchus sussurans		3	1		6	2	I	LC	10

Appendix 1 - continued										
Family	**Species Name**	**PST**	**YSFP**	**YSFN**	**OAF**	**OSFN**	**Forest affiliation**	**Feeding Guild**	**IUCN Status 2012**	**Total**
Galbulidae	*Galbula ruficauda*					2	1	F	LC	2
Icteridae	*Amblycercus holosericeus*	1	1		2	1	1	O	LC	5
	Cacicus uropygialis		3		1	3	2	O	LC	7
	Icterus galbula	1	1	1	1		2	N	LC	4
	Molothrus oryzivorus			1			1	I	LC	1
	Psarocolius decumanus		1				1	I	LC	1
Momotidae	*Momotus momota*			1			1	G	LC	1
Parulidae	*Dendroica pensylvanica*	2	12	10	15	30	1	I	LC	69
	Dendroica petechia	3		1			1	O	EN	4
	Mniotila varia				1	1	2	N	LC	2
	Oporornis philadelphia		1				2	P	LC	1
	Oreothlypis peregrina		1		2		1	O	LC	3
	Phaeothlypis fulvicauda					1	2	O	LC	1
	Seiurus noveborancensis	1		3	1	1	1	O	LC	6
	Setophaga ruticilla			1			2	O	LC	1
	Vermivora chrysoptera		1				1	P	LC	1
	Wilsonia pusilla	1		1	1		1	G	LC	3
Picidae	*Dryocopus lineatus*	4	3		2		2	G	LC	9
	Melanerpes rubricapillus	9	7	4	4	7	1	O	LC	31
	Piculux simplex		1	1		2	2	O	LC	4
	Veniliornis kirkii				1	1	2	O	LC	2
Pipridae	*Manacus aurantiacus*		16	12	2	12	1	P	LC	42
	Pipra mentalis		2	2	1		1	I	LC	5
Polioptilidae	*Polioptila plumbea*					1	2	O	LC	1
Psittacidae	*Amazona autumnalis*		1	2		1	2	I	LC	4
	Pionopsitta haematotis					2	2	O	LC	2
	Pionus senilis				1		1	O	LC	1
Rallidae	*Aramides cajanea*	1		3			1	I	LC	4
Ramphastidae	*Ramphastos swainsonii*	3	5	15	8	9	2	O	LC	40
Thamnophilidae	*Cercomacra tyrannina*					1	2	O	LC	1
	Microrhopias quixensis		3	2		3	1	I	LC	8
	Myrmeciza exsul		2			10	2	I	LC	12
	Taraba major			1			2	I	LC	1
	Thamnophilus bridgesi		2		3	9	2	O	LC	14
	Thamnophilus doliatus				1		2	O	LC	1
Thraupidae	*Cyanerpes lucidus*					2	1	O	LC	2
	Dacnis venusta					1	2	F	LC	1
	Habia atrimaxillaris			2		1	1	O	LC	3
	Piranga rubra			4	7		2	O	LC	11
	Ramphocelus costaricensis	33	48	58	41	14	1	F	LC	194

Appendix 1 - continued

Family	Species Name	PST	YSFP	YSFN	OAF	OSFN	Forest affiliation	Feeding Guild	IUCN Status 2012	Total
Thraupidae	*Sporophila americana*	29	11	12	10	5	1	F	LC	67
	Tachyphonus luctuosus		1		1		2	N	LC	2
	Tangara gyrola			2			1	I	LC	2
	Tangara larvata	4	12	12	5	5	1	N	LC	38
Tinamidae	*Crypturellus soui*					7	2	N	LC	7
	Tinamus major					1	2	I	LC	1
Tityridae	*Myiobius sulphureipygius*			1	1	1	1	I	LC	3
	Onychorhynchus coronatus		1	1		1	1	F	LC	3
	Pachyramphus aglaiae	3	1		2	1	2	F	LC	7
	Pachyramphus polychopterus	1					1	F	LC	1
	Tityra inquisitor				1		2	O	LC	1
Trochilidae	*Amazilia decora*	1	7	3	4	4	2	I	LC	19
	Amazilia tzacatl	3	14	21	14	7	1	I	LC	59
	Florisuga mellivora			1	1		2	O	LC	2
	Heliothryx barroti			1		1	1	O	LC	2
	Phaeochroa cuvierii				1	1	2	O	LC	2
	Phaethornis longirostris		1	1	3	2	1	O	LC	7
	Phaethornis striigularis	1	3	4	8	28	2	O	LC	44
	Thalurania colombica					1	2	O	LC	1
	Threnetes ruckeri		1	2	4	1	2	O	LC	8
Troglodytidae	*Cantorchilus semibadius*		4	18		23	2	I	LC	45
	Thryothorus fasciatoventris		2	1	3	2	2	P	LC	8
Trogonidae	*Trogon bairdii*				1	1	2	O	LC	2
	Trogon rufus		1	2		1	1	O	LC	4
	Trogon violaceus				1		1	O	LC	1
Turdidae	*Turdus assimilis*					1	2	O	LC	1
Tyrannidae	*Attila spadiceus*	1	3	1	4	8	2	I	LC	17
	Camptostoma obsoletum			1			1	N	LC	1
	Capsiempis flaveola		1	2	1		1	I	LC	4
	Empidonax alnorum/Empidonax trailii	3	2		3	1	2	I	LC	9
	Empidonax flaviventris	5	3	2	7	3	1	N	LC	20
	Empidonax minimus	4	1		2		1	I	LC	7
	Megarhynchus pitangua	15	2	3	2	7	1	O	NT	29
	Mionecetes oleagineus		4	9	5		2	O	LC	18
	Myiodynastes luteiventris	2		2			2	I	LC	4
	Myiozetetes granadensis	9	5	6	8	2	1	O	NT	30
	Oncostoma cinereigulare					2	1	O	LC	2
	Ornithion semiflavum	3	4		1	1	1	O	LC	9
	Poecilotriccus sylvia		7	2	4	8	2	O	LC	21
	Rhytipterna holerythra		1				1	I	LC	1

Appendix 1 - continued											
Family	**Species Name**	**PST**	**YSFP**	**YSFN**	**OAF**	**OSFN**	**Forest affiliation**	**Feeding Guild**	**IUCN Status 2012**	**Total**
Tyrannidae	*Todirostrum cinereum*	3	9	7	17	12	1	I	NT	48
	Zimmerius vilissimus		2	1		1	2	I	LC	4
Vireonidae	*Hylophilus decurtatus*		2				1	I	LC	2
	Hylophilus flavipes	1		1	1		1	I	LC	3
	Hylophilus ochraceiceps					1	2	O	LC	1
Total		**255**	**312**	**342**	**293**	**354**				**1556**

Appendix 2. Results of Pearson correlations between habitat variables and species richness of forest specialists and forest generalists. Results printed in bold remained significant after calculating the False Discovery Rate.

Group of bird species	***Forest specialists***			***Forest generalists***		
Habitat variables	***R***	***P***	***FDR-adjusted p-values***	***R***	***P***	***FDR-adjusted p-values***
Herb cover	-0.55	0.011	**0.023**	-0.01	0.953	0.953
Maximal tree height	0.60	0.005	**0.014**	0.51	0.022	**0.038**
Large trees	0.85	<0.001	**<0.001**	-0.02	0.942	0.953
Understory density	-0.61	0.004	**0.014**	-0.09	0.699	0.787
Small trees	0.37	0.104	0.143	0.50	0.023	**0.038**
Canopy closure	0.59	0.006	**0.014**	0.30	0.196	0.252

LEBENSLAUF

Persönliche Daten

Zuname	**REYES PAEZ**
Vorname	**Andrés Felipe**
Akademischer Grad	**B. Sc. in Biologie**
Adresse	**Andergasse 38/30** **1170 WIEN**
Telefon	**+43 681 10707297**
E-Mail	**andres.reyes@gmx.at**
Geburtsdatum	**17. Juli 1983**
Geburtsort	**Bogotá, KOLUMBIEN**

Studienverlauf

2009 – 2013

Masterstudium: Naturschutz und Biodiversitätsmanagement — Universität Wien, Wien, Österreich

Studienschwerpunkte:
- Tierökologie
- Vegetationsökolgie
- Naturschutzbiologie
- Biodiversitätsmanagement
- Landschaftsökologie

2002- 2007

Bachelor in Biologie — Universidad Militar Nueva Granada, Bogotá, Kolumbien

Studienschwerpunkte:
- Zoologie und Vegetationsökologie

- Umwelt- und Naturschutz
- Angewandte Ökologie
- Biodiversität der Tiere
- Agrarwissenschaft: biologische Schädlingsbekämpfung

Bachelorarbeit: Effizienz der Raubmilbe *Amblyseius* sp. für die biologische Bekämpfung von *Tetranychus urticae* (Acari: Tetranychidae) im kommerziellen Rosenanbau.

Schulbildung

1989- 2002	**Hochschulabschluss** — Saint George´s School, Academic School, Bogotá, Kolumbien
1994-1995	**Auslandsschuljahr**: 5. Klasse Abschluss — Marshall Road Elementary School, Fairfax, Virginia, USA

Berufserfahrung und Praktika

2010	**Praktikant**: Nationalpark Hohe Tauern- Matrei in Osttirol, Österreich. Projekt: *Bewertung des Auerwildlebensraumes am „Kleinen Zunig" nach einem Habitat Suitable Index Modell.*
2010	**Feldarbeit für Masterarbeit**: Tropenstation La Gamba, Tres Esquinas, Costa Rica.
2006	**Praktikant**: Universidad Militar Nueva Granada, Bogotá, Kolumbien. Feldarbeit: Bestimmung, Erfassung und Markierung von Fledermäusen in den zentralen Anden Kolumbiens.
2005	**Praktikant**: Universidad Militar Nueva Granada, Bogotá, Kolumbien. Projekt: ***Pflanzen*** *Präferenzen der Familie Gelechiidae Motten um die Entwicklung einer künstlichen Züchtung.*
2003	**Praktikant**: Universidad Militar Nueva Granada, Bogotá, Kolumbien. Projekt: *Wirkung von verschiedenen Konzentrationen von Koffein auf die terrestrischen Mollusken.*

Weitere Qualifikationen

Fremdsprachenkenntnisse

Spanisch	Muttersprache
Englisch	Wort und Schrift (TOEFL iBT:93)

Deutsch	Wort und Schrift (Universitätslehrgang Vorstudienlehrgang, Deutsch, Universität Wien B2)
Französisch	Basis Wort und Schrift (DELF1)

<u>Zusätzliche Kenntnisse</u>

Computerkenntnisse	PC, Microsoft Office, ArcGIS, Statistika, EstimateS, Primer

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Wissenschaftliche Tätigkeiten

<u>Teilnahmen an wissenschaftlichen Konferenzen</u>

2011	**Workshop** für zukünftige Strategien in Österreich für GSPC.
2011	**Tagung**: “Nachhaltige Entwicklung, Ökosystemleistungen und Biodiversität”
2006	**Treffen**: “XLVI Annual Meeting American Phytopathological Society Caribbean Division”.
2006	**Treffen**:“XXVII Annual Meeting – ASCOLFI”
2006	**Workshop**: III Universidad Militar Nueva Granada – Phytopathology International.

<u>Wissenschaftliche Konferenzen mit eigenem Beitrag</u>

2011	**-Vortrag-** **Workshop**: österreichische Tropenforschung - Wissenschaft an der Tropenstation La Gamba. Thema: Die Vielfalt der Vogelwelt in Sekundärwälder der Wert von biologischen Korridoren.
2005	**-Poster-** **Tagung**: “Asociación Colombiana de Entomologia- SOCOLEN” Thema: Effizienz der Prädator Milbe *Amblyseius sp*. für die biologische Bekämpfung von *Tetranychus urticae* (Acari: Tetranychidae) im kommerziellen Rosenanbau.

ANDRES FELIPE REYES PAEZ