THE EFECTIVENESS OF TROPICAL CLOUD FOREST RESTORATION ON BIRD COMMUNITY AT CLOUDBRIDGE NATURE RESERVE, COSTA RICA

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KEY WORDS

Reforestation, land-use change, forest restoration, bird community, landscape composition

INTRODUCTION

All around the world, forest and woodland vegetation have been removed and replaced by agricultural lands, leading to habitat loss and fragmentation (Foley et al. 2005), and decreased biodiversity (Fahrig 2003). In the tropics, more than 7 million hectares of forest were lost between 2000 and 2005, mainly because of land conversion from forest to pastures (FAO 2005). This phenomenon is still a major threat to Neotropical montane cloud forests (Brown et al. 2001). Cloud forests, characterized by a persistent, frequent or seasonal low-level cloud cover usually at the canopy level, represent a habitat of ecological importance for avian conservation, as they maintain a large number of endemic and threatened resident bird species, and provide wintering habitat for many migratory species. In particular, the highlands of Costa Rica and Panama are recognized as an Endemic Bird Area, which is an area where the distributions of two or more restricted-range bird species (breeding range smaller than 50,000 km²) overlap (BirdLife International 2003). Many forest bird species could not survive outside of forest in Costa Rica (Daily et al. 2001). It is therefore important to preserve and restore montane cloud forests in order to enhance biodiversity and protect endemic species associated with this unique habitat. Birds are considered good indicators of habitat change (Bradshaw et al. 2002). Along with biodiversity loss, land-use change has also caused shifts in the guild composition of bird communities. It has reduced the amount of frugivores, nectarivores and insectivores in favor of herbivores (Newbold et al. 2014). Bird species which are large-bodied, sedentary, forest specialists with long generation times, small ranges, small population sizes, and diets of fruit, nectar and invertebrates have been shown to be the most threatened by land-use change (Newbold et al. 2013 ; Barbaro and Van Halder 2009).

Enhancing secondary growth permits the reconnection of forest fragments, allowing forest specialist birds to persist (Stouffer *et al.* 2006). Active restoration, by planting native tree seedlings, is expanding globally and contributes to the reduction of net loss of forest area in several countries (FAO 2005). This conservation strategy could allow the recovery of the Neotropical montane forest landscape matrix over time (Wijdeven and Kuzee 2000 ; Kappelle and Juárez 2006). In the tropics, the main limitation for secondary succession in abandoned pastures is seed availability

(Martínez-Garza and Howe 2003 ; Wijdeven and Kuzee 2000). Indeed, abandoned pastures lack seed banks of forest species (Wijdeven and Kuzee 2000). Animals (birds in particular), as pollinators, seed dispersers and consumers of herbivorous insects (Greenberg *et al.* 2000 ; Van Bael *et al.* 2007 ; Sekercioglu 2006), contribute greatly to forest regeneration. Planting tree seedlings could increase seed dispersal by animals (Lamb *et al.* 2005). It is therefore essential for the long-term success of forest restoration to restore bird communities as well, in order to reestablish the interactions between animals and their environment.

Several studies found that restored forest can constitute habitat for birds, but the success of forest-dependent bird community recovery depends on the structure of the restored forest, plant species composition and age (Munro *et al.* 2011). Indeed, bird community composition depends on canopy cover, structure and species composition of the forest, which are linked to the tree species planted and the age of the forest. Ten years after forest restoration, reforested patches have been shown to recover about 50% of the species found in adjacent forest remnants (Smith *et al.* 2015). Munro *et al.* (2011) found that it takes about 30 years for restored forests to have similar bird communities as the adjacent forest remnants. But the mechanisms driving species assemblage observed at the patch scale might be influenced by factors at the landscape scale and the connectivity between patches (Fahrig 2003; Morrison *et al.* 2010). In fact, landscape effects might contribute more to species assemblage than do fragment size effects (Fahrig 2003). Some authors suggest that the relative importance of habitat factors versus landscape factors change depending on the stage of vegetation succession (Gould and Mackey 2015). However, to my knowledge, little is known about the mechanisms driving birds species assemblage after reforestation, especially at small scales such as the size of a nature reserve (Holl *et al.* 2000).

This study takes place at Cloudbridge Nature Reserve in the Montane cloud forest in Costa Rica. Reforestation started in 2002 to restore forest on pasture lands. Nowadays, much of the reserve has been reforested by planting with tree seedlings of about fifteen native species. More than 270 bird species have been recorded within the reserve since 2002. In order to assess the effect of the forest restoration on the reserve's bird community, a comparison of bird communities between reforested forest patches, natural regrowth patches, and primary forest remnants is needed. Bird species richness and diversity are expected to be higher at patches of intermediate succession stage than at younger patches and remnants, following the intermediate disturbance hypothesis (Connell 1978), as those patches can contain both forest-specialist and disturbance-tolerant species. If the reforested patches is expected to become closer to the one of primary forest as the forest gets older, with more and more disturbance-sensitive species and less and less disturbance-tolerant species. In order to test these hypotheses, I conducted a bird survey between March and April 2016 to compare bird community species richness, and primary forest.

MATERIALS AND METHODS

STUDY SITE

Cloudbridge Nature Reserve is located in San Gerardo de Rivas, Perez Zeledon Province, Costa Rica. It borders Chirripo National Park to the east, a mosaic of agricultural land to the west, and relatively intact forested tracts of land both north and south. The reserve is a mosaic landscape of primary and secondary forests, riparian regions and tree plantations of different age covering about 400 hectares and ranging in elevation from 1550 and 2750 m. In this area, the average rainfall is approximately 4300 m per year and the mean low and high temperatures are 13.4 and 23.1 degrees Celsius.

BIRD SURVEY



FIGURE 1 : BIRD POINT COUNTS LOCATION AT CLOUDBRIDGE NATURAL RESERVE, SAN GERARDO DE RIVAS, PEREZ ZELEDON.

The bird survey was conducted in March and April 2016 during the dry season using the point count technique, as bird data collected by this method can be directly related to habitat (Bibby 2000). To allow for safe and efficient access, all sites were located on existing trails. Twenty-four point counts, separated by a minimum distance of 200 m to ensure data independence (Bibby 2000), were distributed on 5 trails (Figure 1). Each trail was surveyed every week for three weeks per month (5 days per week). Bird point stations on each trail were surveyed from closest to furthest one week, and the opposite direction the following next week. Over 20 minutes, the same observer

recorded all the birds seen and identified at the species level in a radius of 25m, between the ground and the top of the canopy. Each bird station was marked with a fixed sign, which acted as the center of the study area. Only birds observed using the habitat within the study area were included (i.e. birds passing through the study area without stopping were not included). It was assumed that the probability of detection was uniform within this radius (Ralph and Scott 1981; Petit and Petit 2003). Each survey was done between 6am and 10am.

LANDSCAPE VARIABLES



FIGURE 2 : BIRD POINT COUNTS AND LAND COVER TYPE IN A 250M RADIUS AROUND THEM AT CLOUDBRIDGE NATURAL RESERVE.

Land cover mapping was drawn with QGis 2.14.1 based on data collected at the reserve in 2007 and completed by aerial photo interpretation and field validations. Land cover was separated into 7 classes (habitat types): planted forest younger than 10 years, planted forest between 10 and 30 years, natural regrowth between 10 and 30 years, natural regrowth between 30 and 70 years, primary forest (older than 70 years), pastures, and habitation. No planted forest was older than 30 years and no naturally regenerated forest was younger than 10 years or older than 70 years. The percentage of each land cover class in a buffer of 250m around each bird point count (Figure 2) was used for analysis. The 250m buffer was considered the most adapted to the small reserve scale. For each point, the nearest distance from each point count to pastures was calculated. The altitude (from Google Earth) and the habitati

type (land cover class) in which the point was situated were also used for the analysis. Correlations between variables are presented in Appendix 1.

BIRD TRAITS

Species traits considered were diet, migratory status, IUCN status, forest specialization, body mass, generation length and range size (see Table 1 for traits description). Community-Weighted Mean (CWM) trait values were calculated for each site for each trait except for body mass as too many values were not available (47 out of 94). CWM trait represents the dominance of each trait value among the communities. For generation length, value was missing for two species (Flame-throated Warbler, *Parula gutturalis*, and Tropical Parula, *Parula pitiayumi*).

TABLE 1 : BIRD	SPECIES TRA	AITS. THEIR	DESCRIPTION	AND SOURCE.
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Trait	Description	Sources
Diet	Fruits, nectar, invertebrates or	Stiles and Skutch 1989
	omnivore	
Migratory status	Resident or migrant species	BirdLife International 2016
IUCN status	LC: least concern	BirdLife International 2016
	NT: near threatened	
	VU: vulnerable	
	EN: endangered	
	CR: critically endangered	
Forest specialization	None (0)	BirdLife International 2016
	Low (1)	
	Medium (2)	
	High (3)	
Body mass	In g	BirdLife International 2016
Generation length	Number of years between the births	BirdLife International 2016
	of a parent and of a child.	
	Used as a proxy of reproductive rate	
Range size	In km ²	BirdLife International 2016

DATA ANALYSIS

Bird species community composition was analyzed with Correspondence Analysis (CA). The relationship between species community composition and landscape variables was analyzed with Canonical Correspondence Analysis (CCAs). Best-fitting models for landscape variables were obtained by forward selection of significant variables (Blanchet *et al.* 2008). To analyze the relative and independent effect of landscape variables, habitat type and altitude, I used partial CCAs to partition the variance explained by these different groups of variables (Borcard *et al.* 1992). Significance of results was tested with 1000 permutations (P < 0.05). For these multivariate analyses, species occurring in less than two sites were excluded (24 species) (Gomes *et al.* 2008).

To analyze the relationships between the landscape variables and species richness, diversity and CWM traits, I used generalized linear models. I analyzed the effect of habitat type, altitude and landscape variables separately and used a log link with a Poisson error distribution for species richness and an identity link with a normal error distribution

for diversity and CWM traits (forest specialization, generation length and range size). All possible variable combinations were tested, including the null model. Variable correlations were accounted for: correlated variables (|Pearson's r| > 0.6) were never used in the same model. Best-fitting models were determined by the lowest AICc (Akaike's An Information Criterion) score. All variables were standardized in order to compare their possible effect (each variable mean became 0).

R 3.1.2 was used for all data analyses with packages ade4, FD, Ime4, MuMIn and vegan (Barton 2016 ; Dray and Dufour 2007 ; Laliberté and Shipley 2014 ; Oksanen *et al.* 2013). A description of the analysis is given in

Appendix 2.

RESULTS

A total of 880 individual birds were recorded, representing 94 bird species. Twenty-three species were migrants and, seventy-one were residents. There was one vulnerable species (Ruddy Pigeon, *Columba subvinacea*), three near threaded species [Black Guan (*Chamaepetes unicolor*), Golden-winged Warbler (*Vermivora chrysoptera*) and Resplendent Quetzal (*Pharomachrus mocinno*)]. The rest were classified as least concern by the IUCN. Most of the species had a diet based on invertebrates (40 species out of 95). Ten eat mainly fruits and ten mainly nectar. The list of species with their frequency of occurrence, total abundance and characteristics is presented in Appendix 3. The most abundant species were Common Chlorospingus (*Chlorospingus ophthalmicus*), Slate-throated Redstart (*Myioborus miniatus*) and Swainson's Thrush (*Catharus ustulatus*). All the communities were dominated by resident species of least concern (IUCN status). Fourteen sites were dominated by nectivorous species, a site situated in primary forest, but with 62% of natural regrowth between 10 and 30 years.

HABITAT AND LANDSCAPE EFFECTS ON BIRD COMMUNITIES

Species contributing the most to the first CA axis were Elegant Euphonia (*Euphonia elegantissima*) for its negative part and Black-faced Solitaire (*Myadestes melanops*), Flame-throated Warbler (*Parula gutturalis*) and Collared Redstar (*Myioborus torquatus*) for its positive part. Species contributing the most to the second CA axis were White-throated Mountain-Gem (*Lampornis castaneoventris*) and Stripe-tailed Hummingbird (*Eupherusa eximia*), two nectivorous species, for its negative part and Sulphur-winged Parakeet (*Pyrrhura hoffmanni*) for its positive part. Bird community composition was significantly different between habitat type (CCA, 21.87% explained inertia, P < 0.01). The first CA axis differentiates planted forest younger than 10 years, and natural regrowth between 10 and 30 years (negative value), from primary forest, and natural regrowth between 30 and 70 years (positive value). The second axis differentiates primary forest (negative value), from natural regrowth between 10 and 30 years (positive value). Planted forest and natural regrowth of the same age seemed to have different bird communities (Figure 3).



FIGURE 3 : (A) ORDINATION OF BIRD SPECIES ON THE FIRST TWO CORRESPONDENCE ANALYSIS AXIS MADE ON BIRD ABUNDANCES, AND (B) ORDINATION OF SITES REPRESENTED BY HABITAT TYPE (PL1: PERCENTAGE OF PLANTED FOREST YOUNGER THAN 10 YEARS, PL2: PERCENTAGE OF PLANTED FOREST BETWEEN 10 AND 30 YEARS, NR2: PERCENTAGE OF NATURAL REGROTWH BETWEEN 10 AND 30 YEARS, NR3: PERCENTAGE OF NATURAL REGROWTH BETWEEN 30 AND 70 YEARS, PF4: PERCENTAGE OF PRIMARY FOREST). THIS PLAN EXPLAINS 11.87% OF THE TOTAL INERTIA. SPECIES CORRESPONDING TO THE CODES ARE PRESENTED IN APPENDIX 3.



FIGURE 4: BIRD COMMUNITY COMPOSITION INERTIA EXPLAINED BY LANDSCAPE VARIABLES FROM BEST CCA, HABITAT TYPE AND ALTITUDE (* P<0.05, ** P< 0.01).

The altitude explained 9.29% of variance in the species community composition. The best landscape explanatory variables for species community composition explained 18.88% of variance and 15.06% without the variance explained by altitude and habitat type (Figure 4). The best landscape explanatory variables were percentage of

planted forest younger than 10 years (6.2% of variance and 5.86% when variance from the other variables were partialled out), percentage of natural regrowth between 10 and 30 years (6.69% of variance and 6.51% when variance from the other variables were partialled out) and distance to pasture land (6.58% of variance and 5.83% when variance from the other variables were partialled out).

RICHNESS, DIVERSITY AND CWM TRAIT RESPONSES TO HABITAT TYPE AND LANDSCAPE VARIABLES

Neither habitat type nor altitude had an effect on species richness and diversity. Percentage of planted forest younger than 10 years, however, had a positive effect on both of those indices. Diversity also increases with percentage of natural regenerated forest between 10 and 30 years (Table 2).

TABLE 2 : THE BEST GENERALIZED LINEAR MODEL (BASED ON LOWEST AIC) FITTING LANSCAPE VARIABLES ON SPECIES RICHNESS, DIVERSITY AND CWM VALUES OF BIRD COMMUNITIES. FOR EACH MODEL, SIGNIFICANCE LEVELS OF RETAINED VARIABLES ARE GIVEN AS WELL AS THE ESTIMATES FOR THE SIGNIFICANT VARIABLES. NS P>0.01, † P<0.1, * P<0.05, ** P< 0.01, *** P<0.001. AIC_C OF THE SELECTED MODEL, AIC_C OF THE NULL MODEL AND COEFFICIENT OF DETERMINATION BASED ON THE LIKELIHOOD-RATIO TEST (R²) ARE PRESENTED. WHEN NO VALUES ARE INDICATED, THE NULL MODEL HAD THE LOWEST AIC VALUE. D PASTURE: NEAREST DISTANCE TO PASTURE, %PL1: PERCENTAGE OF PLANTED FOREST YOUNGER THAN 10 YEARS, %PL2: PERCENTAGE OF PLANTED FOREST BETWEEN 10 AND 30 YEARS, %NR2: PERCENTAGE OF NATURAL REGROTWH BETWEEN 10 AND 30 YEARS, %NR3: PERCENTAGE OF NATURAL REGROWTH BETWEEN 30 AND 70 YEARS, %PF: PERCENTAGE OF PRIMARY FOREST, %P0: PERCENTAGE OF PASTURE, %H0: PERCENTAGE OF HABITATION.

	D pasture	% pl1	% pl2	% nr2	% nr3	% pf	% p0	% h0	AICc	AIC null	Rc²
Species richness	ns	0.11*	ns	ns	ns	ns	ns	ns	134.78	137.9	0.19
Diversity	ns	0.12**	ns	ns	0.06†	ns	ns	ns	-11.654	-5.3702	0.35
CWM forest specialization	-0.08*	ns	ns	0.07*	0.22 ***	0.22 ***	ns	ns	-39.701	-20.566	0.68
CWM generation length	ns	ns	ns	ns	ns	0.21 ***	ns	ns	2.7946	14.895	0.44
CWM range size	ns	243896†	ns	-386729 **	ns	ns	ns	ns	710.3	719.05	0.41

Forest specialization increases with altitude (P < 0.01) and was the only trait showing a response to altitude. None of the traits were affected by habitat type. CWM forest specialization increased with proximity to pastures, percentage of natural regrowth of both age and primary forest. Percentage of primary forest was the only variable selected in the best-fitted model for CWM generation length (positive effect). Percentage of planted forest younger than 10 years had a positive effect on CWM range size, whereas percentage of natural regrowth between 10 and 30 years had a negative effect on it (Table 2).

DISCUSSION

Both habitat type and landscape factors played an important role in species assemblage. However, habitat type had no effect on species richness, diversity and trait dominance among communities. All the traits considered were affected by landscape variables, mainly the amount of natural regrowth and primary forest present. The amount of pasture land and human habitation were not identified as having an effect on the species traits in any of the models, perhaps because their percentage of cover were too small to have a significant effect.

All the communities were dominated by resident species, which are more at risk of extinction than migratory species according to Owens and Bennett (2000) (but see Henle *et al.* (2004)). Communities were also mainly dominated by species feeding on food sources other than fruits and invertebrates. Food-generalist species have a high probability to occur in a habitat and in high abundance (Newbold *et al.* 2013). But sites in which insectivore species dominated the communities had similar species assemblage than those where more generalist species dominated.

RELATIVE IMPORTANCE OF LANDSCAPE VARIABLES AND HABITAT TYPE ON BIRD COMMUNITIES

The amount of young planted forest (younger than 10 years) and young natural regrowth (between 10 and 30 years), along with the distance to pasture, were the landscape variables that best explained species assemblage. The amount of young planted forest also had a positive effect on species richness and diversity. This response may be caused, according to the intermediate disturbance hypothesis (Connell 1978), by the exploitation of young planted forest resources by species from both natural and disturbed habitats. However, surveys in pasture around the reserve are needed to validate this hypothesis. Diversity also increased with the amount of older natural regrowth (between 30 and 70 years), where disturbance-sensitive forest species can become more abundant than in younger forest. It is also possible that birds are harder to detect where vegetation is dense (Newbold *et al.* 2013). As a result, bird abundance and diversity in old growth forest could be underestimated.

But bird species richness and diversity provide little insight into the habitat value of planted forest for forest species, as Gould and Mackey (2015) found out for post-mining rehabilitation. Investigating functional community composition (using trait species instead of species itself) provides a better understanding of the mechanisms underlying changes in species assemblages when modifications of environmental conditions, including land cover, occur (Devictor *et al.* 2008).

DIFFERENCES BETWEEN FOREST TYPES

When the amount of young planted forest (younger than 10 years) around the bird point station increased, the communities were increasingly dominated by species with large range sizes, which are species less sensitive to landuse change (Newbold *et al.* 2013 ; Barbaro and Van Halder 2009). However, this effect was had little significance. Contrarily, when the amount of natural regrowth increased, the communities were increasingly dominated by species with small range sizes. Species with small range sizes are considered to be more threatened by land-use change because they have more specific habitat requirements than more widespread species (Newbold *et al.* 2013 ; Barbaro and Van Halder 2009). The regeneration of the forest seems thus efficient for the recovery of bird community, but the opposite effect of planted forest suggest that planted and natural secondary forest do not offer the same habitats for birds. Moreover, bird assemblage of young planted forest and young natural regrowth seem to have different species assemblage from the other habitat types and from each other.

Many landscape variables had an effect on forest specialization, which increased with the amount of natural regrowth and remnants. Surprisingly, forest specialization also increased with the proximity to pasture land, although this effect was weaker than the ones of natural regrowth and primary forest. The amount of planted forest showed no effect on this trait.

Only the amount of primary forest had an effect on generation length. Generation length can be used as a proxy for reproductive rate. As the quantity of primary forest increased, the communities were increasingly dominated by slow-reproductive species. Slow-reproductive species are less able to recover after perturbation than fast-reproductive species, and thus are threatened by land-use change (Newbold *et al.* 2013). The primary forest seems essential for the persistence of sensitive slow-reproductive species (Oostra et al. 2008).

Consistently, a significant difference in term of species and functional community composition between planted forest versus natural regrowth and primary forest was observed. This result has been found in other studies (Smith *et al.* 2015 ; Munro *et al.* 2011). Moreover, as natural regrowth becomes older (older than 30 years), the species community composition becomes closer to the primary forest than the planted forest, a finding supported by Stouffer *et al.* (2006). However, the reforestation in the reserve is still recent and the planted areas may need more time to show their full potential for bird community recovery (Munro *et al.* 2011). Borgella and Gavin (2005) showed that temporal scale used to study community responses may lead to differing conclusions.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Planted, natural regrowth and primary forests within the Cloudbridge Nature Reserve show differences in their species and functional community composition. However, as the natural regrowth ages, its community composition may also become closer to that of the primary forest. As the planted forests are still young, their community composition may also become closer to that of the primary forest as they age, and thus may need more time to show an effect on bird community recovery. To fully understand the mechanisms behind bird community restoration after reforestation and natural regrowth, it is essential to consider habitat characteristics such as canopy cover, forest structure, species composition and fruit availability. Only then can we make a full assessment of how successful the reforestation is and what to change in order to improve it. As Sekercioglu (2006) showed in his study, even small forest patches in the mostly deforested Costa Rican agricultural landscape provided essential dietary, microclimatic and nesting resources for bird species sensitive to deforestation. Stiles (1985) found that 70% of Costa Rica's native land birds also use heavily deforested areas, provided that some canopy trees and forest patches remain. It is thus important for bird conservation in a worldwide land-use change context to identify which habitat characteristics can allow those species to live and reproduce in a natural reserve such as Cloudbridge.

REFERENCES

- Barbaro, Luc, and Inge Van Halder. 2009. "Linking Bird, Carabid Beetle and Butterfly Life-History Traits to Habitat Fragmentation in Mosaic Landscapes." *Ecography* 32 (2): 321–333.
- Barton, Kamil. 2016. "MuMIn: Multi-Model Inference. R Package Version 1.15.6. https://CRAN.Rproject.org/package=MuMIn."

Bibby, Colin J. 2000. Bird Census Techniques. Elsevier.

BirdLife International. 2003. BirdLife's Online World Bird Database: The Site for Bird Conservation. BirdLife International Cambridge,, UK.

----. 2016. "IUCN Red List for Birds." http://www.birdlife.org/.

- Blanchet, F. Guillaume, Pierre Legendre, and Daniel Borcard. 2008. "Forward Selection of Explanatory Variables." Ecology 89 (9): 2623–2632.
- Borcard, Daniel, Pierre Legendre, and Pierre Drapeau. 1992. "Partialling out the Spatial Component of Ecological Variation." *Ecology* 73 (3): 1045–1055.
- Borgella, René, and Thomas A. Gavin. 2005. "Avian Community Dynamics in a Fragmented Tropical Landscape." *Ecological Applications* 15 (3): 1062–1073.
- Bradshaw, Anthony D., John Cairns Jr, Richard Hobbs, David W. MacDonald, Thomas P. Moorhouse, Jody W. Enck, Alan Gray, et al. 2002. "Handbook of Ecological Restoration." http://www.jstor.org/stable/pdf/827212.pdf.
- Brown, Alejandro Diego, Maarten Kappelle, M. Kappelle, and A. D. Brown. 2001. "Introducción a Los Bosques Nublados Del Neotrópico: Una Síntesis Regional." *Bosques Nublados Del Neotrópico*, 27–40.
- Connell, Joseph H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." Science 199 (4335): 1302–1310.
- Daily, Gretchen C., Paul R. Ehrlich, and G. Arturo Sanchez-Azofeifa. 2001. "Countryside Biogeography: Use of Human-Dominated Habitats by the Avifauna of Southern Costa Rica." *Ecological Applications* 11 (1): 1–13. doi:10.2307/3061051.
- Devictor, Vincent, Romain Julliard, Joanne Clavel, Frédéric Jiguet, Alexandre Lee, and Denis Couvet. 2008. "Functional Biotic Homogenization of Bird Communities in Disturbed Landscapes." *Global Ecology and Biogeography* 17 (2): 252–261.
- Dray, Stéphane, and Anne-Béatrice Dufour. 2007. "The ade4 Package: Implementing the Duality Diagram for Ecologists." *Journal of Statistical Software* 22 (4): 1–20.
- Fahrig, Lenore. 2003. "Effects of Habitat Fragmentation on Biodiversity." Annual Review of Ecology, Evolution, and Systematics, 487–515.
- FAO, Global Forest Resource. 2005. "Progress Towards Sustainable Forest Management." FAO Forestry Paper 147: 320.
- Foley, Jonathan A., Ruth DeFries, Gregory P. Asner, Carol Barford, Gordon Bonan, Stephen R. Carpenter, F. Stuart Chapin, et al. 2005. "Global Consequences of Land Use." *Science* 309 (5734): 570–574.
- Gomes, Laurens GL, Vicencio Oostra, Vincent Nijman, Antoine M. Cleef, and Maarten Kappelle. 2008. "Tolerance of Frugivorous Birds to Habitat Disturbance in a Tropical Cloud Forest." *Biological Conservation* 141 (3): 860– 871. doi:10.1016/j.biocon.2008.01.007.
- Gould, Susan F., and Brendan G. Mackey. 2015. "Site Vegetation Characteristics Are More Important than Landscape Context in Determining Bird Assemblages in Revegetation." *Restoration Ecology* 23 (5): 670–80. doi:10.1111/rec.12222.
- Greenberg, Russell, Peter Bichier, and Andrea Cruz Angón. 2000. "The Conservation Value for Birds of Cacao Plantations with Diverse Planted Shade in Tabasco, Mexico." *Animal Conservation* 3 (2): 105–112.
- Henle, Klaus, Kendi F. Davies, Michael Kleyer, Chris Margules, and Josef Settele. 2004. "Predictors of Species Sensitivity to Fragmentation." *Biodiversity & Conservation* 13 (1): 207–251.
- Holl, Karen D., Michael E. Loik, Eleanor HV Lin, and Ivan A. Samuels. 2000. "Tropical Montane Forest Restoration in Costa Rica: Overcoming Barriers to Dispersal and Establishment." *Restoration Ecology* 8 (4): 339–349.
- Kappelle, M., and M. E. Juárez. 2006. "Land Use, Ethnobotany and Conservation in Costa Rican Montane Oak Forests." In Ecology and Conservation of Neotropical Montane Oak Forests, 393–406. Springer. http://link.springer.com/chapter/10.1007/3-540-28909-7_30.
- Laliberté, E., and B. Shipley. 2014. "R-Package FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." *R Foundation for Statistical Computing, Vienna, Austria*.
- Lamb, David, Peter D. Erskine, and John A. Parrotta. 2005. "Restoration of Degraded Tropical Forest Landscapes." Science 310 (5754): 1628–1632.

- Martínez-Garza, Cristina, and Henry F. Howe. 2003. "Restoring Tropical Diversity: Beating the Time Tax on Species Loss." *Journal of Applied Ecology* 40 (3): 423–29. doi:10.1046/j.1365-2664.2003.00819.x.
- Morrison, Emily B., Catherine A. Lindell, Karen D. Holl, and Rakan A. Zahawi. 2010. "Patch Size Effects on Avian Foraging Behaviour: Implications for Tropical Forest Restoration Design." *Journal of Applied Ecology* 47 (1): 130–138.
- Munro, Nicola T., Joern Fischer, Geoff Barrett, Jeff Wood, Adam Leavesley, and David B. Lindenmayer. 2011. "Bird's Response to Revegetation of Different Structure and floristics—Are 'restoration Plantings' Restoring Bird Communities?" *Restoration Ecology* 19 (201): 223–235.
- Newbold, Tim, Jörn PW Scharlemann, Stuart HM Butchart, Çağan H. Şekercioğlu, Rob Alkemade, Hollie Booth, and Drew W. Purves. 2013. "Ecological Traits Affect the Response of Tropical Forest Bird Species to Land-Use Intensity." *Proceedings of the Royal Society of London B: Biological Sciences* 280 (1750): 20122131.
- Newbold, Tim, Jörn PW Scharlemann, Stuart HM Butchart, Çağan H. Şekercioğlu, Lucas Joppa, Rob Alkemade, and Drew W. Purves. 2014. "Functional Traits, Land-Use Change and the Structure of Present and Future Bird Communities in Tropical Forests." *Global Ecology and Biogeography* 23 (10): 1073–1084.
- Oksanen, Jari, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, et al. 2013. "Package 'vegan.'" *Community Ecology Package, Version* 2 (9). http://mirror.bjtu.edu.cn/cran/web/packages/vegan/vegan.pdf.
- Oostra, Vicencio, Laurens GL Gomes, and Vincent Nijman. 2008. "Implications of Deforestation for the Abundance of Restricted-Range Bird Species in a Costa Rican Cloud-Forest." *Bird Conservation International* 18 (1): 11–19. doi:10.1017/S0959270908000038.
- Owens, Ian PF, and Peter M. Bennett. 2000. "Ecological Basis of Extinction Risk in Birds: Habitat Loss versus Human Persecution and Introduced Predators." *Proceedings of the National Academy of Sciences* 97 (22): 12144–12148.
- Petit, Lisa J., and Daniel R. Petit. 2003. "Evaluating the Importance of Human-Modified Lands for Neotropical Bird Conservation." *Conservation Biology* 17 (3): 687–694.
- Ralph, C. John, and J. Michael Scott. 1981. "Estimating Numbers of Terrestrial Birds." http://agris.fao.org/agrissearch/search.do?recordID=US201300344698.
- Sekercioglu, C. H. 2006. "Ecological Significance of Bird Populations." Handbook of the Birds of the World 11: 15–51.
- Smith, Geoffrey C., Tom Lewis, and Luke D. Hogan. 2015. "Fauna Community Trends during Early Restoration of Alluvial Open Forest/woodland Ecosystems on Former Agricultural Land." *Restoration Ecology* 23 (6): 787–799.
- Stiles, F. Gary. 1985. "Conservation of Forest Birds in Costa Rica: Problems and Perspectives." *ICBP Technical Publication* 4: 141–168.
- Stiles, F. Gary, and Alexander Frank Skutch. 1989. *Guide to the Birds of Costa Rica*. Comistock. http://agris.fao.org/agris-search/search.do?recordID=US201300640055.
- Stouffer, Philip C., Richard O. Bierregaard, Cheryl Strong, and Thomas E. Lovejoy. 2006. "Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments." *Conservation Biology* 20 (4): 1212–1223.
- Van Bael, Sunshine A., Peter Bichier, and Russell Greenberg. 2007. "Bird Predation on Insects Reduces Damage to the Foliage of Cocoa Trees (Theobroma Cacao) in Western Panama." *Journal of Tropical Ecology* 23 (6): 715–719.
- Wijdeven, Sander MJ, and Mirjam E. Kuzee. 2000. "Seed Availability as a Limiting Factor in Forest Recovery Processes in Costa Rica." *Restoration Ecology* 8 (4): 414–424.

APPENDIX

APPENDIX 1 : PEARSON CORRELATION COEFFICIENTS BETWEEN LANDSCAPE VARIABLES. SIGNIFICANT COEFFICIENTS ARE PRESENTED IN BOLD (P < 0.05). %PL1: PERCENTAGE OF PLANTED FOREST YOUNGER THAN 10 YEARS, %PL2: PERCENTAGE OF PLANTED FOREST BETWEEN 10 AND 30 YEARS, %NR2: PERCENTAGE OF NATURAL REGROTWH BETWEEN 10 AND 30 YEARS, %NR3: PERCENTAGE OF NATURAL REGROWTH BETWEEN 30 AND 70 YEARS, %PF: PERCENTAGE OF PRIMARY FOREST, %PO: PERCENTAGE OF PASTURE, %H0: PERCENTAGE OF HABITATION.

	altitude	distance to pasture	%pl1	%pl2	%nr2	%nr3	%pf	%p0
distance to pasture	0.73							
%pl1	-0.33	-0.27						
%pl2	-0.42	-0.44	-0.28					
%nr2	-0.41	-0.2	-0.05	-0.19				
%nr3	0.41	0.1	-0.23	0.2	-0.71			
%pf	0.32	0.57	-0.2	-0.43	0.08	-0.53		
%p0	-0.37	-0.66	-0.15	0.65	0	-0.04	-0.32	
%h0	-0.32	-0.34	-0.21	0.89	-0.24	0.15	-0.34	0.56

APPENDIX 2 : ANALYSIS USED FOR THIS STUDY.

Analysis	R package	R function	Description	References
Correspondence Analysis	ade4	dudi.coa	Ordination techniques in which	Dray <i>et al.</i> 2007
			rare species weight more on the	
			axis than more common ones.	
Canonical correspondence	vegan	cca	Very popular ordination	Oksanen et al. 2013
analysis and partial canonical			techniques to analysis the effect	
correspondence analysis			of environmental variables on	
			communities.	
Fitting Generalized Linear	stats	glm	Used to fit generalized linear	Dobson and Barnett
Models			models, specified by giving a	2008
			predictor and a description of the	
			error distribution.	

APPENDIX 3 : BIRDS SPECIES OCCURRENCE, ABUNDANCE AND CHARACTERISTICS. SPECIES NAMES ARE ACCORDING TO BIRDLIFE INTERNATIONAL.

English name	Scientific name	Code	Occurrence	Abundance	Status	IUCN	Diet	Forest specialization	Body mass (g)	Generation lenght	Range size (km²)
Acorn Woodpecker	Melanerpes formicivorus	ACWP	8	3	resident	LC	invertebrates	high	NA	5.6	1500000
Boat-billed Flycatcher	Megarynchus pitangua	BBFC	4	1	resident	LC	invertebrates	low	63.4	3.6	13200000
Blue-crowned Motmot	Momotus coeruliceps	BCMM	4	4	resident	LC	omnivore	medium	141.6956482	3.6	38300
Brown-capped Vireo	Vireo leucophrys	BCVI	46	30	resident	LC	invertebrates	medium	12.3	4.2	575000
Black-cheeked Warbler	Basileuterus melanogenys	BCWA	12	6	resident	LC	invertebrates	high	11.8	3.9	4800
Buff-fronted Foliage-gleaner	Philydor rufum	BFFG	4	1	resident	LC	invertebrates	high	25	4.7	2190000
Black-faced Solitaire	Myadestes melanops	BFSO	42	20	resident	LC	fruits	high	32.1	4.5	31900
Bay-headed Tanager	Tangara gyrola	BHTA	4	3	resident	LC	omnivore	medium	NA	4.9	3990000
Black Guan	Chamaepetes unicolor	BLGU	4	1	resident	NT	fruits	high	32.1	4.5	31900
Blue Seedeater	Amaurospiza concolor	BLSE	4	2	resident	LC	omnivore	medium	13.1	3.8	201000
Blackburnian Warbler	Dendroica fusca	BLWA	8	2	migrant	LC	invertebrates	medium	NA	3.6	1910000
Black-throated Green Warbler	Dendroica virens	BTWA	21	8	migrant	LC	invertebrates	medium	NA	3.6	1480000
Black-and-White Becard	Pachyramphus albogriseus	BWBE	8	2	resident	LC	omnivore	high	17.3	4.6	342000
Black-and-White Warbler	Mniotilta varia	BWWA	8	2	migrant	LC	invertebrates	medium	10.9	4.6	3230000
Chestnut-capped Brush-finch	Arremon brunneinucha	CCBF	17	4	resident	LC	invertebrates	medium	41.5	3.8	617000
Clay-colored Thrush	Turdus grayi	ССТН	12	4	resident	LC	invertebrates	low	NA	6.5	1060000
Chiriqui Quail-dove	Zentrygon chiriquensis	CHQD	12	3	resident	LC	omnivore	high	308	4.6	16400
Cherrie's Tanager	Ramphocelus costaricensis	CHTA	4	1	resident	LC	omnivore	low	NA	3.7	17800
Common Chlorospingus	Chlorospingus ophthalmicus	COCH	79	65	resident	LC	omnivore	medium	NA	3.7	582000
Collared Redstar	Myioborus torquatus	CORS	12	7	resident	LC	invertebrates	medium	10.5	3.5	5300
Collared Trogon	Trogon collaris	COTR	17	4	resident	LC	omnivore	high	64.19999695	7.3	6800000
Dusky-capped Flycatcher	Myiarchus tuberculifer	DCFC	8	2	migrant	LC	invertebrates	medium	18.41	5.1	10600000
Elegant Euphonia	Euphonia elegantissima	ELEU	46	28	resident	LC	fruits	medium	NA	3.5	463000
Emerald Toucanet	Aulacorhynchus prasinus	EMTO	54	31	resident	LC	omnivore	medium	179.2040863	7	420000
Flame-colored Tanager	Piranga bidentata	FCTA	21	13	resident	LC	omnivore	medium	36.57	4.1	399000
Fiery-throated Hummingbird	Panterpe insignis	FTHU	4	1	resident	LC	nectar	medium	NA	4.2	8300
Flame-throated Warbler	Parula gutturalis	FTWA	8	3	resident	LC	invertebrates	medium	9.5	NA	3900
Golden-browed Chlorophonia	Chlorophonia callophrys	GBCH	12	5	resident	LC	fruits	medium	25.8	3.7	17400
Golden-bellied Flycatcher	Myiodynastes hemichrysus	GBFC	25	12	resident	LC	omnivore	medium	NA	3.6	16600
Gray-breasted Wood-wren	Henicorhina leucophrys	GBWW	17	6	resident	LC	invertebrates	high	NA	3.6	714000
Green-crowned Brilliant	Heliodoxa jacula	GCBR	8	2	resident	LC	nectar	high	NA	4.2	63200
Gray-headed Tanager	Eucometis penicillata	GHTA	4	1	resident	LC	omnivore	medium	NA	3.7	5710000
Green Hermit	Phaethornis guy	GRHE	17	4	resident	LC	nectar	medium	NA	4.2	555000
Great Kiskadee	Pitangus sulphuratus	GRKI	29	18	migrant	LC	invertebrates	low	63.79	3.6	16100000
Golden-crowned Warbler	Basileuterus culicivorus	GRWA	21	5	resident	LC	invertebrates	medium	NA	3.9	8380000
Golden-winged Warbler	Vermivora chrysoptera	GWWA	25	9	migrant	NT	invertebrates	medium	NA	3.8	943000
Hairy Woodpecker	Leuconotopicus villosus	HAWP	12	3	resident	LC	invertebrates	high	51.7	4.9	13300000
Magnificent Hummingbird	Eugenes fulgens	MAHU	8	2	migrant	LC	nectar	high	NA	5.1	854000
Mountain Elaenia	Elaenia frantzii	MOEL	8	2	resident	LC	invertebrates	medium	NA	4.6	259000
Ochraceous Wren	Troglodytes ochraceus	OCWR	12	3	resident	LC	invertebrates	high	NA	3.5	17300

English name	Scientific name	Code	Occurrence	Abundance	Status	IUCN	Diet	Forest specialization	Body mass (g)	Generation lenght	Range size (km²)
Olivaceous Woodcreeper	Sittasomus griseicapillus	OLWC	4	1	resident	LC	invertebrates	medium	NA	4.1	12000000
Olive-striped Flycatcher	Mionectes olivaceus	OSFC	4	1	resident	LC	fruits	medium	16.4	4	745000
Palm Tanager	Thraupis palmarum	PATA	4	1	migrant	LC	omnivore	medium	NA	4	12200000
Paltry Tyrannulet	Zimmerius vilissimus	PATY	25	7	resident	LC	omnivore	medium	NA	3.6	288000
Peg-billed Finch	Acanthidops bairdi	PBFI	4	2	resident	LC	omnivore	medium	NA	3.8	4700
Philadelphia Vireo	Vireo philadelphicus	PHVI	25	10	migrant	LC	invertebrates	high	NA	4.2	673000
Rose-breasted Grosbeak	Pheucticus ludovicianus	RBGB	4	1	migrant	LC	omnivore	medium	42	4.7	2130000
Rufous-browed Peppershrike	Cyclarhis gujanensis	RBPS	8	4	resident	LC	invertebrates	medium	NA	5.2	13500000
Rufous-breasted Wren	Thryothorus rutilus	RBWR	17	4	resident	LC	invertebrates	medium	16.5	4	206000
Ruddy-capped Nightingale-thrush	Catharus frantzii	RCNT	8	4	resident	LC	omnivore	medium	28.9	4.2	245000
Resplendent Quetzal	Pharomachrus mocinno	REQU	4	1	resident	NT	omnivore	high	NA	7.3	149000
Red-faced Spinetail	Cranioleuca erythrops	RFST	8	3	resident	LC	invertebrates	high	16.9	3.8	70100
Red-headed Barbet	Eubucco bourcierii	RHBA	50	19	resident	LC	omnivore	high	37	8.5	235000
Rough-legged Tyrannulet	Phyllomyias burmeisteri	RLTY	4	1	migrant	LC	omnivore	high	11.1	3.6	856000
Rufous-tailed Hummingbird	Amazilia tzacatl	RTHU	12	3	resident	LC	nectar	medium	NA	3.4	1030000
Ruddy Pigeon	Columba subvinacea	RUPI	25	10	migrant	VU	fruits	high	NA	6.6	6900000
Streak-breasted Treehunter	Thripadectes rufobrunneus	SBTH	4	1	resident	LC	invertebrates	high	56.2	3.8	17600
Slaty-capped Flycatcher	Leptopogon superciliaris	SCFC	4	2	resident	LC	omnivore	high	11.7	3.6	616000
Scintillant Hummingbird	Selasphorus scintilla	SCHU	50	27	resident	LC	nectar	low	NA	4.7	9400
Spot-crowned Woodcreeper	Lepidocolaptes affinis	SCWC	21	6	resident	LC	invertebrates	medium	NA	4.1	187000
Streak-headed Woodcreeper	Lepidocolaptes souleyetii	SHWC	12	5	resident	LC	invertebrates	medium	27.5	4.1	1480000
Slaty Antwren	Myrmotherula schisticolor	SLAW	4	1	resident	LC	invertebrates	high	9.6	5.1	491000
Speckled Tanager	Tangara guttata	SPTA	21	5	resident	LC	fruits	low	NA	4.9	365000
Spotted Wood-quail	Odontophorus guttatus	SPWQ	8	3	resident	LC	omnivore	high	NA	3.9	339000
Scarlet-thighed Dacnis	Dacnis venusta	STDA	21	12	resident	LC	fruits	medium	NA	3.7	201000
Stripe-tailed Hummingbird	Eupherusa eximia	STHU	17	8	resident	LC	nectar	high	NA	4.2	175000
Slate-throated Redstart	Myioborus miniatus	STRS	79	64	resident	LC	invertebrates	medium	9	3.5	1240000
Streaked Saltator	Saltator striatipectus	STSA	17	5	resident	LC	invertebrates	low	39	4.1	859000
Silver-throated Tanager	Tangara icterocephala	STTA	58	44	resident	LC	omnivore	medium	NA	4.9	74200
Summer Tanager	Piranga rubra	SUTA	17	4	migrant	LC	omnivore	medium	28.2	3.8	3270000
Sulphur-winged Parakeet	Pyrrhura hoffmanni	SWPA	25	39	resident	LC	fruits	medium	82.2	6	8000
Swainson's Thrush	Catharus ustulatus	SWTH	58	57	migrant	LC	omnivore	high	NA	4.3	2890000
Tennessee Warbler	Vermivora peregrina	TEWA	58	47	migrant	LC	omnivore	medium	8.9	3.8	1350000
Townsend's Warbler	Dendroica townsendi	TOWA	21	5	migrant	LC	invertebrates	medium	NA	3.4	920000
Tropical Kingbird	Tyrannus melancholicus	TRKB	4	1	migrant	LC	omnivore	low	37.4	4.2	14700000
Tropical Parula	Parula pitiayumi	TRPA	12	3	resident	LC	omnivore	medium	6.7	NA	8360000
Tropical Pewee	Contopus cinereus	TRPE	8	3	migrant	LC	invertebrates	medium	11.6	3.5	5650000
Three-striped Warbler	Basileuterus tristriatus	TSWA	17	5	resident	LC	invertebrates	medium	NA	3.9	467000
Tufted Flycatcher	Mitrephanes phaeocercus	TUFC	12	6	resident	LC	invertebrates	medium	NA	3.6	599000
Violet Sabrewing	Campylopterus hemileucurus	VISW	8	2	resident	LC	nectar	medium	NA	4.2	314000
Volcano Hummingbird	Selasphorus flammula	VOHU	4	1	resident	LC	nectar	low	2.65	4.7	4600
Western Wood-pewee	Contopus sordidulus	WEWP	4	1	migrant	LC	invertebrates	medium	13.1	3.4	3360000

English name	Scientific name	Code	Occurrence	Abundance	Status	IUCN	Diet	Forest specialization	Body mass (g)	Generation lenght	Range size (km²)
Wilson's Warbler	Wilsonia pusilla	WIWA	75	45	migrant	LC	invertebrates	medium	7.2	3.6	1370000
White-naped Brush-finch	Atlapetes albinucha	WNBF	12	3	resident	LC	omnivore	medium	33.1	3.8	56600
White-throated Mountain-Gem	Lampornis castaneoventris	WTMG	21	14	resident	LC	nectar	medium	NA	4.5	1500
White-throated Thrush	Turdus assimilis	WTTH	4	1	resident	LC	omnivore	medium	NA	6.7	645000
White-winged Tanager	Piranga leucoptera	WWTA	12	7	resident	LC	omnivore	medium	NA	4.1	566000
Yellow-bellied Flycatcher	Empidonax flaviventris	YBFC	21	5	migrant	LC	omnivore	medium	11.8	3.7	680000
Yellowish Flycatcher	Empidonax flavescens	YEFC	38	18	resident	LC	omnivore	medium	NA	3.7	165000
Yellow-faced Grassquit	Tiaris olivaceus	YFGQ	8	2	resident	LC	fruits	none	8.3	3.4	966000
Yellow-rumped Warbler	Dendroica coronata	YRWA	4	2	migrant	LC	invertebrates	medium	NA	3.5	6260000
Yellow-thighed Finch	Pselliophorus tibialis	YTFI	33	24	resident	LC	omnivore	medium	NA	3.8	6600
Yellow-throated Vireo	Vireo flavifrons	YTVI	8	2	migrant	LC	invertebrates	medium	18	4.2	1470000
Yellow-winged Vireo	Vireo carmioli	YWVI	17	5	resident	LC	invertebrates	medium	NA	4.2	4200