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The responses of understorey birds to forest fragmentation, logging and wildfires: An Amazonian synthesis

J. Barlow[a,b,*], *C.A. Peres*[a], *L.M.P. Henriques*[b], *P.C. Stouffer*[c,d], *J.M. Wunderle*[e]

[a]*Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom*
[b]*Museu Paraense Emílio Goeldi (MPEG), Coordenação de Ciências da Terra e Ecologia, Av. Perimetral 1901, Bairro Terra Firme, Belém-Pará 66077-530, Brazil*
[c]*School of Renewable Natural Resources, 227 RNR Building, Louisiana State University, Baton Rouge, LA 70803-6202, USA*
[d]*Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia, CP 478, Manaus, AM 69011-970, Brazil*
[e]*International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 507, Palmer, Puerto Rico 00721, United States*

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ABSTRACT

We combine mist-net data from 24 disturbance treatments taken from seven studies on the responses of understorey Amazonian birds to selective logging, single and recurrent wildfires, and habitat fragmentation. The different disturbance treatments had distinct effects on avian guild structure, and fire disturbance and the isolation of forest patches resulted in bird communities that were most divergent from those in continuous, undisturbed forest in terms of their species composition. Although low-intensity logging treatments had the least noticeable effects, the composition of understorey birds was still markedly different from the composition in undisturbed forest. This analysis demonstrates the importance of preventing habitat fragmentation and the spread of fires in humid tropical forests, and highlights the need for more research to determine the long-term suitability of large areas of degraded forest for forest birds.

1. Introduction

Although tropical forests continue to be threatened by high rates of deforestation (Skole and Tucker, 1993; Whitmore, 1997; Laurance et al., 2001a), the area of remaining forest that is degraded by anthropogenic disturbance each year is much larger than that converted to alternative land uses (Skole and Tucker, 1993; Barreto et al., 2004). These contemporary forms of forest disturbance affect resource availability and change the physical environment, and may alter the density, biomass or spatial distribution of the biota (White and Pickett, 1985; Walker and del Moral, 2003). The composition and structure of tropical forests and their soils are altered as a result of selective logging, wildfires and edge-effects (e.g. Uhl and Buschbacher, 1985; Cochrane and Schulze, 1998; Pinard et al., 2000; Fimbel et al., 2001; Malcolm, 2001; Putz et al.,

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* *Corresponding author*: Tel.: +44 1603 591426/592549; fax: +44 1603 501327.
E-mail address: J.Barlow@uea.ac.uk (J. Barlow).

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2001; Laurance et al., 2002; Fredericksen and Pariona, 2002; van Nieuwstadt, 2002; Barlow and Peres, 2004a), while deforestation affects the dynamics of the matrix habitat, which can increase fragment isolation (Stouffer and Bierregaard, 1995a,b; Gascon et al., 2000). However, little is known about the relative severity of these different forms of disturbance. We address this by using mist-net data from seven different studies that examined the responses of understorey birds to selective logging, fire, and fragmentation (see Tables 1 and 2). We provide a quantitative appraisal of the relative severity of these different types of disturbance, and assess their implications for conservation and future research priorities.

Deforestation and land-use change has led to the creation of many small forest isolates in the highly fragmented landscapes along active frontiers (Peres and Michalski, in press), contributing to the creation of up to 20,000 km of forest edges each year in the Brazilian Amazon alone (M. Cochrane and D. Skole, pers. comm.). Logging operations have also been expanding dramatically in the Amazon in recent years (Laurance, 1998) with the annual extraction of approximately 7 million trees worth $2.5 billion (Lentini et al., 2003). The intensity of these logging practices vary greatly, and although 80% of all logging operations are estimated to be illegal and poorly executed (Laurance, 1998), the recent designation of 50 million ha of National forests (12% of the Brazilian Amazon) indicates that reduced impact methods could soon be implemented across large tracts of tropical forest (Veríssimo et al., 2002; Veríssimo and Barreto, 2004).

Selective logging and fragmentation also reduce forest flammability thresholds (Uhl and Buschbacher, 1985; Holdsworth and Uhl, 1997; Cochrane and Laurance, 2002), and combined with droughts induced by ENSO (El-Niño Southern Oscillation) events have led to a substantial increase in the prevalence of fires in humid tropical forests in recent years. Although 40,000 km^2 of Amazonian forest are estimated to have burned during the 1998 dry season (Diaz et al., 2002), the potential extent of wildfires is much greater. As many as 1.5 million km^2 could become highly vulnerable to wildfires during ENSO years (Nepstad et al., 2001), and 259,000 km^2 of forest along the 'deforestation arc' are estimated to be at risk from recurrent fires (Cochrane, 2001).

The effects of these disturbances on forest wildlife have been quantified across many geographic regions and for many taxa (Putz et al., 2001 and Fimbel et al., 2001 for selective logging, Turner, 1996 and Laurance et al., 2002 for fragmentation, and Barlow and Peres, 2004a for fires). Birds are one of the best known of these tropical taxa (Dunn, 2004), and the extent to which tropical forest avifaunas are affected by current anthropogenic activities has been related to the extraction rate and the degree of collateral damage in selective logging operations (Johns, 1991; Mason, 1996), the initial burn severity and the resulting tree mortality from fires (Barlow and Peres, 2004b), and the size of forest fragments (Bierregaard and Lovejoy, 1989; Stouffer and Borges, 2001). However, the relative effects of these different disturbance types are harder to predict, as forest wildlife may respond to the composition of the surrounding landscape, or the extent of disturbance-induced regeneration (Farhig, 2003). A quantitative assessment of the relative severity of these different structural forms of disturbance is vital if conservation strategies are to be effectively prioritised.

2. Methods

All data comes from primary forest *terra firme* sites where bird capture data were available from undisturbed forest and forest disturbed by fragmentation, fire, or selective logging (see Fig. 1). We minimised the geographic variation in species composition and the potential influence of any variation in historical environmental stability on species resilience (Danielsen, 1997; Jones et al., 2001) by restricting the analysis to Amazonia. Sites were located (from east to west) in or near Paragominas (Kranz, 1995), the Tapajós National Forest (Henriques and Wunderle unpublished data), the Tapajós-Arapiuns Extractive Reserve (Barlow et al., 2002; Barlow and Peres, 2004b), about 80 km north of Manaus (BDFFP; Guilherme and Cintra, 2001), and the Imataca Forest Reserve, Venezuela (Mason, 1996).

The undisturbed forest treatments that were used as controls were located within the same landscapes as the disturbance treatments. Selectively logged forests are defined as those where the selective felling of species of commercial value had occurred (i.e. patch cuts), though we also include three silvicultural treatments – pre-harvest liberation thinning (girdling of non-commercial tree species in an attempt to increase growth rates and densities of commercially viable

Table 1 – Methodological differences between studies

Study	Hours nets were open[a]	Number of nets per sample	Other methodological details
Mason (1996)	0600–1430	18–21	Gaps and logging roads avoided
Barlow and Peres (2004b)	0600–1800	24	Large tree falls and existing trails avoided
Barlow et al. (2002)	0600–1800	24	Large tree falls and existing trails avoided
Kranz (1995)	0600–1200	20	Gaps avoided
Guilherme and Cintra (2001)	0600–1200	n.a.	Nets located along established tracks
BDFFP	0600–1400	8 or 16[a]	Isolates of different ages; most isolates more than 100 m from continuous forest
Wunderle et al. (in press)	0600–1500	64	Nets arranged in groups of two, stratified design targeted forest matrix, natural treefalls and logging gaps

All studies focused on single disturbance events, with the exception of Kranz (1995), where burned forests had been logged prior to the fire.
n.a., not available.
a BDFFP used eight nets per netline in 1 ha fragments and 16 nets per netline in 10 and 100 ha fragments.

Table 2 – Studies and disturbance types used in the analysis

Treatment code[c]	Study	Disturbance	Years since disturbance	Total net hours	Number of local spatial replicates
t1	Guilherme and Cintra (2001)	None	–	1440	3
t2	Guilherme and Cintra (2001)	Selectively logged (all trees = 55 cm DBH)	10	1440	3
t3	Guilherme and Cintra (2001)	Selectively logged (all trees = 50 cm DBH)	10	1440	3
t4	Guilherme and Cintra (2001)	Selectively logged (all trees = 40 cm DBH)	8	1440	3
t5	Guilherme and Cintra (2001)	Selectively logged (all trees = 55 cm DBH)	4	1440	3
t6	Guilherme and Cintra (2001)	Girdling of tree species without commercial value	11	1440	3
t7	Wunderle et al. (in press)	None	–	7168	2
t8 – a	Wunderle et al. (in press)	Selectively logged (under FLONA management)	2	3584	2
t9 – b	Wunderle et al. (in press)	Selectively logged (under FLONA management)	3	3584	2
t10	Mason (1996)	None	–	~5000	6
t11 – a	Mason (1996)	Selectively logged	<1	~1250	2
t12 – b	Mason (1996)	Selectively logged	5–6	~2500	2
t13	Mason (1996)[a]	Logged with vines cut	5	~1250	2
t14	Mason (1996)[a]	Logged with enrichment strips	5–6	~2000	2
t15	Barlow and Peres (2004b)	None	–	7200	10
t16 – a	Barlow et al. (2002)	Once-burned	1	5760	8
t17 – b	Barlow and Peres (2004b)	Once-burned	3	8640	12
t18	Barlow and Peres (2004b)	Twice-burned	3	4320	6
t19	Kranz (1995)	None	–	720	3
t20	Kranz (1995)	Selectively logged and once-burned	1	720	3
t21	BDFFP[b]	None	–	4096	1
t22 – a	BDFFP[b]	1 ha fragments	1	3368	5
t23 – b	BDFFP[b]	1 ha fragments	3	1415	5
t24 – c	BDFFP[b]	1 ha fragments	5	1345	5
t25 – a	BDFFP[b]	10 ha fragments	1	12239	4
t26 – b	BDFFP[b]	10 ha fragments	3	2579	4
t27 – c	BDFFP[b]	10 ha fragments	5	2485	4
t28 – a	BDFFP[b]	100 ha fragments	1	10006	2
t29 – b	BDFFP[b]	100 ha fragments	3	2644	2
t30 – c	BDFFP[b]	100 ha fragments	5	1922	1

a Time since logging only – the additional silvicultural practices of vine cutting and enrichment strips occurred 1 year and 3 years prior to sampling, respectively.
b Biological dynamics of forest fragment project (BDFFP).
c Letters denote temporal replicates of the same spatial samples.

species; Guilherme and Cintra, 2001), the post-harvest cutting of vines (to minimise competition faced by commercially valuable trees; Mason, 1996) and the post-harvest creation of enrichment strips (3 m × 100 m strips placed 50 m apart, and planted with commercially desirable species; Mason, 1996). Forest isolate data are from the three fragment sizes (1, 10 and 100 ha) examined in the Biological Dynamics of Forest Fragment Project (BDFFP hereafter) (Bierregaard et al., 2001). Two wildfire regimes are examined – low-intensity surface wildfires in forest that had burned only once in living memory, and higher intensity recurrent fires in forests that burned twice in the last 12 years. Flame heights rarely exceed 30 cm in once-burned forest. Fires in forests burning for a second time are typically more intense, with flames occasionally reaching into the canopy (e.g. Cochrane and Schulze, 1998).

Understorey birds are suitable for this kind of analysis as they are good indicators of disturbance in tropical forests, responding to changes in local vegetation structure (Mason, 1996; Pearman, 2002; Barlow et al., 2002; Barlow and Peres, 2004b), landscape scale processes (Stouffer and Bierregaard, 1995a,b; Robinson, 1999; Pearman, 2002), and floristic composition and the availability of food resources (Bersier and Meyer, 1994; Barlow and Peres, 2004b). Furthermore, Amazonian birds are relatively well studied from a taxonomic and ecological standpoint (Cohn-Haft et al., 1997; Terborgh, 1985; Terborgh et al., 1990; Oren and Parker, 1997), allowing a species classification into foraging and dietary guilds (see Table 3). We use the guild classification of Terborgh et al. (1990), with information on additional species extracted from Sick (1997); Hilty and Brown (1986); Thiollay (1994), and Ridgley and Tudor (1989, 1994). Guilds are a useful tool for examining community changes in species-rich environments (Terborgh and Robinson, 1986), facilitating comparisons between communities that differ in species composition. The classification

Table 3 – Foraging and dietary guild classifications, and results from correlations between guild abundance (standardised between studies by using the proportion each guild contributed to each sample, n = 30), and MDS axis scores 1 and 2 (see Fig. 2)

Foraging and dietary guild	Guild code	MDS axis 1		MDS axis 2	
		r	*p*	*r*	*p*
Arboreal frugivore	FA	−0.12	0.519	**0.61**	**<0.001**
Terrestrial frugivore	FrT	0.26	0.167	−0.25	0.178
Arboreal granivore	GA	**0.59**	**0.001**	0.25	0.179
Terrestrial granivore	GrT	0.06	0.768	**0.44**	**0.016**
Ant-following insectivore	IAF	**−0.90**	**<0.001**	0.14	0.475
Arboreal gleaning insectivore	IAG	**0.75**	**<0.001**	−0.18	0.330
Arboreal sallying insectivore	IAS	−0.20	0.288	**−0.56**	**0.001**
Internal bark-searching insectivore	IBI	**0.65**	**0.000**	0.33	0.076
Bark-searching insectivore	IBS	−0.08	0.655	**−0.63**	**<0.001**
Dead leaf gleaning insectivore	IDL	−0.33	0.078	−0.15	0.435
Terrestrial gleaning insectivore	ITG	0.19	0.316	**−0.40**	**0.029**
Terrestrial sallying insectivore	ITS	0.06	0.753	−0.39	0.035
Arboreal nectarivore	NA	**0.60**	**<0.001**	**0.44**	**0.014**
Arboreal omnivore	OA	0.08	0.683	0.24	0.199

Statistics not shown for diurnal raptors, nocturnal raptors and aquatic guilds.

of Stotz et al. (1996) was also used to group species by their sensitivity to disturbance.

Mist-netting is a useful technique for sampling the non-vocal and secretive understorey birds (Karr, 1981), which are often the most susceptible to forest disturbance (Johns, 1991; Aleixo, 1999). A number of studies based on point counts were excluded from this analysis, as this method has yet to be used to examine the effects of fires or fragmentation in Amazonian forests. Furthermore, abundance estimates from mist-netting and point-counts often differ (Lambert, 1992), while direct observations may be biased when established trails and logging roads were used to sample birds (Johns, 1989; Thiollay, 1992). One of the key advantages of mist-netting is that it is more robust to differences in observer ability than techniques involving direct observation. Finally, as mist-netting targets small understorey species, these results are largely independent of the potentially confounding factor of subsistence hunting, which is one of the most pervasive anthropogenic influences on larger vertebrates throughout Amazonia (Peres and Lake, 2003).

All studies were conducted in the forest understorey using similar nets with the same mesh size (36 mm). However, they still varied in their methodology (Table 1), and capture success can still be highly variable (see Remsen and Good, 1996), depending on (among other things) the spatial configuration of the nets, the season when netting occurred, the time of day when nets were opened, the number of days that net-lines were operated in the same place, and whether nets were placed along established or new trails. Therefore, although all capture data were converted to captures per 1000 mist-net hours (hereafter, mn-h) to compare between samples with different sizes (mn-h), it was also necessary to standardise the data within Primer v.5 in order to compare guild abundances between studies with different capture rates. Unstandardised data were used in all analysis where disturbed forest samples were compared directly with their local control sample.

Because studies differed in sample effort, understorey bird composition and diversity, all disturbed forest samples were compared with the undisturbed forest sample from the same study. The % dissimilarity between the community composition of each disturbed forest sample and the undisturbed forest control was calculated using the Bray-Curtis similarity index, comparing all captures identified to species level. The use of the Bray-Curtis index as our primary measure of disturbance severity was supported by highly significant correlations between this and other measures of avifaunal responses to disturbance. These include the % change (from undisturbed forest) in the abundance of species classified by Stotz et al. (1996) as disturbance sensitive ($r = -0.734$, $n = 24$, $p = <0.001$), changes in the % dissimilarity of understorey and terrestrial species only ($r = 0.91$, $n = 24$, $p = <0.001$), the number of shared species ($r = -0.46$, $n = 24$, $p = <0.026$), and the Jaccard dissimilarity index ($r = 0.88$, $n = 24$, $p = <0.001$). The severity of the effects (average % dissimilarity from primary forest) were compared with an ANOVA test, with disturbance type (fragmentation, logging or low-intensity fire) as the independent variable, and time since disturbance entered as a covariate.

Non-metric multi dimensional scaling (MDS) was used to ordinate samples based on the relative abundance of foraging and dietary guilds. All MDS was undertaken in PRIMER v.5 (Clarke, 1993) using the Bray-Curtis similarity index. A plot with 2 axes was preferred over a plot with 3 axes as the stress was already below 0.2, and the addition of a third axis did little to reduce it further (Clarke, 1993). Plots were rotated to display the highest amount of variance on axis 1. MDS was preferred over other ordination methods because fewer assumptions are made over the shape of guild responses, although similar ordinations were achieved using other methods such as Canonical correspondence analysis (CCA) using CANOCO v.4.5 (Ter Braak and Smilauer, 1998). PRIMER v.5 was also used to conduct ANOSIM (Analyses of Similarity; Clarke and Green, 1988) to test for significant differences

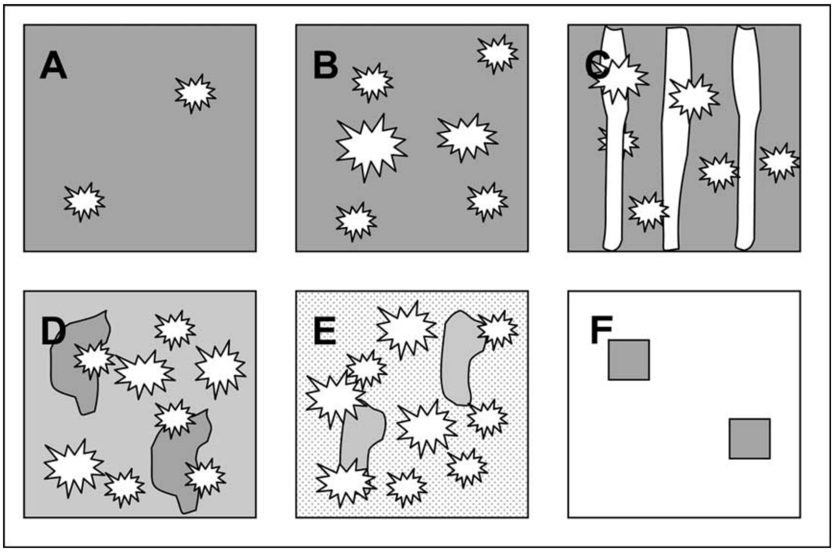

Fig. 1 – A schematic representation of the forms of habitat degradation in Amazonian forests examined here, from: (A) undisturbed forest (intact canopy with natural tree fall gaps), (B) selectively logged forest, (C) selectively logged forest with enrichment strips, (D) once-burned forest (a more open canopy punctuated by large treefall gaps, and patches of unburned forest), (E) twice-burned forest (a very open canopy disrupted by many large tree fall gaps, and a few areas of lightly burned forest), and (F) forest isolates, with relatively intact canopies (at the time of sampling).

between disturbance types, and to calculate the index of multivariate dispersion (Warwick and Clarke, 1993). The influence of the different foraging and dietary guilds in determining the MDS ordination were examined by correlating guild change with the MDS axes. (see Fig. 2)

3. Results

This analysis combined data from over 100,000 mn-h of sampling effort (Tables 1 and 2), resulting in the capture of 279 species. Only 10% of the species (26) were captured in all studies. However, the community composition (calculated from the abundance of the 17 guilds in Table 3) of undisturbed forest plots was similar across sites, despite these regional differences in species composition and the methodological differences between studies (Table 1). All six undisturbed forest samples clustered closely together in the MDS ordination (Fig. 2), and had a lower index of dispersion than any of the disturbance types (Index of Multivariate Dispersion for samples was 0.57 in undisturbed forest; 1.05 in logged forest; 1.08 in forest fragments; 1.10 in once-burned forest). Furthermore, greater geographic distance between undisturbed sites did not lead to significantly lower similarity between the bird communities (pairwise comparisons between the Bray-Curtis similarity and the actual distance between sites: two-tailed test, $r_s = -0.25$, $n = 15$, $p = 0.37$).

3.1. *Differences between disturbance types*

The three forms of disturbance (logged, burned and fragmented forest), all tended to form discrete clusters in the MDS ordination, although selectively logged forest and silviculture samples were statistically indistinguishable from control samples (Table 4). However, they were considerably more dispersed in MDS space (Fig. 2), and logged forest samples with high levels of canopy perforation and understorey perturbation (such as those with additive silvicultural practices such as enrichment strips; t14 in Fig. 2) ordinated closer to the once-burned forest samples than those with lower rates of forest disturbance, such as girdling (t6 in Fig. 2). Burned and fragmented forests grouped separately along MDS axis 2, and were significantly different from each other, as well as from the logged and control samples (Fig. 2, Table 4).

3.2. *Avifaunal dissimilarity between disturbance types*

All disturbance samples were considerably less similar to the neighbouring undisturbed control samples than the background levels of spatial and temporal dissimilarity measured within undisturbed forest (Fig. 3). There were significant differences between the average severity of disturbance types, despite using a very coarse classification: selective logging had the least influence on the % dissimilarity of understorey birds from the undisturbed controls, while fire disturbance had the greatest effect (mean ± SE difference from undisturbed forest in logged forest = 35.7 ± 6.4% ($n = 11$); forest fragments = 49.7 ± 15.6% ($n = 9$); once-burned forest = 54.1 ± 1.6% ($n = 3$); twice-burned forest = 89.2% ($n = 1$); ANOVA (excluding twice-burned forest, and with time since disturbance included as a covariate; time; $F_{1,\ 19} = 0.28$, $p = 0.60$; disturbance category; $F_{2,\ 19} = 5.05$, $p = 0.017$). The variation within disturbance types was high, and although low-intensity selective logging and silvicultural treatments had the least effect on understorey bird composition, the creation of enrichment strips after logging altered the avifauna to a similar extent as low-intensity surface fires and the isolation of 10 and 100 ha fragments (Fig. 3).

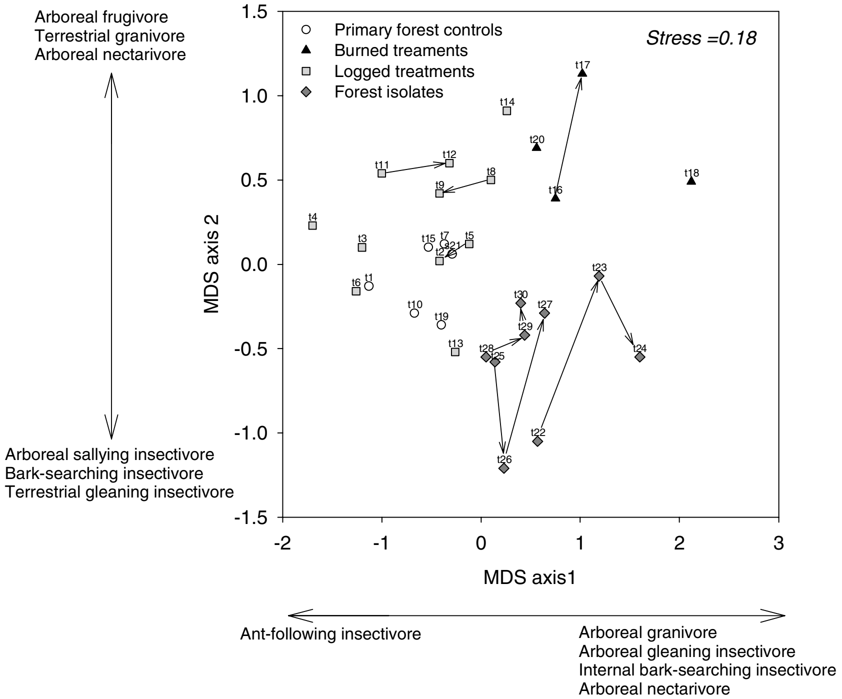

Fig. 2 – MDS ordination of 24 disturbance samples and six undisturbed forest controls, ordinated by similarity based on the abundance of foraging and dietary guilds. There were significant differences between groups (ANOSIM, global $R = 0.42$, $p = 0.001$), and only undisturbed controls and logged forest samples were statistically indistinguishable (see Table 4). Lines link temporal replicates of the same sample. See Table 2 for disturbance codes.

Selective logging, fragmentation, and surface fires also appeared to have distinct effects on avian guild structure across the range of temporal classes examined (Fig. 2). Axis 1 is a strong correlate of disturbance severity, and the disturbed forest samples correlated very highly with the % dissimilarity of species composition from primary forest shown in Fig. 3 ($r = 0.86$, $n = 24$, $p < 0.001$). These differences along axis 1 were driven by strong declines in ant-following insectivores, and increases in arboreal nectarivore, internal bark-searching insectivore, arboreal gleaning insectivores and arboreal granivores (Fig. 2, Table 3). Axis 2 was not correlated with overall disturbance severity ($r = -0.04$, $n = 24$, $p = 0.87$), but was associated with declines in external bark-searching and arboreal sallying insectivores, and strong increases with arboreal frugivores (Table 3).

4. Discussion

This cross-site comparison between the effects of selective logging, forest fragmentation and wildfires revealed considerable differences in the relative severity of their short-term impacts upon understorey bird assemblages. First we examine the differences in avian responses between disturbance types, and then discuss the implications of these results for conservation planning in tropical forests, and highlight future research priorities.

Table 4 – Analyses of similarity (ANOSIM) and analyses of variance (ANOVA) results for comparisons between 30 mist-net samples grouped by treatment type (grouped as PF – undisturbed primary forest, LF – logged forest, BF – once-burned forest, and FR – forest fragments)

Comparison	ANOSIM		ANOVA Tukeys post-hoc	
	r	p	p – Axis 1	p – Axis 2
PF–LF	−0.08	0.79	Ns	Ns
PF–BF	0.91	0.012	0.005	0.016
PF–FR	0.44	0.001	0.001	Ns
LF–BF	0.58	0.003	0.002	Ns
LF–FR	0.55	0.001	<0.001	<0.001
BF–FR	0.40	0.045	Ns	<0.001

ANOSIM was conducted on the similarity matrix based on the Bray-Curtis similarity index. ANOVA results shown are Tukeys post-hoc tests from comparisons using MDS axis scores. The twice-burned forest sample was excluded from this analysis because $n = 1$.

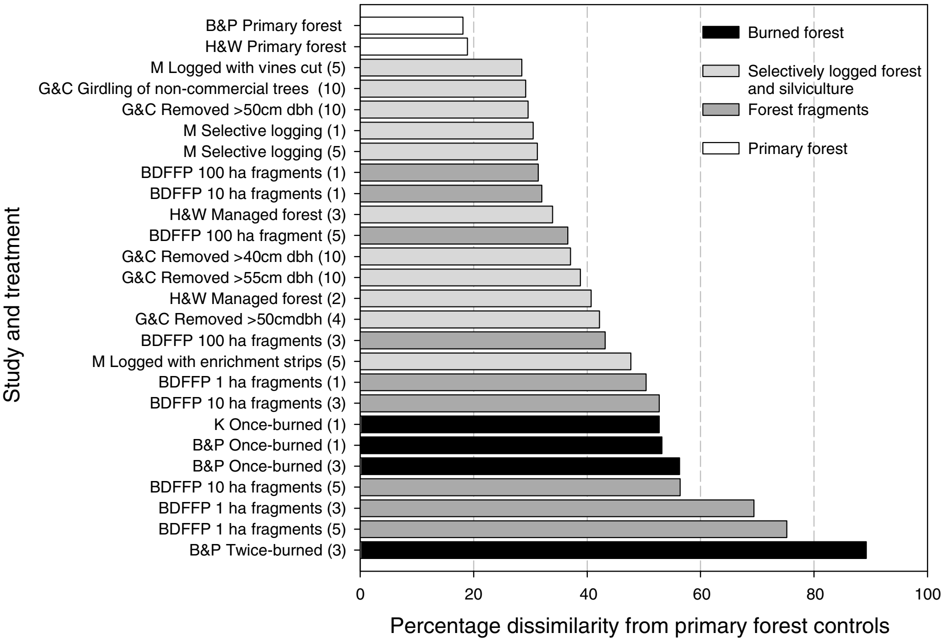

Fig. 3 – The % dissimilarity (Bray-Curtis) of the avifauna (all identified captures) in 24 disturbed forest samples from their undisturbed forest controls. The number of years since disturbance are indicated in brackets. The two primary forest bars show average dissimilarity values in undisturbed primary forest, derived from a temporal comparison between the same plots sampled 2 years apart (Barlow and Peres, 2004b), and a spatial comparison between two sites sampled simultaneously.

4.1. *Responses to anthropogenic disturbance*

The assumption that the composition of guilds sampled by mist-nets is similar across the Amazonian primary forests where these studies took place was supported. Undisturbed primary forest samples clustered together in the MDS ordination and had a low index of dispersion. For instance, there was no significant relationship between the geographic distance between sites and the similarity of the undisturbed forest samples at each site. Most of the differences between studies can therefore be attributed to the disturbance type regime rather than to the differences between their methodologies or the potential effect of geographic location.

Logging, fires and fragmentation differed from each other in terms of their average severity (Fig. 3) and in their effects on guild composition. While burning and the creation of small fragments were similar in terms of their severity (see axis 1, Figs. 2 and 3), they were significantly different on axis 2, reflecting the high post-fire abundance of guilds such as granivores, frugivores and nectarivores, which can benefit from intermediate levels of disturbance such as natural tree fall gaps, soil disturbance, canopy perforation or edge creation (Levey, 1988; Restrepo et al., 1999; Barlow and Peres, 2004b; Wunderle et al., 2005).

4.2. *Implications for the conservation of forest birds*

Determining the relative severity of anthropogenic influences in tropical forest is an important step if conservation action is to be effectively implemented. We assess each disturbance type in turn, examining the conservation implications of their continued spread across tropical forests.

4.2.1. *Selective logging*

Selective timber harvest is an important economic activity in tropical forests, where it has received considerable attention from ecologists and economists, and been promoted as the least environmentally damaging of the financially viable land uses (Pearce et al., 1999). Although the effect of low-impact logging on species composition was clearly detectable here (Fig. 3), the effects of logging were generally smaller than other disturbance types, supporting claims that carefully managed selective logging operations can help maintain relatively high levels of biodiversity. However, it should be recognised that these results may not be representative of large areas of logged forests far from recolonisation sources, and that the effects of repeated timber harvest over variable time intervals remain unknown (Bawa and Seidler, 1998). Furthermore, it is essential that logged forests are carefully managed to prevent fires, haphazard human settlements, fragmentation, and hunting, all of which are associated with most contemporary logging activities (Laurance, 1998), and can be extremely detrimental for forest wildlife.

4.2.2. *Silviculture*

Some logging operations are modified by silviculture in an attempt to increase future commercial returns, or minimise collateral damage. The evidence from Mason (1996) suggests that the post-felling creation of enrichment strips increases the degree to which the bird assemblage diverges from those of undisturbed forest, and should be discouraged if biodiversity conservation is placed above economic yield. Paradoxically, vine cutting after logging appeared to reduce the effects of the logging operation (Mason, 1996), possibly by preventing the post-disturbance dominance of vines (Laurance et al., 2001b). However, any slight benefits for understorey birds should be balanced against the potential loss of many liana-dependent species. Although the girdling of non-commercial species produced one of the least noticeable effects, this was sampled before the remaining commercially viable species were subsequently felled and removed (Guilherme and Cintra, 2001), when much higher levels of disturbance would occur.

4.2.3. *Forest fragmentation*

Many bird studies report detrimental responses to the isolation of tropical forest patches (Bierregaard and Lovejoy, 1989; Stratford and Stouffer, 1999; Stouffer and Borges, 2001; Robinson, 1999; Lambert and Collar, 2002). We show that the community responses (in terms of the % difference from primary forest) for 1–100 ha plots are comparable to those found following low-intensity wildfires, providing a strong argument against the creation of small forest isolates. Furthermore, results from the BDFFP fragments should be considered as conservative compared to forest isolates created through road building and the expansion of cattle ranching, cash crops, and mining operations. This is because (1) non-experimental fragments are often highly irregular in shape, and have much higher edge-area ratios than the square fragments studied in the BDFFP; (2) almost all ‘real world’ fragments created outside of experimentally controlled situations are subjected to high levels of associated anthropogenic disturbance events such as selective logging, hunting and fires (Cochrane and Laurance, 2002; Lambert and Collar, 2002; Peres and Michalski, in press); (3) BDFFP fragments were located close to source populations in continuous primary forest, and are not representative of fragments in the active deforestation frontiers of southern and eastern Amazonia (Peres and Michalski, in press); (4) we only include data from 1 to 5 years following isolation, before the ecological implosion of isolates (Laurance et al., 1997; Gascon et al., 2000; Laurance et al., 2002) when most avian extinctions are known to occur (Brooks et al., 1999; Robinson, 1999; Ferraz et al., 2003).

4.2.4. *Surface wildfires*

The spread of fires into primary forests should be seen as one of the greatest threats to the conservation of the understorey forest birds: low-intensity fires in unlogged and logged-and-burned forests altered avifaunal composition of forests to a similar extent as the most severe forms of selective logging (with additional post-felling silvicultural practices) and the smallest fragment sizes (Fig. 3). As forests affected by logging or by edge-dependent effects of fragmentation are more likely to burn than undisturbed primary forest (Uhl and Buschbacher, 1985; Holdsworth and Uhl, 1997; Cochrane et al., 1999; Nepstad et al., 1999; Cochrane and Laurance, 2002), these results strongly suggest that any edge-creation or logging should take into account the vulnerability of forests to fire. Furthermore, because even undisturbed forest can burn during severe ENSO-related droughts (Peres, 1999; Barlow and Peres, 2004a), haphazard development should be restricted and ignition sources controlled in seasonally-dry forests that have low flammability thresholds, such as those on sandy soils (Nepstad et al., 1998).

Furthermore, many forests have already succumbed to fire, setting in motion a positive feedback process that renders them increasingly likely to burn again (Cochrane et al., 1999; Nepstad et al., 1999). Such recurrent fires were by far the most severe form of forest degradation examined here, reinforcing the need for the careful control of large-scale forest disturbance in fire-sensitive areas. We suggest that the creation of large primary forest reserves or National Forests along developing frontiers may be the most effective way of preventing haphazard frontier expansion and the associated spread of wildfires.

4.3. *Analytical limits and future research priorities*

This analysis focused on guild and community level responses, allowing comparisons between studies with different sample sizes and from forests containing different species. However, this approach had important limitations, and many of the species-level responses to disturbance were not investigated. Furthermore, we would expect more differences among guild responses to different forms of disturbance to emerge with increased replication, a better understanding of heterogeneity within disturbance types, and a finer classification of disturbance classes. A number of further caveats are worth considering.

Temporal change: Because of a lack of long-term data, this study was focused on the short-term effects of disturbance. Temporal shifts in community structure are an integral part of post-disturbance responses (Bierregaard and Lovejoy, 1989; Thiollay, 1992; Stouffer and Bierregaard, 1995b; Wunderle, 1995; Mason, 1996; Ferraz et al., 2003; Barlow and Peres, 2004b), and were also evident here within this study (Fig. 2). However, small sample sizes and uneven temporal replication meant we were unable to examine the potential interaction between disturbance type and the post-disturbance temporal changes in bird communities. Moreover, from a conservation perspective longer term data are required to accurately compare the prospects for the post-fire recovery of forest wildlife, and assess the long-term sustainability of repeated timber harvests.

Species persistence: The presence of a species in an area does not necessarily mean that they are suitable for its long-term persistence (O’Brien et al., 2003), particularly as these studies focused on areas of disturbed forest that were near source populations in primary forest.

Vegetation structure: Although all studies reported at least some data on forest structure, the variables measured often differed and it was not possible to use these to make quantitative comparisons with changes in the avifauna. Interpretation of results in the future will be greatly enhanced by the collection (and reporting) of a number of standardised forest structure variables, such as the number of live trees, stand basal area, canopy cover, and understorey vegetation density.

Sampling methodology: Although mist-netting allowed us to compare data from seven studies, it can also be biased (see Section 2 and Remsen and Good, 1996). While studies based on standardised point counts were insufficient to be included in this analysis, their future inclusion would add important information on species rarely captured in mist-nets.

Synergistic effects: The disturbance types examined here rarely occur independently of each other (e.g. logging and fragmentation lead to fires, and fragments are frequently logged; e.g. Cochrane and Laurance, 2002; Peres and Michalski, in press). However, very few studies address the effects of two or more co-occurring disturbance events, which may have synergistic and increasingly detrimental effects on forest wildlife.

5. Conclusion

It is self-evident that management strategies that succeed in reducing the: (1) removal rates and damage during logging operations, (2) creation of forest fragments, or (3) the extent of burn coverage and the severity of fires will prove beneficial for disturbance-sensitive forest wildlife. However, by comparing their relative severity, this analysis highlights the extremely damaging nature of forest fires and the isolation of small fragments, and also suggests that low-intensity and carefully managed logging practices could play an important role in Amazonian forest wildlife conservation if used as an economically viable complement to the preservation of pristine forest. Forests managed for selective logging will prove especially useful if these are located in areas that would otherwise be subjected to haphazard and illegal frontier advance.

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REFERENCES

Aleixo, A., 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. Condor 101, 537–548.

Barlow, J., Haugaasen, T., Peres, C.A., 2002. Effects of ground fires on understorey bird assemblages in Amazonian forests. Biol. Conserv. 105, 157–169.

Barlow, J., Peres, C.A., 2004a. Ecological responses to El Niño-induced surface fires in central Amazonia: management implications for flammable tropical forests. Phil. Trans. R. Soc. Lond. B 359, 367–380.

Barlow, J., Peres, C.A., 2004b. Avifaunal responses to single and recurrent wildfires in Amazonian forests. Ecol. Appl. 14, 1358–1373.

Barreto, P., Souza Jr., C., Anderson, A., Salomão, R., Wiles, J., 2004. Human Pressure on the Brazilian Amazon Forest Biome. IMAZON/World Resource Institute, Belém, Pará.

Bawa, K., Seidler, R., 1998. Natural forest management and conservation of biodiversity in tropical forests. Conserv. Biol. 12, 46–55.

Bersier, L.F., Meyer, D.R., 1994. Bird assemblages in mosaic forests - the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecol. Int. J. Ecol. 15, 561–576.

Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R., 2001. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press.

Bierregaard, R.O., Lovejoy, T.E., 1989. Effects of forest fragmentation on Amazonian understorey bird communities. Acta Amazonica 19, 215–241.

Brooks, T.M., Pimm, S.L., Oyugi, J.O., 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13, 1140–1150.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Australian J. Ecol. 18, 117–143.

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a biological effects study. Marine Ecol. Programme Series 46, 213–226.

Cochrane, M.A., 2001. In the line of fire – understanding the impacts of tropical forest fires. Environment 43, 28–38.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P., Davidson, E.A., 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284, 1832–1835.

Cochrane, M.A., Laurance, W.F., 2002. Fire as a large-scale edge effect in Amazonian forests. J. Tropical Ecol. 18, 311–325.

Cochrane, M.A., Schulze, M.D., 1998. Forest fires in the Brazilian Amazon. Conserv. Biol. 12, 948–950.

Cohn-Haft, M., Whittaker, A., Stouffer, P.C., 1997. A new look at the species-poor central amazon: the avifauna north of manaus, Brazil. Ornithol. Monographs 48, 205–235.

Danielsen, F., 1997. Stable environments and fragile communities: does history determine the resilience of avian rain-forest communities to habitat degradation? Biodiv. Conserv. 6, 423–433.

Diaz, M.C.V., Nepstad, D., Mendonça, M.J.C., Seroa da Motta, R., Alencar, A., Gomes, J.C., Ortiz, R.A., 2002. O Prejuízo Oculto do Fogo: Custos Econômicos das Queimadas e Incêndios Florestais na Amazônia. Unpublished manuscript.

Dunn, R.R., 2004. Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds and lepidoptera. Forest Ecol. Manage. 191, 215–224.

Farhig, L., 2003. Effects of habitat fragmentation on biodiversity. Ann. Rev. Ecol., Evol. Syst. 34, 487–515.

Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L., Lovejoy, T.E., 2003. Rates of species loss from Amazonian forest fragments. Proc. Natl. Acad. Sci. U.S.A. 100, 14069–14073.

Fimbel, R.A., Grajal, A., Robinson, J.G., 2001. Logging-wildlife issues in the tropics – an overview. In: Fimbel, R.A., Grajal, A., Robinson, J.G. (Eds.), The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. Columbia University Press, New York.

Fredericksen, T.S., Pariona, W., 2002. Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian tropical forest. Forest Ecol. Manage. 171, 223–230.

Gascon, C., Williamson, G.B., da Fonseca, G.A.B., 2000. Receding forest edges and vanishing reserves. Science 288, 1356–1358.

Guilherme, E., Cintra, R., 2001. Effects of intensity and age of selective logging and tree girdling on an understorey bird community composition in central Amazonia, Brazil. Ecotropica 7, 77–92.

Hilty, S.L., Brown, W.L., 1986. A Guide to the Birds of Colombia. Princeton University Press, Princeton, NJ.

Holdsworth, A.R., Uhl, C., 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. Ecol. Appl. 7, 713–725.

Johns, A.D., 1989. Recovery of a Peninsular Malaysian rainforest avifauna following selective timber logging: the first 12 years. Forktail 4, 89–105.

Johns, A.D., 1991. Responses of Amazonian rain-forest birds to habitat modification. J. Tropical Ecol. 7, 417–437.

Jones, M.J., Sullivan, M.S., Marsden, S.J., Linsley, M.D., 2001. Correlates of extinction risk of birds from two Indonesian islands. Biol. J. Linnean Soc. 73, 65–79.

Karr, J.R., 1981. Surveying birds in the tropics. Studies Avian Biol. 6, 548–553.

Kranz, R.H., 1995. Tree Seedling Regeneration and Bird Communities after Wildfire in a Selectively Logged Rain Forest in the Eastern Amazon. University of Wisconsin-Madison.

Lambert, F.R., 1992. The consequences of selective logging for Bornean lowland forest birds. Phil. Trans. R. Soc. Lond. B 335, 443–457.

Lambert, F.V., Collar, N.J., 2002. The future for Sundaic lowland forest birds: long-term effects of commercial logging and fragmentation. Forktail 18, 127–146.

Laurance, W.F., 1998. A crisis in the making: responses of Amazonian forests to land use and climate change. Trends Ecol. Evol. 13, 411–415.

Laurance, W.F., Albernaz, A.K.M., Da Costa, C., 2001a. Is deforestation accelerating in the Brazilian Amazon? Environ. Conserv. 28, 305–311.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Rankin-de-Merona, J.M., Gascon, C., Lovejoy, T.E., 1997. Biomass collapse in Amazonian forest fragments. Science 278, 1117.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618.

Laurance, W.F., Perez-Salicrup, D., Delamonica, P., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L., Lovejoy, T.E., 2001b. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82, 105–116.

Lentini, M., Verissimo, A., Sobral, L., 2003. Fatos Florestais da Amazônia. Instituto do homem e meio ambiente da Amazônia (IMAZON), Belém, Brazil.

Levey, D.J., 1988. Tropical wet forest treefall gaps and distributions of understorey birds and plants. Ecology 69, 1076–1089.

Malcolm, J.R., 2001. Extending models of edge effects to diverse landscape configurations, with a test form the neotropics. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), Lessons from Amazonia: The Ecology and Conservation of a Fragmented forest. Yale University Press, New Haven and London, pp. 346–357.

Mason, D., 1996. Responses of venezuelan understorey birds to selective logging, enrichment strips, and vine cutting. Biotropica 28, 296–309.

Nepstad, D., Carvalho, G., Barros, A.C., Alencar, A., Capobianco, J.P., Bishop, J., Moutinho, P., Lefebvre, P., Silva, L.S., 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecol. Manage. 154, 395–407.

Nepstad, D., Moreira, A., Verissimo, A., Lefebvre, P., Schlesinger, P., Potter, C., Nobre, C., Setter, A., Krug, T., Barros, A.C., Alencar, A., Pereira, J.R., 1998. Forest fire prediction and prevention in the Brazilian Amazon. Conserv. Biol. 12, 951–953.

Nepstad, D.C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., Brooks, V., 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398, 505–508.

O'Brien, T.G., Kinnaird, M.F., Nurcahyo, A., Prasetyaningrum, M., Iqbal, M., 2003. Fire, demography and the persistance of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. Anim Conserv. 6, 115–121.

Oren, D.C., Parker, I.T.A., 1997. Avifauna of the Tapajos National Park and vicinity, Amazonain Brazil. Ornithol. Monographs 48, 493–525.

Pearce, D., Putz, F.E., Vanclay, J., 1999. A sustainable forest future. Working paper GEC 99-15. Centre for Social and Economic Research on the Global Environment, Norwich, UK.

Pearman, P.B., 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understorey. Ecol. Monographs 72, 19–39.

Peres, C.A., 1999. Ground fires as agents of mortality in a Central Amazonian forest. J. Tropical Ecol. 15, 535–541.

Peres, C.A., Lake, I.R., 2003. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. Conserv. Biol. 17, 521–535.

Peres, C.A., Michalski, F., in press. Synergistic effects of habitat disturbance and hunting in Amazonian forest fragments. In: laurance, W.F., Peres, C.A. (Eds.), Emerging threats to tropical forests.

Pinard, M.A., Barker, M.G., Tay, J., 2000. Soil disturbance and post-logging forest recovery on bulldozer paths in Sabah, Malaysia. Forest Ecol. Manage. 130, 213–225.

Putz, F.E., Blate, G.M., Redford, K.H., Fimbel, R., Robinson, J., 2001. Tropical forest management and conservation of biodiversity: an overview. Conserv. Biol. 15, 7–20.

Remsen, J.V., Good, D.A., 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113, 81–398.

Restrepo, C., Gomez, N., Heredia, S., 1999. Anthropogenic edges, treefall caps, and fruit-frugivore interactions in a neotropical montane forest. Ecology 80, 68–685.

Ridgley, R.S., Tudor, G., 1989. The Birds of South America the Oscine Passerines. University of Texas, Austin, Texas.

Ridgley, R.S., Tudor, G., 1994. The Birds of South America. The Suboscine Passerines. University of Texas, Austin, Texas.

Robinson, W.D., 1999. Long-term changes in the avifauna of Barro-Colorado Island, Panama, a tropical forest isolate. Conserv. Biol. 13, 5–97.

Sick, H., 1997. Ornitologia Brasileira: Uma Introdução. Universidade de Brasilia, Brasilia.

Skole, D., Tucker, C., 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. Science 260, 905–1910.

Stotz, D.F., Fitzpatrick, J.W., Parker, T.A., Moskovits, D.K., 1996. Neotropical Birds. Ecology and Conservation. University of Chicago Press, Chicago.

Stouffer, P.C., Bierregaard, R.O., 1995a. Effects of forest fragmentation on understorey hummingbirds in Amazonian Brazil. Conserv. Biol. 9, 1085–1094.

Stouffer, P.C., Bierregaard, R.O., 1995b. Use of Amazonian forest fragments by understorey insectivorous birds. Ecology 76, 2429–2445.

Stouffer, P.C., Borges, S.H., 2001. Conservation recommendations for understorey birds in Amazonian forest fragments and secondary areas. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), Lessons from Amazonia: The ecology and Conservation of a Fragmented Forest. Yale University Press, pp. 248–261.

Stratford, J.A., Stouffer, P.C., 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. Conserv. Biol. 13, 1416–1423.

Ter Braak, C.J.F., Smilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco: Software for Canonical Community Ordination (version 4). Centre for Wageningen, Wageningen.

Terborgh, J., 1985. Habitat selection in Amazonian birds. In: Cody, M.L. (Ed.), Habitat Selection in Birds. Academic Press Inc., New York, pp. 311–338.

Terborgh, J., Robinson, S., 1986. Guilds and their utility in ecology. In: Kikkawa, J., Anderson, D.J. (Eds.), Community Ecology: Pattern and Process. Blackwell Scientific Publications, Melbourne, pp. 65–90.

Terborgh, J., Robinson, S.K., Parker, T.A., Munn, C.A., Pierpont, N., 1990. Structure and organization of an Amazonian forest bird community. Ecol. Monographs 60, 213–238.

Thiollay, J.M., 1992. Influence of selective logging on bird species-diversity in a Guianan rain-forest. Conserv. Biol. 6, 47–63.

Thiollay, J.M., 1994. Structure, density and rarity in an Amazonian rain-forest bird community. J. Tropical Ecol. 10, 449–481.

Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33, 200–209.

Uhl, C., Buschbacher, R., 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the Eastern Amazon. Biotropica 17, 265–268.

van Nieuwstadt, M.G.L., 2002. Vertical gradient in viable seed density and germination after fire in the seed bank of a lowland dipterocarp rain forest. In: van Nieuwstadt, M.G.L. (Ed.), Trial by Fire. Postfire Development of a Tropical Dipterocarp Forest. Utrecht University, pp. 83–94.

Veríssimo, A., Cochrane, M.A., Souza, C., 2002. National forests in the Amazon. Science 297, 1478.

Veríssimo, A.B., Barreto, P., 2004. National Forest in the Brazilian Amazon: opportunities and challenges. In: Zarin, D., Alavalpati, J., Putz, F., Schimink, M. (Eds.), Working Forest in the America Tropics: Conservation through Sustainable Management? Columbia University Press, New York, pp. 31–40.

Walker, L.R., del Moral, R., 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge.

Warwick, R.M., Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. J. Experimen. Marine Biol. Ecol. 172, 215–226.

White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. pp. 3–13.

Whitmore, T.C., 1997. Tropical forest disturbance, dissappearance, and species loss. In: Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago.

Wunderle, J.M., 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: The first 18 months. Condor 97, 879–896.

Wunderle, J.M., Henriques, L.M.P., Willig, M.R. Short-term responses of birds to forest gaps and understory: an assessment of reduced impact logging in a lowland Amazon forest. Biotropica, in press.

Wunderle, J.M., Willig, M.R., Henriques, L.M.P., 2005. Avian distribution in treefall gaps and understorey of terra firme forest in the lowland Amazon. Ibis 147, 109–129.