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Bird community responses to reduced-impact logging in a certified forestry concession in lowland Bolivia

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ABSTRACT

We studied bird community composition and abundance within the logged and unlogged forest areas of a certified forestry concession in lowland Bolivia. The logged forest was harvested using reduced-impact logging techniques between one and four years previously. We used canonical correspondence analysis to describe the relationship between selected environmental variables and bird species abundance data, and the Indicator Value procedure to test for associations between bird species and the logged and unlogged habitats. Approximately one-third of birds were restricted to either the logged or unlogged areas, with 20% of all species only encountered in, or significantly more abundant in, the unlogged areas of the concession. The majority of birds found in significantly higher abundance in the unlogged areas of the concession were associated with forest habitats dominated by large trees, or a high diversity of trees, providing dense canopy cover and deep leaf litter, with an understorey dominated by ferns. Over 40% of bird species that were significantly associated with the unlogged areas of the concession are of conservation concern. In contrast, the majority of birds associated with the logged areas of the concession are known to be relatively resilient to human disturbance. The majority of species which exhibited significant lower abundances in the logged areas of the concession belonged to insectivorous or frugivorous feeding guilds. We discuss whether current management practices within this certified concession are sustainable and how our results can be used to guide future research and inform better practice.

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1. Introduction

Reduced-impact logging (RIL) is a modified form of selective logging that is increasingly employed in tropical forests. It

incorporates a variety of techniques aimed at lowering levels of damage to the residual stand (Putz et al., 2001). These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of

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logging roads (Heinrich, 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). However, reduced-impact logging is still a form of commercial forestry that increases the frequency and extent of canopy discontinuities (Jackson et al., 2002). These changes to vegetation structure can alter microclimatic conditions, including temperature, wind and humidity levels (Pinard and Cropper, 2000; Asner et al., 2004b). The capacity of these forests to retain their original complement of biodiversity is not well known (Bojanic and Bulte, 2002; Dauber et al., 2005).

Birds are an ideal taxon for assessing the impacts of logging on biodiversity in tropical forests, as bird community composition can be strongly influenced by disturbance to forest vegetation structure (Wiens, 1992; Mason and Thiollay, 2001; Barlow and Peres, 2004). Birds also perform vital ecological functions in tropical forests and have roles as pollinators, seed dispersers, and predators (Stiles, 1983). Furthermore, quantitative assessment of the IUCN red list shows that the threat status of the world's birds has steadily worsened since 1988 (Butchart et al., 2004), with 93% of threatened forest avifauna found in tropical forests (Birdlife-International, 2004).

Studies of conventional selective logging suggest that disturbance to vegetation structure and microclimate affects bird species in a variety of ways, and is highly dependent on the guild being considered (Mason, 1996; Woltmann, 2003; Wunderle et al., 2006). For instance, because reproductive activity in understorey plants is positively correlated with increased irradiance (Costa and Magnusson, 2003), members of some avian guilds (e.g. frugivores, nectarivores) can increase in abundance following selective logging due to the increased availability of nectar and fruit in areas of canopy discontinuity (Mason, 1996; Wunderle et al., 2006). In contrast, understorey insectivores are particularly susceptible to disturbance associated with selective logging (Mason and Thiollay, 2001; Sekercioglu et al., 2002; Sodhi et al., 2004; Barlow et al., 2006; Barlow et al., 2007; Gray et al., 2007). Members of this guild may be physiologically intolerant to increased variation in temperature and humidity levels associated with decreased canopy continuity (Karr and Brawn, 1990; Mason, 1996; Sekercioglu et al., 2002; Barlow and Peres, 2004). Each species may react differently to a given forest disturbance depending (in part) on its foraging behavior, habitat specialization, and physiological sensitivity to microclimatic changes (Thiollay, 1992; Sekercioglu et al., 2002). For these reasons, studies of bird species' responses to tropical forest disturbance have reported negative or positive impacts depending on the extent of disturbance, and the species pool being considered (Hill and Hamer, 2004).

There are over 1400 species of bird known from Bolivia, with the majority of species found in the sub-tropical and tropical forests of the lowlands (Pacheco, 1998). Almost half of these areas are now granted to forestry concessions (Mostacedo and Fredericksen, 1999). In 1996, a new forestry law was enacted to promote the sustainable harvesting of timber (Mostacedo and Fredericksen, 1999). To achieve bestmanagement practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering over 2.2 million hectares had obtained certification by the Forest Stewardship Council (FSC, 2005).

We suggest that there is a need to evaluate the compatibility of reduced-impact logging with biodiversity maintenance. In this paper, we use a reduced-impact logged sub-tropical forest in Santa Cruz province, lowland Bolivia, as a case study to examine: (i) differences in avian diversity and community composition in logged and unlogged forests; and (ii) the potential conservation related repercussions of any observed differences.

2. Methods

2.1. Site description

Our study area was located in the subtropical humid forest of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100,000 ha forestry concession "La Chonta". This is owned and managed by Agroindustria Forestal La Chonta (509,000–545,000 easting, 8,275,500–824,900 northing; Fig. 1). The forest has an average elevation of 320 m (range 230–390 m). The soils consist of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean annual temperature is 25 °C with a mean annual precipitation of approximately 1560 mm. The region experiences a distinct dry season from May to October. The entire concession was subjected to legal and illegal selective logging of mahogany (Swietenia macrophylla), and spanish cedar (Cedrela odorata) 10–25 years prior to this study. The concession was certified by SmartWood in 1998.



Fig. 1 – Map of Bolivia with approximate location of the la Chonta forestry concession indicated within the department of Santa Cruz.

2.2. Harvesting procedure

Approximately 2500 ha is harvested annually over three contiguous 850 ha blocks (\sim 4 km \times 2 km), yielding 50,000 m³ of timber. Eighteen commercial tree species were harvested during the time of this study (2003–2004) including Ficus boliviana, *Hura crepitans, Terminalia oblonga, Pseudolmedia laevis, Cariana ianeirensis,* and *Cariniana estrellensis.* Average harvest intensity in this forest is approximately 4 trees/ha (Jackson et al., 2002). The forestry company Agroindustria Forestal La Chonta conducts inventories of harvestable trees one year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except F. boliviensis and H. crepitans, which are harvested above 70 cm dbh. One in five harvestable trees is required by law to be left as a seed tree. During pre-harvesting inventory, trees selected for felling are cleared of all vines around the bole.

The forestry company uses a 'fishbone' harvesting strategy with a single primary north-south road bisecting each 850 ha block. Skid trails are located 100–150 m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during felling. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25–30 years.

2.3. Survey design

Logging blocks were harvested systematically in the La Chonta concession (see Fig. 2). Logging related disturbance was



Fig. 2 – Schematic diagram representing relative location of reduced-impact logged blocks (labeled with year of harvest) and unlogged sites used in this study within the La Chonta concession, Department of Santa Cruz, Bolivia. The 'S' symbol represents transects cut within each block. Five points, comprising one representative of each of the five vegetation categories, was place along each of three east/ west transects of each 'S'. The east/west transects are \sim 1 km in length. Unlogged areas are to be harvested between 2004 and 2007.

adjacent to, but south and west of, our unlogged control blocks. We therefore acknowledge the theoretical possibility that any observed differences between bird communities found within the harvested and unharvested blocks of the concession, could be the product of a priori spatial variation in vegetation. However, unlogged areas of the concession were destined to be logged shortly after completion of our research. As such, their "unlogged" status was not indicative of associated differences in vegetation type. Second, tree species composition and abundance was consistent between the unharvested areas of the residual stand and the unlogged forest (A. Felton unpublished data). Third, a stratified-random sampling design was used which incorporated commercial tree species occurrence, vegetation height, and disturbance type. This design increased the likelihood that logged and unlogged survey points were appropriate for comparison, and accounted for natural variation in vegetation structure. This experimental design also addressed the concern that selective logging disproportionately disturbs forest with commercial densities of harvestable trees, and any random placement of survey points within the harvested blocks was unlikely to sample habitat directly comparable to that found within the unlogged forest blocks.

We defined five habitat categories: 1. 'target' points (T) with vegetation height over 20 m and possessing one of five commercial tree species (Ficus boliviensis, H. crepitans, C. estrellensis, C. ianeirensis, T. oblonga) of harvestable size; 2. 'future' points (F) from 12 to 20 m in height and possessing a commercial tree of the afore mentioned five species not yet of harvestable size but above 30 cm dbh; 3. 'non-target' points (N) of less than 12 m in height and not possessing a tree-fall gap caused by the felling of a tree (in the harvested blocks) or a natural tree fall (in the unlogged blocks) of greater than 50 cm dbh; and 5. 'road' points (R) located on a primary north-south logging road in the logged forest.

In each logging block, one to two clusters of 15 survey points, representing three of each of the five habitat categories, were randomly chosen from available alternatives (as identified during preliminary vegetation surveys) and located along three \sim 1 km long transects (see Fig. 2).We placed survey points at least 300 m apart and at least 500 m from the edge of neighbouring treatment blocks. This design was repeated until 180 survey points were designated for the logged area. The equivalent survey design was repeated in the unlogged forest for the total of 360 survey points used in the study. In the logged forest, the 'target' category was represented by seed trees left by loggers to aid regeneration. Trees not harvested due to undesirability (e.g. insufficient bole length or malformation) were not included in this category. In the residual stand of the logged forest, the edge of 'target', 'non-target', and 'future' points were located at least 15 m away from skid trails or logging gaps. All habitat categories (other than 'road' points) were located at least 250 m from logging roads.

2.4. Bird surveys

We used the point-count method of surveying bird species abundance at each of the 360 survey points. Distance to individual birds from the observer (A.F.) was grouped into two radius intervals: 0–20 m and 20 m to infinity (as per Bibby et al., 2000). The closer distance interval (0–20 m) was used in conjunction with vegetation surveys to couple observations with measured habitat variables (see Felton et al., 2008), whereas the unlimited detection results (0 m – infinity) were used for general bird community comparison between the logged and unlogged areas of the concession. Our data could be used to obtain bird density estimates if used in conjunction with Distance software (Buckland et al., 1993). However, we refrain from such analyses due to currently unresolved issues relating to the validity of the program's underlying assumptions (see Barry and Walsh, 2001). As such, we use our survey results as a surrogate of relative abundance, rather than as estimates of absolute density.

We conducted surveys from December to February of the 2003–2004 wet season. We began surveys at first light (5:45–6:00 am), and continued until approximately 10:30 am. This period overlapped with the daily peak in bird vocal activity. A day's survey consisted of visiting three points of each of the five habitat types (15 points in total). Each point was surveyed for 12 min. We included birds flushed from the survey point on approach by the observer, while birds flying over the survey area were not included in the analysis. We only undertook surveys if the weather was fine (e.g. no rain or high wind).

Due to the density of forest vegetation, most identifications were made acoustically, rather than visually. When there was potential for confusion regarding the number of calling individuals, the most conservative option was used. Recordings were made using a Sony TCM 5000 tape-recorder attached to a Sennheiser ME66 microphone. These recordings were used as a supplement to in-the-field identification of vocalizing species. For species that we were unable to identify in the field, symbolic representations of songs were noted, in addition to notes on the recording time, direction, and estimated distance to the call. This enabled us to match subsequent identifications with abundance and distance information. Unknown recordings were identified using the CD-ROM Birds of Bolivia, 2.0 (Mayer, 2000), or by an expert (B.H).

2.5. Measurement of vegetation structure and floristics

We conducted vegetation structure and floristic surveys during June and July 2004 within the 360 survey points. To reduce the effects of seasonal variation, logged and unlogged areas were surveyed on alternate days, as were blocks logged in different years. At each survey point, we marked a 20 m \times 20 m quadrat within which all trees, palms, poles and snags were counted if part of their bole encroached on the quadrat. Trees (>10 cm dbh) were identified to species-level by botanists from the Instituto Boliviano de Investigación Forestal (IBIF). We defined poles as trees less than 10 cm dbh but taller than 3 m. We counted palms up to 3 m in height were, with palms over this height also identified to species. We also took three measurements of vegetation structure from four equidistant markers located 7 m from the quadrat center. We used a 2 m rope held vertically and marked at 10 cm intervals to assess understorey density of vegetation, we. We held the rope in the centre of the quadrat with the number of bands visible from each of the four markers counted by the observer which provided our index of understorey density. We measured canopy height at each marker using a clinometer and a laser rangefinder. We also quantified canopy cover at each marker using a densiometer.

We defined a 2×2 m plot at each of the four markers. In each plot, we estimated the percentage cover of grasses, ferns, palms, seedlings, dead wood, soil, rock, sand, *Erythrochiton fallax* (Rutaceae), *Heliconia* spp. (Heliconiaceae), other herbs, and vines. Vine coverage was divided into two classes: 0-1 m ("vine low") and 1-2 m above ground ("vine high"). For further details of vegetation surveys see Felton et al. (2006).

2.6. Statistical analysis

We assessed the thoroughness of our bird sampling in the logged and unlogged forests using sample-based rarefaction curves constructed with the Mao Tau function in EstimateS v.8 (Colwell, 2005). We used the Indicator Value (IndVal) procedure (Dufrêne and Legendre, 1997) to test associations between individual bird species and the logged and unlogged areas of the concession. Higher Indicator Values therefore indicate species which are more representative for the given habitat. A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results ($\alpha = 0.05$).

We used canonical correspondence analysis (CCA ter Braak, 1986) to describe the relationship between selected environmental variables and bird data (0-20 m). CCA is a multivariate ordination technique that uses information on species' abundances at sites and the environmental variables at those sites, to produce an ordination of species distributions using nonlinear, unimodal responses (Wiens et al., 2001; Gunnarsson et al., 2006). CCA is especially useful for analyzing species-environment relationships (Palmer, 1993; Hobson et al., 2000; Grand and Cushman, 2003). All analyses were carried out using the ADE4 software package available online within the statistical analysis software R. As our vegetation structure measurements were undertaken within areas of 20×20 m, the usefulness of CCA in our study diminishes for species with individual distributions influenced by structural and floristic variables operating at larger spatial scales (see Felton et al., 2008).

3. Results

There are several assumptions inherent in the point count survey technique that can potentially bias a study's results and should be acknowledged prior to their interpretation (Bibby et al., 2000). Of principle relevance to our study, logging associated changes to vegetation structure could bias the detectability of some bird species when comparisons are made between vegetation types that differ in their relative openness. We cannot account for the exact impact of this potential bias in our results. However, we suggest that the experimental design employed in this study minimized the affect of such biases in all but two of our five surveyed habitat types (both logging roads and logging gaps were more open than their unlogged counterparts). Furthermore, encounter rates for species within the logged and unlogged areas of the concession demonstrated a consistent pattern of disturbance sensitive species being encountered more frequently in the unlogged areas and disturbance associated species being encountered more frequently in the logged areas. As our assessment of results is primarily concerned with changes to species composition, we feel confident that our interpretation of the data is robust to potential biases, with alternative explanations of our results less parsimonious. During point count surveys, we identified 5062 birds, belonging to 158 species, and 35 families. For a complete list of all species found during this study within the La Chonta concession and their relative abundance see Felton et al. (2007). In the unlogged forest 133 species were identified, of which 27 species were not found in the logged forest. In the logged forest, 132 species were identified, of which 24 species were not found in the unlogged forest. The results of samplebased rarefaction curves (Fig. 3) indicate that our sampling efforts were sufficient due to their rapid approach to asymptote.



Fig. 3 – Sample-based rarefaction curves calculated using Mao Tau as per Colwell (2005) for unlogged and logged forest points within the La Chonta concession Bolivia. The squares (unlogged) and diamonds (logged) represent individual point count results used for the accumulation curve and the dashed lines are the 95% confidence intervals. The x-axis is scaled to show the number of individuals encountered.

Table 1 – The nine bird species with the highest indicator value (IV) for unlogged habitats and subsequently the seven bird species with the highest indicator value (IV) for logged habitats, representing the degree to which a given species is associated with unlogged (U) versus logged (L) areas in the La Chonta concession, Department of Santa Cruz, Bolivia

Family	Common name	Scientific name	Unlogged	Logged	IV	P value	Sensitivity	Foraging guild
Formicariidae	Black-faced antthrush	Formicarius analis	33	14	11.31	0.003	М	Terrestrial
								insectivore
Falconidae	Barred forest-falcon	Micrastur ruficollis	9	0	5	0.004	М	Raptor
Picidae	Red-necked woodpecker	Campephilus rubricollis	27	8	9.86	0.004	Н	Bark insectivore
Ramphastidae	Channel-billed toucan	Rhamphastos vitellinus	34	13	9.24	0.005	Н	Frugivore/omnivore
Columbia	Gray-fronted dove	Leptotilla rufaxilla	49	28	13.79	0.02	М	Frugivore
Thamnophilidae	Spot-backed antbird	Hylophylax naevia	18	6	5.83	0.02	Н	Gleaning insectivore
Thraupinae	Guira tanager	Hemithraupis guira	8	1	11.96	0.02	L	Gleaning insectivore
Ramphastidae	Red-billed toucan	Ramphastos tucanus	41	18	9.65	0.02	Н	Frugivore
Polioptilidae	Long-billed gnatwren	Ramphocaenus	38	22	11.96	0.02	L	Gleaning insectivore
		melanurus						
Thamnophilidae	Black-throated antbird	Myrmeciza atrothorax	10	39	14.15	0.0001	L	Gleaning insectivore
Tinamidae	Little tinamou	Crypturellus soui	13	26	8.15	0.03	L	Terrestrial granivore
Parulinae	Golden-crowned warbler	Basileuterus culicivorus	21	36	12.28	0.01	М	Insectivore/omnivore
Picidae	Yellow-tufted woodpecker	Melanerpes cruentatus	12	35	12.83	0.002	L	Arboreal omnivore
Cardinalinae	Buff-throated saltator	Saltator maximus	0	9	5	0.003	L	Arboreal omnivore
Troglodytidae	Moutached wren	Thryothorus genibarbis	15	29	9.15	0.03	L	Gleaning insectivore
Columbidae	Scaled pigeon	Columba speciosa	26	39	12.67	0.036	М	Frugivore

A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results (α = 0.05). The number of observations for a given species in unlogged or logged surveys is also presented. "Sensitivity" to disturbance ratings are low (L), medium (M) and high (H), as per Stotz et al. (1996).

We present the IndVal scores to indicate the relative contribution of bird species to the established differences in bird community composition between the logged and unlogged areas (Table 1). Random reallocation permutations demonstrated that nine bird species were significantly associated with the unlogged areas of the concession, whereas seven bird species were significantly associated with the logged areas (Table 1). Bird species considered to exhibit a 'high' sensitivity to disturbance (Stotz et al., 1996), were prevalent amongst those species significantly associated with the unlogged areas (40% of species), and absent amongst species significantly associated with the logged areas (Table 1). Birds belonging to the insectivorous or frugivorous feeding guilds were more likely to be significantly associated with the unlogged areas than the logged areas. The only granivore that demonstrated a significant difference between the disturbed and undisturbed areas was primarily associated with logged areas of the concession. The four forest-falcon species, barred forest-falcon (Micrastur ruficollis), collared forest-falcon (Micrastur semitorquatus), lined forest-falcon (Micrastur gilvicollis), and bat falcon (Falco rufigularis), were observed only in unlogged sites.

Vegetation structure variables differed in their relationship to the first and second axes of the CCA ordination (Fig. 3). The first canonical axis (eigenvalue = 0.11) distinguished between sites with more trees, greater tree diversity, closed canopy, low vines, and deeper leaf litter in the positive direction, from those with more disturbed ground (soil) and coverage by ferns, *Heliconia* spp., and palms in the negative direction. Unlogged habitat categories primarily had positive scores on the first canonical axis, with logged sites possessing positive scores (Fig. 3).

The second canonical axis (eigenvalue = 0.095) primarily described changes in openness of the understorey and associated differences in the dominance of different understorey vegetation types (Fig. 3). Along this second axis, sites dominated by seedlings and low vines in the negative direction



Fig. 4 – Plot scores (linear combination of variable scores) for the first two axes of canonical scores from CCA analysis for vegetation variables and habitat categories in the logged and unlogged forest of the La Chonta Concession Bolivia.



Fig. 5 – Average scores are presented for bird species in the first two axes of the CCA analysis. Only those bird species that were significantly associated with the unlogged areas of the La Chonta Concession Bolivia as determined using the IndVal technique are shown. See Table 1 for details relating to the bird species represented.

were distinguished from sites dominated by ferns and trees in the positive direction. Habitat categories associated with logging disturbance were situated along the negative aspect of the second canonical axis, with unlogged categories located along the positive axis (Fig. 3).

Bird species found in significantly higher abundance in the unlogged area were primarily distributed positively along the first and second canonical axis (Fig. 4). The bird species recorded at significantly higher abundance in the logged area were primarily associated with negative scores on the first canonical axis and consistently associated with negative scores on the second canonical axis (Fig. 5).

4. Discussion

We found that bird communities significantly differed in composition between the logged and unlogged areas of the La Chonta concession. Approximately 20% of species were exclusive to or significantly more abundant in the unlogged areas. Furthermore, over 40% of bird species that exhibited a significant association with the unlogged area (Table 1) are considered to be highly sensitive to human disturbance, and of conservation concern (Stotz et al., 1996). In contrast, those species which were significantly associated with the logged areas (Table 1) are primarily species that are known to be relatively resilient to human disturbance (Thiollay, 1992; Canaday, 1996; Stotz et al., 1996; Marsden et al., 2001). Recently Gray et al. (2007) analyzed the results of 57 published studies of avian feeding guild responses to tropical forest disturbance and determined that the abundance of avian granivores tends to increase significantly, whereas insectivores and frugivores tend to decrease significantly. Our findings are consistent with their results. We suggest that despite the employment of reduced impact logging procedures and the awarding of certification status to this concession, logging associated

disturbance has still been sufficient to significantly alter resident bird community composition (see Fig. 6).

The majority of those birds found in significantly higher abundance in the unlogged areas of the La Chonta concession were associated with forest habitats dominated by large trees, or a high diversity of trees, providing dense canopy cover and deep leaf litter, with an understorey dominated by ferns (Figs. 3 and 4). These conditions are not indicative of the habitats created by logging activities. In La Chonta, skid trails, roads and landings disturb 25% of ground area with an additional 25% of the canopy opened due to tree felling (Jackson et al., 2002). Furthermore, logging gaps differ significantly from natural tree-fall gaps in size and the density and composition of understorey vegetation (Felton et al., 2006). The introduction of logging roads and skidder trails, as well as the increased frequency and extent of tree-fall gaps, all contribute to a reduction in canopy continuity and the increased prevalence of forest area in early successional stages.

How a bird species responds to forest disturbance can be dictated, at least in part, by their direct physiological sensitivity to associated changes in microclimate (Thiollay, 1992). Birds that forage exclusively in the lower understorey can be physiologically and behaviorally specialized for lower-light conditions (Stratford and Robinson, 2005). Neotropical species that evolved in the relatively stable forest understorey may be particularly intolerant to changes in microclimate (Canaday, 1996; Stratford and Robinson, 2005). Increased canopy-discontinuity that fragments these low light habitats may thereby reduce the availability of suitable foraging conditions for light-sensitive species.

For example, several insectivores, including the blackfaced antthrush (Formicarius analis), were significantly less abundant in the harvested blocks of this study. Their apparent decline may be the result of three interrelated aspects of anthropogenic disturbance. First, members of this feeding



Fig. 6 – Average scores are presented for bird species in the first two axes of the CCA analysis. Only those bird species that were significantly associated with the logged areas of the La Chonta Concession Bolivia as determined using the IndVal technique are shown. See Table 1 for details relating to the bird species represented.

guild are predicted to be particularly intolerant of habitat above threshold levels of irradiance (Stratford and Robinson, 2005; Gray et al., 2007). Logging may therefore reduce the availability of adequate microclimatic foraging conditions with resultant impacts on insectivore population abundance (Barlow et al., 2006). Second, increased irradiance may also result in the loss of food resources, with xeric conditions in the understorey reducing the composition and abundance of arthropod food resources (Karr and Brawn, 1990; Rosenberg, 1990; Mason, 1996; Barlow et al., 2002). Third, the presence of logging roads may have served to reinforce these declines.

In a study by Sekercioglu et al. (2002), the authors suggest that *F. analis* is unable to recolonize suitable habitat within fragmented landscapes because their sensitivity to altered microclimates prevents them from crossing deforested areas. Previous research has established that roads as narrow as 10 m can act as barriers to dispersal for understorey insectivores in the Neotropics (Develey and Stouffer, 2001). Logging roads in La Chonta average 11.3 m in width (Jackson et al., 2002) and are therefore potentially acting as linear barriers, severely restricting the ability of *F. analis* and other sensitive understorey species (e.g. the spot-backed antbird Hylophylax *naevia*) to re-colonize suitable habitats.

Another bird species encountered significantly more often in the unlogged areas of the concession was the barred forestfalcon *M. ruficollis*. Our results suggest that this forest raptor may be adversely affected by reduced-impact logging because of its strong association with closed canopy forests. Forest falcons, such as *M. ruficollis*, are morphologically adapted to living and hunting in forest environments, possessing short wings and long tails that aid maneuverability in dense vegetation (Jullien and Thiollay, 1996). As such, their non-detection within harvested blocks may be due to an overall decline in the suitability of appropriate vegetation structure, as has been the suggested reason for forest raptor declines from other logged sites (Jullien and Thiollay, 1996).

Their absence from logged forest also may be associated with a lack of suitable nesting trees. One study conducted in Guatemala found that the majority of M. *ruficollis* nesting hollows were located in the cavities of trees belonging to the genus *Cedrela*, and were over the minimum diameter cut size used at La Chonta (Thorstrom et al., 1990). As both *Cedrela fisilis* and *C. odorata* are harvested in the La Chonta concession (Park et al., 2005), it is possible that logging operations are reducing nesting options in harvested blocks. Notably three other species of falcon (collared forest-falcon (*M. semitorquatus*), lined forest-falcon (*M. gilvicollis*), and bat falcon (*F. rufigularis*)) were also undetected within the harvest blocks.

Two large-bodied canopy feeding frugivores also appeared to be disproportionately sensitive to the reduced-impact logging conducted within this forest. Both the channel-billed toucan *Ramphastos vitellinus* and the white-throated toucan *Ramphastos tucanus*, were significantly less common in the harvested blocks of the concession. R. vitellinus and R. tucanus are both primarily frugivorous canopy feeders (Remsen et al., 1993; Galetti et al., 2000). They are of special interest to forest managers because toucans are considered to be very effective seed dispersers (Snow, 1981). The beak of the toucan is large and dexterous and enables the toucan to consume fruit of varying sizes, from many different tree species (Galetti et al., 2000). Furthermore, their movement across large territories (estimated to be ca. 40–50 ha in the Peruvian Amazon (Terborgh et al., 1990)) increase the dispersal and associated survival rates of seeds for timber tree species such as Virola *surinamensis* (Howe et al., 1985). In the case of this timber species, toucans were far more effective than smaller frugivorous birds at dispersing seeds to areas where they experienced lower mortality rates (Howe et al., 1985).

The primarily frugiviorous diet of R. vitellinus and R. tucanus raises the possibility that their reduced abundance results from a reduced availability of fruit. Many of the timber tree species harvested in La Chonta are important fruit sources for frugivorous birds (Mostacedo and Fredericksen, 1999; Park et al., 2005). This is especially the case for the large free-standing fig F. boliviana. Fig trees are regularly considered keystone plant resources (e.g. Leighton and Leighton, 1983; Terborgh, 1986) because their asynchronous fruiting habits, large size and copious fruit production (Janzen, 1979) enable them to provide fruit during periods when other fruit resources are inadequate (Terborgh, 1986). Harvesting the largest individuals of F. boliviana and other timber species that produce fruit consumed by birds (e.g. P. laevis), may therefore be reducing the availability of fruit during these periods of scarcity.

4.1. Conservation and management implications

There is currently active promotion of claims that RIL procedures applied within FSC certified concessions "conserve forest biodiversity" (FSC, 2002, 2006) and can be considered to be "sustainable forest management" (WWF, 2007). In comparison to the impacts of conventional selective logging practices often encountered in the tropics, these statements may be considered reasonable. However, to suggest with any confidence that a particular forestry management technique conserves forest biodiversity and/or is ecologically sustainable would need to be supported by decades of research necessarily encompassing several harvesting cycles (Hartshorn, 1995). As such, general claims regarding the capacity of certified RIL concessions to maintain biodiversity are currently unsubstantiated, with potentially serious repercussions if incorrect. First, unrealistic expectations regarding the biodiversity value of forests logged using RIL techniques could result in RIL entering fragile and biodiverse ecosystems where logging should be excluded. Second, these claims could provide a misleading perspective regarding the contribution that RIL is making to counteract the loss of biodiversity from large areas of disturbed tropical forest. For instance, in this study several species of conservation concern were either not encountered, or encountered in significantly lower abundances within the logged areas of the concession.

Keller et al. (2007) argues that we must accept that forests selectively logged for commercial quantities of timber will "be different" from those that are not managed for commercial use. We agree with this assessment. However, we also suggest that what is acceptably "different" from a relatively pristine state must be clearly defined, and can not differ to the point of being unsustainable, especially for certified concessions. Unfortunately, the results of several studies suggest that current management practices employed within the La Chonta certified concession are not sustainable.

The dominance of non-commercial pioneer plant species in logging gaps (Park et al., 2005), lack of adequate regeneration for most commercial species (Pariona et al., 2003), and current projections of dramatic declines in the volume of future harvests (Dauber et al., 2005), are strong indications that currently employed logging practices in this concession are unsustainable. If the forest continues to be harvested at a rate that exceeds its capacity to regenerate, then eventually reductions in timber yield will lower the economic incentives for maintaining the concession. Under these circumstances there is a significant risk that the concession could be converted to potentially more profitable land-uses, such as agriculture or pastural lands. This would result in the degradation and clearing of a far higher percentage of the original forest than found in even the most exploitative of selective logging operations. Inevitably such a landscape transformation would equate with a substantial loss of forest dependent biota, including many of the bird species currently found within the La Chonta concession. It is our view that the types of changes to forestry practice which may redress this imbalance between harvesting rates and forest regeneration will potentially also benefit some of the bird species that appear to be adversely affected by current logging activities. This is because the same altered microclimatic conditions that disadvantage the regeneration of some commercial tree species (see Felton et al., 2006), also appear to be unfavourable to some forest-dependent avian taxa.

For example, nearly one quarter of all skid trails in the La Chonta concession are dead-ends or short cuts and are not used for the transportation of logs (Jackson et al., 2002). These unnecessary trails are causing 79% of all ground area disturbance outside of the marked trail network (Jackson et al., 2002). Correcting this problem would substantially reduce the extent of damage to forest understorey, and limit the amount of disruption to canopy continuity. These changes would also help to reduce incidental damage to commercial tree species in advanced stages of regeneration (see Felton et al., 2006), and potentially redress one of the causal processes behind avian species declines.

Consideration should also be given to the true long term costs and benefits of harvesting the free-standing fig species *F. boliviana*. This tree species regularly achieves a dbh of >200 cm and possesses a crown often exceeding 30m in diameter (Felton pers. obs.). The harvesting of this tree is disproportionately contributing to canopy discontinuity (Felton et al., 2006), and potentially removing a valuable keystone fruit resource for the frugivorous species of this forest. As the seed dispersing activities of both *R. vitellinus* and *R. tucanus* are presumably contributing to forest regeneration, there is the possibility that reducing the numbers of these large avian frugivores could have negative effects on the ecology of this forest.

It is currently unknown whether the processes that are causal to the observed differences in bird community composition will have time to recover between timber harvests, or be exacerbated by subsequent harvests. If the processes that are leading to the apparent declines of some bird species within the harvested areas of the concession are operating at a temporal scale that allows for recovery within the projected logging rotation cycle, then it is possible that at least some bird species may be able to maintain viable populations by moving from areas currently being harvested to regenerating or pristine areas of the concession (Wunderle et al., 2006). However, if some bird species are declining as a result of causal processes that will not be rectified, or in fact will be exacerbated with each consecutive harvest, then further changes to bird communities can be expected unless logging practices are altered and/or rotation times extended. Further research assessing longer-term changes to the bird community needs to be conducted so that we can determine to what extent these scenarios are occurring in La Chonta. Subsequently, species orientated research could be used to identify the causal processes behind declines (Lindenmayer et al., 2007) so that contributing factors to these declines can be minimized through negotiations with concession managers.

5. Conclusion

There is increasing evidence that reduced-impact logging of tropical forests causes less damage to forest structure in the tropics than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). Furthermore, prohibitions on hunting are laudable improvements that contribute to the conservation of birds and mammals of this and other certified forestry concessions (Wilkie et al., 1992; Peres 1997, 2000). However, achieving such improvements relative to the exploitive nature of conventional selective logging can come with the risk of complacency. There is as yet insufficient data to suggest that RIL is a panacea for combining the commercial need for forest products with the need to maintain those ecosystems that provide them. Our findings suggest that at least some bird species, representing a range of ecological guilds, are at risk of decline in tropical forestry concessions that employ RIL techniques. Minimizing unnecessary skidder activity, restricting or preventing the harvest of F. boliviana, and ensuring that regular feedback occurs between those assessing ecological responses and those regulating the way in which logging activities are conducted, may help to rectify the causal processes underlying these observed changes. With more knowledge, and strong links between science and policy, it is possible that any necessary adjustments can be made, and RIL can be seen as the first step towards the difficult and complex goal of achieving ecologically sustainable forestry in the tropics.

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