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Bird community responses to disturbance in a forestry concession in lowland Bolivia

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Abstract. Bird community characteristics of three sites with different levels of disturbance were studied using transect surveys during the dry season in a subtropical humid forest in Bolivia. One area had been unintentionally burned 4 years prior and selectively harvested (DIS) 1 year prior to sampling. A second area had been selectively harvested 1 year prior to sampling and had no recent history of fire (HAR). Species richness, as assessed by species–time curves and rarefaction, was higher in both altered areas than in undisturbed forest (INT). In general, frugivores and omnivores were more abundant in both altered areas compared to intact forest. Canopy frugivores, understory omnivores and multiple-strata omnivores were most abundant in HAR. Canopy frugivores, near-ground insectivores, understory and multiple-strata omnivores were least abundant in INT, although INT had the highest abundances of canopy insectivores and near-ground omnivores. Richness and abundance of widespread species with low habitat specificity was higher in both areas that experienced disturbance compared to intact forest. Differences in bird community structure between disturbed and intact forest at this site are attributed primarily to the addition of widespread species with less narrow habitat requirements, and possibly to changes in the distribution of different food types.

Introduction

Habitat alteration or destruction, particularly in Neotropical forest regions, continues to be a cause of conservation concern (Stotz et al. 1996; BirdLife International 2000). The most dramatic changes to bird communities are brought about by forest removal (‘clearcutting’) or conversion to farmland (Terborgh 1989), but the specific effects of forest isolation and patch size are less clear (e.g., Terborgh and Weske 1969; reviews in Wiens 1989; Bierregaard 1990; Laurance and Bierregaard 1997; Stratford and Stouffer 1999; Maldonado-Coelho and Marini 2000; Stouffer and Borges 2000). Results of several studies on the effects of selective harvesting of trees on bird communities suggest that (1) changes in bird communities are highly variable, and (2) changes in bird communities following selective tree removal are influenced by a variety of factors, including harvest intensity, time since harvesting, landscape context, and post-harvest land-use patterns (Johns 1986, 1991; Rappole and Morton 1985; Thiollay 1989a, 1992, 1994, 1997, 1999; Silva and Strahl 1991; Mason 1996; Aleixo 1999; Stratford and Stouffer 1999). Perhaps the most consistent finding of selective logging studies is an increase in the numbers and abundances of widespread species with low habitat specificity (Johns 1991; Mason 1996; Thiollay 1994, 1997; Canaday 1997; Aleixo 1999).

Among the land-locked countries of the world, Bolivia has the highest documented avian diversity – over 1300 species – and the lowland forests of Amazonia contain approximately one-third of these (Remsen and Traylor 1989; Armonía 1995). These forests are increasingly subject to conversion and selective harvesting. However, many forest species are extremely difficult to census; their population densities and conservation status are unknown (e.g., many raptors; Thiollay 1989b, 1994; Bierregaard 1998). The forests of northeastern Bolivia lie along several continental-scale areas of endemism (Haffer 1985) and thus contain unique species assemblages. Even though bird community composition is reasonably well documented in these forests, specific and sub-specific limits are not, and more detailed studies are likely to reveal an even higher level of biodiversity than currently recognized. Numerous studies throughout South America have recently documented previously unrecognized species and subspecies, even from relatively well-studied areas (e.g., Parker and O'Neill 1985; Bierregaard et al. 1997; Fitzpatrick and Stotz 1997; Graves 1997; Isler et al. 1997, 1999; Krabbe and Schulenberg 1997; Schulenberg and Parker 1997).

I studied forest bird communities in a commercial lowland forest in Departamento Santa Cruz, Bolivia during the dry season of 1999. In this paper, I compare avian community and species abundance patterns between a relatively undisturbed area and two areas with different histories of disturbance. Specifically, I address the questions: How does avian diversity and/or species composition differ between areas with two different types of disturbance and areas of undisturbed forest? Are there differences between guild characteristics of areas that differ in their disturbance history?

Methods

The study site, La Chonta (15°45′ S, 62°45′ W), is a forestry concession approximately 31 km northeast of Acensión de Guarayos, Departmento Santa Cruz, Bolivia, at an elevation of approximately 300 m a.s.l. The mean annual temperature is 25.3 °C and varies little seasonally. Mean annual rainfall is 1562 mm year^{-1}, the majority of which occurs between September and May. The site is classified as humid subtropical forest (Pinard et al. 1999) and has relatively low relief; mean canopy height is ca. 25 m. Common commercial tree species are *Ficus glabrata, Ficus* spp., *Terminalia oblonga, Hura crepitans, Cariniana estrellensis, C. ianeirensis, Schizolobium amazonicum, Pouteria nemorosa, Pseudolmedia laevis*, and *Centrolobium microchaete*. Of the 100000 ha in the concession, 71% is scheduled to be selectively harvested; the remaining 29% mostly includes areas that have low commercial tree densities and also 20 m buffer zones around permanent streams. The entire concession had been subject to both legal and illegal harvesting of Mahogany (*Swietenia macrophylla*) and Spanish Cedar (*Cedrela odorata*) 20 years prior to this study. Because neither of these species typically occurs in high densities, their removal probably did not have a large impact on forest structure. The concession is surrounded on three sides by intact forest; the western edge borders on extensively cleared agricultural areas. The distance between the areas surveyed and this non-forest habitat was a minimum of 17 km. At the time the bird surveys were conducted, 7000 ha (7%) of the concession had been selectively harvested, most since 1997.

Two areas that differed in their history of disturbance were surveyed and compared with undisturbed forest. The burned and harvested site (hereafter DIS) had been unintentionally burned in 1995 when fires used for agricultural purposes by local people spread into this part of the forest. The area was subsequently selectively harvested ($\bar{x} = 2.81$ trees ha^{-1}, volume $= 9.32\ m^3\ ha^{-1}$ removed) in 1998. The actual extent of the fires within this 800 ha section is difficult to assess, although effects of the fire on commercial tree densities are reflected in pre-harvest inventory data (see Pinard et al. 1999). The harvested-only site (HAR) did not have a recent history of fire, and was selectively harvested ($\bar{x} = 5.17$ trees ha^{-1}, volume $= 17.16\ m^3\ ha^{-1}$ removed) in 1998. The intact forest site (INT) was part of a large ($>$1000 ha) unharvested area with tree species composition similar to that of both DIS and HAR before they were altered by fire and harvesting. All three sites were within 12 km of each other. The INT site was not entirely unaffected by human activities; as part of a pre-harvest treatment in INT, vines associated with trees to be harvested had been cut, though not removed, 1 year prior to this study.

I used canopy gaps, one of the most obvious changes in forest structure after selective harvesting or fires, as a coarse measure of structural differences between the three sites. I define ‘gap’ as an area of at least 5 m^2 in which the vegetation reaches a maximum height of 5 m. For each 625 m^2 block (25 × 25 m; $n = 27$ blocks $transect^{-1}$) on each side of the transect, I estimated the area occupied by gap as 0, 25, 50, 75 or 100%. The measure makes no distinction between natural and anthropomorphic gaps, but is used here as an index of canopy heterogeneity.

Bird surveys

Bird surveys were conducted between 31 July and 15 October 1999, which constitutes the majority of the dry and, generally, non-breeding season at La Chonta. In contrast to birds of temperate areas, birds in tropical forests tend to be vocal year-round and have a much greater tendency to maintain permanent territories (Morton 1996). Thus, it is likely that the majority of species present at the site were detected during the course of this study.

Estimating densities of birds in tropical forests is notoriously difficult, and it is generally accepted that methods relying heavily on detection of vocalizations are most inclusive and thus preferred when time is short and observers are few (reviews in Karr 1981; Terborgh et al. 1990; Johns 1991; Parker 1991; Blake 1992; Remsen 1994; Thiollay 1997; dos Anjos and Boçon 1999; but see Rappole et al. 1998). Although these types of surveys may over-sample some groups and under-sample others to largely unknown degrees (e.g., Whitman et al. 1997), there is little reason to suspect that employing identical methods using a single observer would not produce comparable results.

I used a transect method similar to that of Kendeigh (1944) and Emlen (1977). Eight 650-m transects were located opportunistically along old secondary skidder trails, and along timber survey paths. Locating transects along pre-existing trails is often undesirable (Bibby et al. 2000). However, the fine network of unplanned skidder paths in the disturbed areas produced a habitat that was almost entirely 'edge'; few areas in HAR and DIS were greater than 50 m from a skidder path. There were two transects each in INT and HAR, and four transects in DIS. The number of transects in each habitat was restricted by logistical constraints such as limited access to the sites and having only a single observer. All transects were at least 350 m (perpendicular distance) from each other; transects along the same trail were at least 100 m (from the end of one to the beginning of the next) from each other. Transects were generally straight, and flagged at 25 m intervals. Transect width was 50 m on either side for most species. Because the vocalizations of some families are easily detected at much greater distances, transect width for the following families was set at 100 m on either side: tinamous (Tinamidae), diurnal raptors (Accipitridae and Falconidae), guans (Cracidae), wood-quails (Odontophoridae), parrots (Psittacidae), pigeons and doves (Columbidae), owls (Strigidae) and nightjars (Caprimulgidae). Within comparisons presented here, equal areas (13 or 26 ha for the above-mentioned families) were surveyed for equal amounts of time (19.5 h; see section Data analysis).

During each survey, I recorded each bird seen or heard within the survey area. I did not include birds flying over or through the survey area in density calculations. For each bird detected, I noted the species, time, method of detection (seen, heard or both), the side of the transect and the nearest flag. For each detection, I estimated the perpendicular distance from the transect to the bird in the following categories: 0, 5, 10, 25, 50 and 100 m (the latter category only for the families listed above). Prior to collecting data, I spent 6 weeks at La Chonta and nearby forests practicing distance estimation with common species seen and heard at measured distances and I am confident that most individuals could be reliably assigned to these categories.

Data were dictated quietly into a microcassette recorder. Within each 45-min survey, I did not record individuals or flocks suspected of being previously recorded. Although I tried to be conservative, it is possible that some quickly moving or wide-ranging birds may have been counted more than once. A few unidentified vocalizations were tape-recorded and identified later whenever possible; unidentified vocalizations constituted less than 5% of the individuals detected during surveys.

A complete daily census along a transect consisted of five surveys: three in the morning and two in the evening. Together, these times include the peaks of vocal activity for most species (Terborgh et al. 1990; Parker 1991; Blake 1992). Surveys were timed around sunrise and sunset and starting times were adjusted for changing day length. Pre-dawn surveys began 1 h before sunrise and nearly the entire survey was conducted in total darkness. Dawn surveys began at sunrise, and post-dawn surveys began 1 h after sunrise. Dusk surveys began shortly before sunset and ended at last light. Evening surveys began 1 h after sunset. Each survey lasted 45 min, during which I walked the entire transect very slowly (ca. 0.9 km h^{-1}), stopping frequently to listen. I used a flashlight during pre-dawn and evening surveys to look for eye shine and to navigate the transect. Surveys along a particular transect were generally conducted on the same day.

Morning surveys were replicated three times (i.e., three pre-dawn, three dawn surveys, etc. from each transect). Towards the end of the study period, noise from cicadas (Insecta: Cicadidae) made evening surveys ineffective, and these were discontinued after two replications. Using the program Distance (Thomas et al. 1998), I calculated the density of each species or guild with a sufficient number of detections using the one survey from each day that had the maximum number of individuals detected. In other words, density estimates for each species and guild were generated using data collected during times of peak detectability. For all analyses, I excluded migrant species from northern regions (e.g., *Myiodynastes luteiventris*, *Tyrannus* spp.) from analyses because these species only began arriving during the last week of field work, and not all transects were visited when these migrants were present.

Data analysis

Census data from all transects were initially subjected to cluster analysis (between-groups linkage, squared Euclidean distance) to justify pooling data from transects within each habitat (Ludwig and Reynolds 1988; Borges and Stouffer 1999). Cluster analysis revealed that all DIS transects were more similar to each other compared to any other transect (Figure 1), and I conclude that the main result of sampling a greater area in DIS was greater precision of density estimates. Rarefaction curves were generated for each sample in order to compare species richness for a standard sample size (Ludwig and Reynolds 1988). In order to standardize this analysis by area surveyed, I randomly divided the four DIS samples into two groups and calculated rarefaction curves separately.

Community analyses of tropical avifaunas are made difficult by the large number of species involved. A relatively large proportion of forest species in any Neotropical forest are, at the scale of most investigations, rare and patchily distributed (Karr 1977). Guild signatures, in which species are grouped according to ecological characteristics, are a useful aid in examining large-scale ecological differences between areas with few species in common, and guild analysis has become a widely used tool for describing and comparing bird communities (e.g., Karr et al. 1990; Terborgh et al. 1990; Stotz et al. 1996; Thiollay 1997; Borges and Stouffer 1999). All species at La Chonta were assigned to guilds based on diet and forest stratum or foraging substrate according to published evidence, supplemented by personal observations (Karr et al. 1990; Parker et al. 1996; Cohn-Haft et al. 1997). Guild signatures of the three areas were compared in terms of species richness and estimated densities. Lastly, I compared densities of the most common species in INT

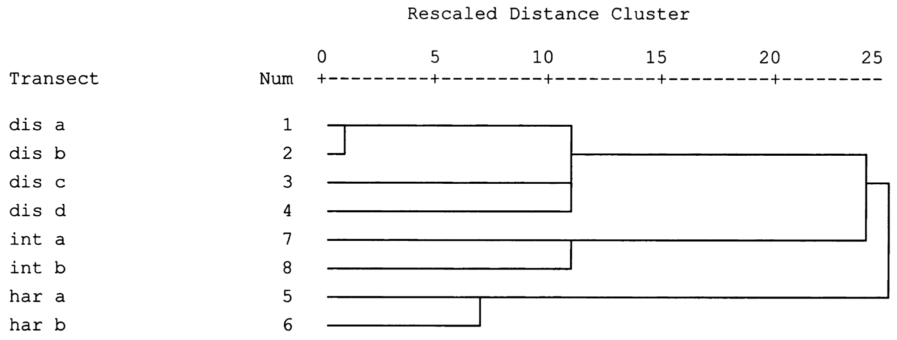

Figure 1. Dendrogram showing relationships (squared Euclidean distance) between bird census data (estimated population density of each species) from eight transects in three forest types at La Chonta. dis = burned and subsequently selectively harvested, int = intact forest, har = selectively harvested.

with those in altered areas, and also present densities of the most abundant species in altered areas. A G-test with Bonferroni correction for multiple comparisons was used to test for differences between estimated densities of guilds and species in each area (Sokal and Rohlf 1995).

Results

The mean amount of forest in gap phase was significantly lower in INT than in all other areas (ANOVA $F_{3,432} = 44.09$, $P < 0.001$; Sidak test for planned comparisons, $P < 0.001$, Figure 2), indicating that gross changes to forest structure following disturbance in HAR and DIS were similar.

Census data

Of the 245 species detected at La Chonta during 46 days of field work, 174 (71%) were detected during surveys. Of the remaining 71 species, 43 (61%) were very rare (detected fewer than five times during the study period), 18 (25%) were typical of habitats not quantitatively surveyed (e.g., aquatic habitats, large clearings), 7 (10%) were migrants not included in analyses, and 3 (4%) were species typically only detected soaring during midday. Thus, approximately 80% of the species expected in the habitats sampled were detected during surveys. However, most results presented here are heavily influenced by the 10–15 most common species in each area; these relatively abundant species were likely effectively sampled [cf. 'core species' of Remsen (1994) and Borges and Stouffer (1999)].

Community comparisons

Shannon-Wiener H' values were similar for the three habitats (INT = 4.26, HAR = 4.38, DIS = 4.61) and are comparable to values from several other Neotropical

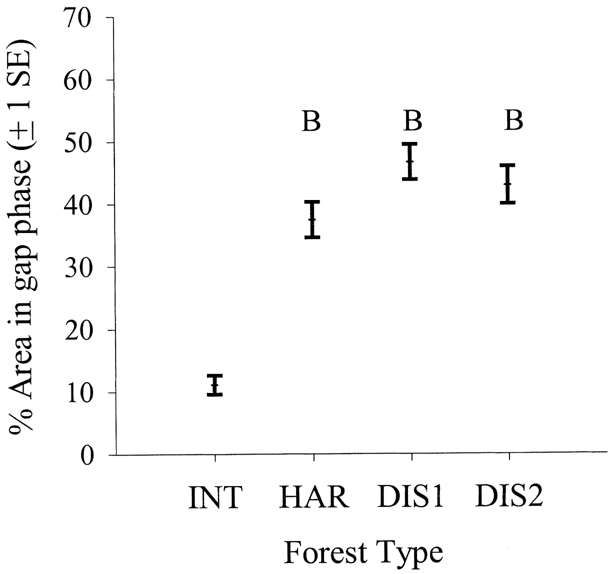

Figure 2. Mean percent (±1 SE) of forest in gap phase in four samples of equal area in three forest types at La Chonta. Bars that have the same letter above them are not significantly different from each other (ANOVA on square root-transformed data; Sidak correction for multiple comparisons $P < 0.001$). Forest types are as follows: INT = intact, HAR = selectively harvested, DIS1 and DIS2 = two samples from burned and subsequently selectively harvested forest.

lowland forest studies [summarized in Aleixo (1999)]. Species richness estimates from rarefaction curves indicate that HAR and DIS contained more species than INT (Figure 3). Detectability was slightly lower in INT compared to DIS and HAR as measured by the proportion of detections made by sight only (0.06 in INT versus ca. 0.12 in DIS and HAR). However, only a few rarely detected species in DIS and HAR (e.g., *Harpagus bidentatus*, *Accipiter superciliosus*) were detected by sight only that were not detected in INT.

Guild analysis

Differences between the forest types in the number of species within each guild were not apparent. Analysis of the numbers of individuals within each guild showed that INT contained the highest densities of canopy insectivores and ground/near-ground omnivores, but that INT generally had significantly fewer individuals from most other guilds with adequate sample sizes (Table 1). Of 12 species for which densities could be calculated for all three habitats, three were significantly more abundant in INT compared to either disturbed habitat, and three were more abundant in HAR and DIS than in INT (Table 2). However, eight additional species were common in INT but not detected frequently enough to estimate density in at least one of the altered habitats. I interpret such few (or even no) detections as indicative of a species genuinely rare in that habitat. Taking this into account, several other

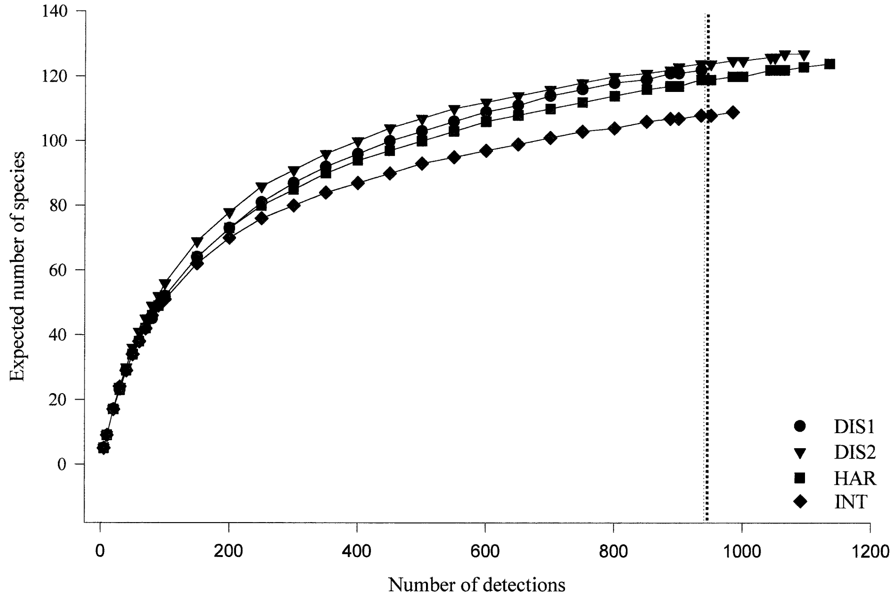

Figure 3. Rarefaction curves for the expected number of bird species in four samples from equal areas in three different forest types at La Chonta. Habitat types are the same as in Figure 2. The dotted line indicates the standard sample size of 935 detections.

Table 1. Estimated densities (individuals 100 ha^{-1} ±1 SE) of 13 bird guilds at La Chonta.

Diet/stratum	INT	HAR	DIS	Sig.
Frugivores				
Canopy	156(54)	286(101)	270(62)	**
Multiple	23(11)	51(19)	52(14)	**
Insectivores				
Bark	77(24)	85(24)	85(18)	
Canopy	113(30)	51(23)	86(20)	**
Ground/near ground	115(32)	173(44)	395(66)	**
Multiple	61(20)	43(14)	68(21)	*
Understory	305(54)	242(126)	368(48)	**
All insectivores	672(160)	594(231)	1000(173)	**
Nectarivores/Insectivores	182(45)	69(22)	155(26)	**
Omnivores				
Canopy	73(27)	57(27)	168(37)	**
Ground/near ground	175(44)	45(15)	54(22)	**
Multiple	66(22)	145(36)	118(41)	**
Understory	128(33)	233(46)	191(31)	**

Habitat codes are as follows: INT = intact, undisturbed forest; HAR = selectively harvested one year prior; DIS = selectively harvested 4 years prior and subsequently unintentionally burned. Species are listed in decreasing abundance in INT. Guilds listed are those for which accurate densities could be calculated for all three habitats and which are not the only guilds present at La Chonta. Estimated densities were compared with a *G* test (df = 2). * = significant at P = 0.05, ** = significant at P = 0.001.

Table 2. Estimated densities (individuals 100 ha^{-1} ±1 SE) of bird species common in at least one habitat at La Chonta.

Species	INT	HAR	DIS	Sig.
Tangara chilensis	129(37)	97(48)	67(33)	**
Myiornis ecaudatus	114(65)	53(25)	80(27)	**
Phaethornis spp.[a]	103(38)	–[b]	34(12)	**
Habia rubica	98(35)	64(28)	21(9)	**
Herpsilochmus rufomarginatus	77(28)	39(18)	131(29)	**
Xiphorhynchus guttatus	64(21)	54(19)	54(14)	
Myiarchus tuberculifer	56(22)	–	22(9)	**
Basileuterus culicivorus	54(25)	36(17)	32(12)	*
Myiopagis gaimardii	51(20)	–	34(11)	
Thamnophilus schistaceus	49(21)	33(18)	32(12)	
Rhytipterna simplex	41(17)	–	–	n/a[c]
Nyctiphrynus ocellatus	39(13)	34(12)	18(7)	*
Columba speciosa	39(15)	76(34)	45(13)	*
Momotus momota	39(19)	69(23)	113(22)	**
Myrmeciza hemimelaena	36(18)	–	94(33)	**
Trogon collaris	34(17)	33(17)	–	
Tinamus tao	18(8)	nd[d]	7(4)	*
Penelope jacuacu	17(9)	40(15)	42(10)	**
Crypturellus undulatus	17(8)	–	20(6)	
Otus watsonii	14(7)	20(8)	17(6)	
Turdus amaurocholinus	–	80(37)	139(32)	**
Myrmeciza atrothorax	–	117(36)	209(52)	**
Pteroglossus castanotis	–	61(25)	51(23)	
Crypturellus soui	–	12(7)	23(7)	
Ramphocelus carbo	–	–	151(51)	n/a
Turdus hauxwelli	–	46(20)	–	n/a
Saltator maximus	–	–	68(23)	n/a
Hylophilus muscicapinus	–	–	25(12)	n/a
Thryothorus guarayanus	nd	nd	50(18)	n/a

Habitat codes are as in Table 1. Species listed are those for which accurate densities could be calculated using the program Distance. Estimated densities were compared with a *G* test. * = significant at $P = 0.05$, ** = significant at $P = 0.001$. [a] Includes *P. ruber* and *P. hispidus*. [b] Density estimate not calculated (too few detections). [c] No test performed. [d] Species never detected in habitat.

species were common in INT but rare in disturbed habitat. Moreover, several species were quite common in at least one of the disturbed habitats and too rare in INT to estimate their densities, and most of these species are known to be tolerant of moderate habitat disturbance.

Discussion

Community comparisons

At La Chonta, guild composition and rank abundances of common species were found to differ between two areas with different disturbance histories (DIS and

HAR) and relatively undisturbed intact forest (INT). These results are likely related to both the type of disturbance (fire and logging in DIS versus logging only in HAR) and the time since the initial disturbance (4 years in DIS versus 1 year in HAR). The finding that species richness was lowest in intact forest is consistent with the 'intermediate disturbance' hypothesis of Connell (1978) and the notion that increased habitat heterogeneity is correlated with increased diversity (Karr and Roth 1971; Roth 1976; Willott et al. 2000). Not surprisingly, increased species richness in altered areas was largely the result of the addition of widespread habitat generalists. Tree removal and fire at La Chonta produced areas that consisted almost entirely of edge habitat, and areas without dense understory vegetation were rare outside of undisturbed forest. Of 22 species detected at La Chonta listed by Parker et al. (1996) as indicators of disturbed habitats, 15 (68%) were absent from intact forest, three (14%) were less abundant in intact forest, and only three either showed no differences in abundance or showed ambiguous trends. In some cases, species substitution was apparent at the generic level. For example, estimated densities of *Tangara chilensis* were reduced in altered areas, where *T. mexicanus, T. nigrocincta, T. gyrola* and *T. cyanicollis* were commonly observed. The latter three species were never observed in intact forest and the former only very rarely so. *Tangara chilensis* is primarily a bird of the forest, whereas the four other species are typically found in semi-open areas (Isler and Isler 1987; Ridgley and Tudor 1989). Only one species listed as a disturbance indicator by Parker et al. (1996; *Piaya cayana*) appeared to be more abundant in intact forest than in disturbed areas.

Some of the observed differences in guild signatures between the three habitat samples were influenced considerably by single species, suggesting that guild analyses are but a first step in evaluating gross differences between bird communities (Martin and Karr 1986). The understory omnivore *Momotus momota* was largely responsible for the greater abundance of its guild in areas that experienced disturbance. In contrast, other understory omnivores, such as *Lipaugus vociferans*, *Trogon collaris*, *T. curucui* and *Turdus hauxwelli*, were more frequently detected in HAR and INT than in DIS. The reduced number of near-ground insectivores in INT was mostly due to the near-absence of *Myrmeciza atrothorax* and low numbers of *Hypocnemis cantator*. Both species were commonly observed in weedy edges near canopy gaps and logging roads, and this microhabitat is far more abundant in areas that have experienced disturbance (personal observation).

Significantly more canopy and multiple-strata frugivores were detected in disturbed areas than in undisturbed forest. Although I did not collect data on fruit abundance and distribution in the three forest types at La Chonta, published evidence from other Neotropical studies allows for some speculation on the distribution of frugivores. Strict frugivores and other species that include fruit in their diets are typically less sedentary than insectivores (Karr 1976; Martin and Karr 1986; Stouffer and Bierregaard 1993), and this is likely related to the often temporally patchy distribution of trees bearing fruit (Levey 1988b; Gautier-Horn and Michalaud 1989). Some of the tree species harvested at La Chonta (*Ficus* spp., *Pseudolmedia laevis*) produce fruits that are consumed by birds (personal observation); removal of these trees would be expected to reduce the numbers of frugivores.

However, it is possible that unharvested individual plants responded to disturbance by producing more fruit, perhaps as a result of competitive release following harvesting, or, in DIS, as a response to an increase in available nutrients that typically follows fire (Pyne et al. 1996). These types of short-term responses by plants could not only substantially increase the amount of fruit available in an area, but this fruit would likely be produced more synchronously than the often patchy distribution of trees within a closed forest (Moermond and Denslow 1985; Loiselle and Blake 1991; personal observation). Moreover, plants producing large crops of fruit consumed by birds are frequently more common in forest gaps and along edges (Levey 1988a, 1988b; Loiselle and Blake 1991). In Costa Rica, the greater abundance of fruit-bearing plants in secondary habitats was positively correlated with frugivore abundance (Blake and Loiselle 1991). The abundance of fruit-consuming birds in disturbed areas at La Chonta would thus be expected to decline as the area reverts to mature forest, as was found in Costa Rica (Loiselle and Blake 1994). This pattern appeared to hold true for certain groups of frugivores and omnivores at La Chonta, where abundances were highest in HAR, intermediate in DIS and lowest in INT. Still, without data from disturbed areas prior to disturbance, causal inferences about the effects of disturbance are not possible. It should also be noted that the relationship between logging, fruit-producing plants and frugivorous birds is far from resolved: studies indicate that patterns observed in Neotropical studies may not apply to all tropical forests (e.g., Plumptre et al. 2001; Zakaria and Francis 2001).

Conservation implications

Although few species found in intact forest were entirely absent from disturbed forest, the abundances of several sensitive or poorly known species differed between habitats. It is important to note that the majority of species at La Chonta remain poorly studied, and their specific tolerances of disturbance are not well known. For example, although I could not generate density estimates for species flying over the study area, the poorly known *Chaetura egregia* was detected commonly and almost exclusively over intact forest. Such an observation is striking and likely meaningful because visibility (and therefore detectability of aerial species) was much greater over HAR and DIS compared to INT. The persistence and even increased abundance of several large game species (including the habitat-sensitive *Penelope jacuacu*; Parker et al. 1996) in disturbed habitats is encouraging, but may also be partially due to the currently very low hunting pressure at La Chonta (see Borges 1999). In tropical areas, hunting pressure typically increases as new roads provide easy access to forests (Silva and Strahl 1991; Rumiz et al. 2001).

Lack of knowledge of the natural history of many species and lack of long-term data from most areas makes it difficult to know whether differences observed in short-term studies such as this persist into the future. Changes in bird communities following moderate disturbance may remain detectable for many years, even if no additional disturbances occur. In French Guiana, Thiollay (1997) found that differences between avifaunas of logged and unlogged forests were greater 10 years following harvesting than at 3–4 years after harvesting. For long-lived species such as parrots, for example, changes in population sizes might not be detectable for a time span much greater than the duration of most studies. Although ground and near-ground insectivores were most abundant in disturbed areas at La Chonta (and this was heavily influenced by a single species *Myrmeciza atrothorax*), some terrestrial insectivores, such as *Corythopis torquata* and *Hylophylax naevia*, appeared to avoid disturbed areas at La Chonta. These and other terrestrial insectivores have been found to be sensitive to disturbance in Brazil (Johns 1991; Aleixo 1999; Stratford and Stouffer 1999), Venezuela (Mason 1996), French Guiana (Thiollay 1997), and Malaysia (Johns 1986). The precise causes of this pattern are unclear, although it may be linked to an avoidance of areas with high stem densities (Marra and Remsen 1997; Merry 2001), which are often found in gaps and early successional areas.

Geographic or temporal variation in the behavior of some species further contributes to the difficulty in assessing the conservation implications of disturbance ecology studies. Several species reported to be associated mainly with bamboo elsewhere (e.g., *Nonulla ruficapilla*, *Hemitriccus flammulatus*, *Ramphotrigon fuscicauda*; Parker 1984; Ridgley and Tudor 1994) appeared to be associated with older treefall gaps with high vine densities at La Chonta, where bamboo was absent from the forest. Similarly, no ant swarms were detected until the beginning of the rainy season in mid-October, yet species often associated with ant swarms elsewhere (e.g., *Dendrocincla fuliginosa, Dendrocolaptes picumnus*, *D. certhia*, *Hylophylax poecilinota*; Willis 1982; Ridgley and Tudor 1994; Parker et al. 1996) were present and fairly common at La Chonta throughout the study period.

The addition of widespread habitat generalist species to the avifauna of disturbed areas at La Chonta is symptomatic of the complicated ways in which bird communities respond to habitat disruption and the ways these changes are perceived by conservation planners and land managers. At first glance, moderate disturbance has the effect of increased local bird diversity. However, it is not yet sufficiently clear that this increased diversity persists, or is even desirable, as most of the species added to these avifaunas are widespread and at very low risk of global or even local extinction. If undisturbed habitat fragments that support species with narrower habitat requirements are too small or too isolated, the ultimate product of widespread habitat disturbance is reduced avian diversity at the local and, eventually, at the regional scale.

Finally, whether the integrity of forest bird communities can be preserved following selective tree harvesting depends not only on the type and extent of the initial harvest, but also on what long-term management practices are implemented following the initial harvest. At La Chonta, 30-year harvest rotations are planned (Empresa Agroindustrial La Chonta Ltda 1998). Some tree species, such as *Ficus*, regenerate and recruit poorly in these forests, and even though gaps may improve *Ficus* regeneration (Fredericksen et al. 1999), the number of mature individuals bearing large quantities of fruit would likely not return to pre-harvest levels within this time frame. Furthermore, when tree species that are currently commercially valuable are depleted, loggers often begin harvesting less valuable species as well

(T. Fredericksen, personal communication) and, ultimately, conversion to pasture for cattle or agriculture frequently becomes the only profitable option for landowners (Terborgh 1989). Thus, while an initial selective harvest may not alter forest bird communities irrevocably, economic practices that often follow the opening of an area to logging often have more far-reaching consequences for tropical forest birds.

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