Effects of forest disturbance and habitat loss on avian communities in a Neotropical biodiversity hotspot

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ABSTRACT

Regenerating forests are increasingly ubiquitous in tropical landscapes. They hold great conservation potential and there is demand for assessments of their biodiversity value. Forest disturbance and forest loss often occur together, yet few studies attempt to disentangle their separate effects on biological communities. In the Ecuadorian Chocó, a biodiversity hotspot, we sampled understory birds in patches with increasing levels of disturbance (old-growth, selectively-logged, and secondary forests) within contiguous forest and in fragments. Species richness increased with disturbance but decreased with habitat loss, with a 75% reduction in endemic and threatened species in fragments compared to contiguous forest. This reduction in richness was most pronounced in secondary forest fragments, suggesting that disturbance and habitat loss interact synergistically to maximally reduce avian biodiversity. Species composition was strongly affected by habitat loss and, to a lesser extent, disturbance, with forest fragments and secondary forests presenting distinct communities dominated by generalists with medium-to-low sensitivity to anthropogenic disturbance and reduced proportions of endemics and endangered species. Capture rates also decreased (non-significantly) with habitat loss, and the relative abundance of dietary guilds varied in response to both habitat loss and disturbance. Our study shows that regenerating patches surrounded by contiguous forest can sustain high biodiversity levels and, when past habitat disturbance is mild, present similar communities to old-growth forests. In contrast, forest loss caused reductions in richness (especially in more disturbed patches), profound changes in community composition, and loss of species of conservation concern. These results underscore the importance of considering landscape context when evaluating the conservation value of disturbed forests.

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1. Introduction

Anthropogenic habitat modification in the tropics has generated intense concern because these regions suffer the highest rates of forest loss, fragmentation, and degradation (FAO, 2010) yet house most described and undescribed species (Joppa et al., 2011). On the other hand, reforestation and natural forest expansion have contributed to a global reduction in net forest loss in the last 20 years (FAO, 2010); e.g., secondary succession was estimated to replace one in every 6–7 ha of tropical forest cleared (Wright, 2005). While this rate does not offset the loss of primary forest, it calls attention to the potential that disturbed forests (here defined as forests that have been impacted by anthropogenic stressors such as fire, selective or extensive logging and are currently in regeneration) may hold for biodiversity and essential ecosystem

services. For example, disturbed forests may serve as species refugia and increase beta-diversity (Dent and Wright, 2009; Edwards et al., 2011), increase landscape connectivity (Stouffer and Bierregaard, 1995), preserve animal-mediated ecosystem processes (Schleuning et al., 2011), and sequester atmospheric carbon (Wright, 2005).

The value of disturbed forests as a conservation asset is vigorously debated (Wright, 2005; Barlow et al., 2007a,b; Dent and Wright, 2009; Didham, 2011; Gibson et al., 2011). Although recent studies have identified significant conservation benefits (Dent and Wright, 2009; Edwards et al., 2011), more information is needed to accurately gauge the conservation value of regenerating forests relative to primary forests. In particular, despite a large recent body of work on the effects of forest loss on biodiversity (reviews by Laurance and Bierregaard, 1997; Ewers and Didham, 2006; Fahrig, 2003), we know surprisingly little about how it interacts with habitat disturbance. Habitat disturbance and habitat loss are often correlated across landscapes (Harrison and Bruna, 1999; Laurance et al., 2002), yet very few studies have formally attempted to

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disentangle their independent and synergistic effects on biological communities or processes (Lees and Peres, 2006; Cornelius, 2008; Peters et al., 2008; Schleuning et al., 2011).

We examined changes in understory bird communities in response to both habitat disturbance and habitat loss (*sensu* Fahrig, 2003) in northwest Ecuador, at a transition zone between the Tumbesian and Chocó biogeographic zones, both characterized by high levels of endemism, diversity, and threat (Orme et al., 2005; Devenish et al., 2009). Birds are well suited for this as they are reliable indicators of broader biodiversity trends (Barlow et al., 2007a). The study took place within the Mache-Chindul Reserve, which contains some of the largest remaining tracts of primary forest in the region, but suffers from historical and ongoing deforestation. Human settlements in the study area consist mainly of small, traditional communities, and despite the presence of indigenous or long-standing (>200 years) populations, most land conversion occurred after the 1980s, with the advent of large immigration waves by mestizo 'colonos' (Sierra and Stallings, 1998). Deforestation and logging activities in the study region are largely non-organized and small-scale in nature, carried out by local landowners.

To examine the effects of intensity of habitat disturbance, we compared forest patches in three *habitat types*: (1) OG: old-growth forest, (2) SL: regenerating selectively-logged, and (3) CC: regenerating clear-cut (i.e., secondary) forests. To test for the effect of habitat loss, we compared patches in two *landscape types*: (1) contiguous forest (patches within a matrix of old-growth forest) and (2) fragmented forest (isolated patches within a matrix of pasture/agriculture). We sampled multiple replicates of each habitat type in each of the two landscape types to evaluate the following predictions: (a) richness and capture rates decrease with increasing disturbance (OG > SL > CC forest) and with habitat loss (contiguous forest > fragments); and (b) community similarity to contiguous OG forest (control treatment) decreases with intensity of habitat modification (highest for SL contiguous forest, lowest for CC fragments). In doing so, our broader objective was to assess the relative importance of habitat disturbance versus habitat loss on avian communities. If disturbance is more important, we expect that richness, capture rates, and community similarity will follow the pattern OG contiguous $\geqslant$ OG fragmented > SL contiguous $\geqslant$ SL fragmented > CC contiguous $\geqslant$ CC fragmented. In contrast, if habitat loss is more important, we might expect OG contiguous $\geqslant$ SL contiguous $\geqslant$ CC contiguous > OG fragmented $\geqslant$ SL fragmented $\geqslant$ CC fragmented.

2. Methods

2.1. Study site

The study was conducted in a ~12 000 ha area around Bilsa Biological Station (BBS; 79°45′W, 0°22′N, 330–730 m a.s.l.), a 3500-ha private reserve established in 1994 by Fundación Jatun Sacha and located within the larger Mache-Chindul Reserve (~120 000 ha), Esmeraldas and Manabi Provinces, Ecuador (Fig. 1). Mean annual temperature is 23–26 °C; mean annual precipitation is 2000–3000 mm, with a January–June wet season and a July–December dry season, each presenting a peak in avian breeding activity (February–May and October–November; J. Karubian and L. Carrasco, unpublished data). BBS is a comprised of a complex matrix of contiguous OG forest inter-digitated with SL or CC forests that were cut 19–30 years ago and abandoned to regenerate naturally. BBS contains some of the last large remnants of premontane wet forest in NW Ecuador and has been identified as critically important for the conservation of this megadiverse ecosystem (BirdLife International and Conservation International, 2005; Devenish et al., 2009). The surrounding areas within the Mache-Chindul Reserve have been extensively deforested for use in small-scale agriculture and cattle ranching within the last 40 years (Charlat et al., 2000), resulting in a series of forest fragments with varying structural complexity. In this study, we use OG forest within BBS as our control treatment; however, given the size of BBS, it is possible that this site has been impacted by the reduced extent of overall forest in the region, such that extinctions have already occurred and 'pristine' avifauna is no longer present (Lees and Peres, 2006). As there is virtually no comprehensive baseline records that pre-date deforestation in this area, we cannot evaluate the extent of these effects.

2.2. Habitat characterization

We established 79 habitat sampling points at 200 m intervals along >15 km of existing trails within contiguous forest, covering ~1/3 of BBS (Fig. 1). Habitat type at each point was classified as OG (44 points), SL (16 points), or CC forest (19 points) based on knowledge of land use history and visual inspection of forest structure (canopy height, size of trees, understory density, etc.). To validate this classification, for each point we recorded the number of medium and large-sized trees (DBH of 10–50 cm within a 10 m-radius plot and with DBH $\geqslant$ 50 cm within a 20 m-radius plot, respectively), canopy height (estimated visually), percent of canopy cover (100 − average of densiometer measures taken on four cardinal directions), and elevation (measured with a Garmin GPS unit). After variables were transformed as necessary to ensure normality, a discriminant analysis (DA) was employed to assess if habitat sampling points could be confidently assigned to habitat type categories based on these structural variables. In each site where birds were sampled, we recorded habitat variables (above) from each of three plots located at either extreme and in the center of our mist netting area; inter-plot distance was 100 m. The validated DA model previously built was then applied to bird sampling sites to objectively classify their predominant habitat type.

2.3. Bird sampling

Understory birds were sampled with ground-level mist-nets (12 × 2.5 m) in contiguous forest (BBS) and forest fragments around BBS. All sampling was conducted by LC, who has over a decade of experience working with the local avifauna; digital vouchers and genetic samples were collected. Sampling in BBS contiguous forest was carried out from October 2004 – August 2007 at 15 netting stations (Fig. 1) separated by ~1400 m on average (230–3200 m); this distance was similar for stations in the same (1479 ± 670 m, mean ± 1 SD) or different habitat types (1379 ± 680 m). All netting stations were surrounded by qualitatively similar habitat for at least 200 m in all directions from the center of the net lines with one exception, CC3, which was a patch of secondary forest approximately 200 × 200 m surrounded by OG forest on all sides (see Section 3). During each sampling session, eight mist-nets were setup along a 200-m linear transect and operated between 06:30–13:30 h for three consecutive days (one sampling session = three days). Sampling was rotated across netting stations, such that each station was sampled 5–8 times in total, and the total number of sampling sessions was similar across habitat types (OG, 33; SL, 32; CC, 34). Outside BBS, we sampled 13 forest fragments 3–48 ha in size (average ± 1 S.D. 20 ± 16 ha) located 0.6–7.7 km from BBS (average: 4.4 ± 2.2 km; Fig. 1, Supplementary material Table 1). Each fragment was sampled with eight mist-nets during a single sampling session (three days) between August 2010 and February 2011 or January 2012. Due to the lack of adequate cloud-free satellite imagery in the region, fragment area was measured directly, using GPS tracks obtained by walking the perimeter of fragments; we did not map unsampled fragments in the area. During exploratory analyses, we did not detect seasonality effects on species composition. Among
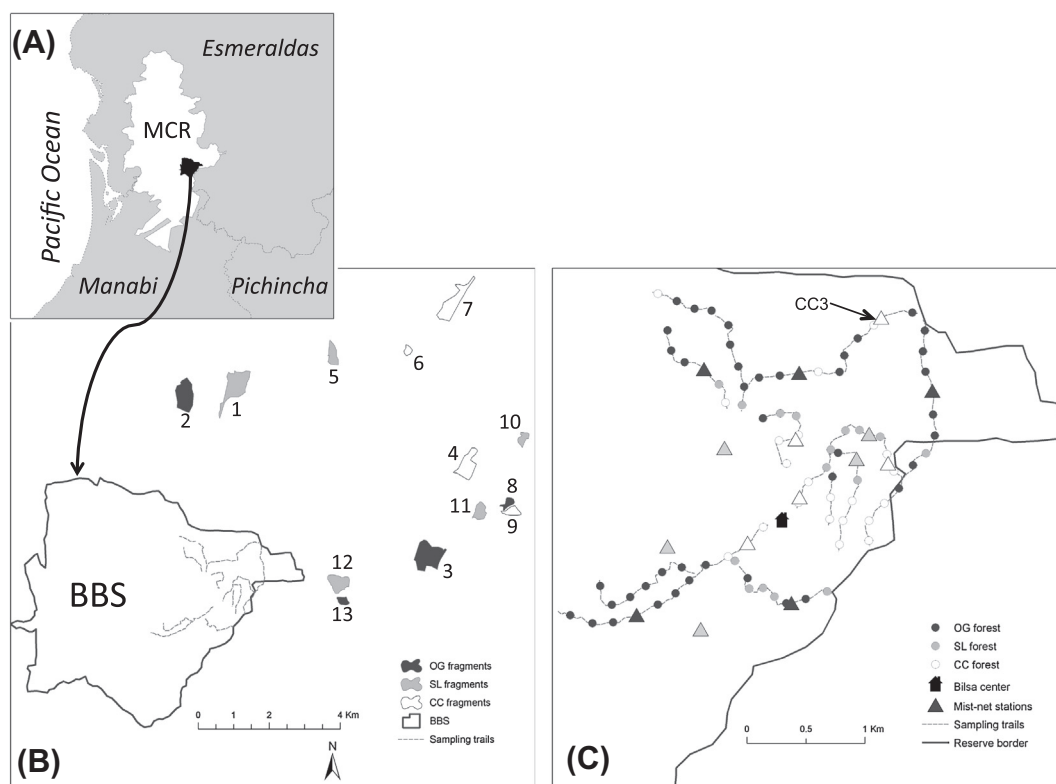
Fig. 1. Map of the study area. (A) Location of Bilsa Biological Station (BBS) within the Mache-Chindul Reserve (MCR) in Esmeraldas and Manabi provinces, NW Ecuador; (B) location of 13 forest fragments sampled around BBS; (C) habitat sampling points (circles) and mist-netting stations (triangles) inside BBS. In the legend, OG = old growth, SL = selectively-logged, CC = regenerating clear-cut (secondary) forests. CC3 is a small patch of CC forest (∼200 × 200 m) surrounded by OG (see text).

∼1000 individuals captured in BBS that were recaptured at least once, 83% were never recaptured in a different netting station, suggesting that, although some movement exists between netting stations, it is not likely to significantly change the results. We recorded no recaptures between the sampled fragments.

Pros and cons of mist-net bird sampling have been extensively discussed elsewhere (Karr, 1981; Levey, 1988; Blake and Loiselle, 1991; Blake and Loiselle, 2001). Most relevant to this study is the concern that perceived differences in avian communities may be due to biases in capture probability of canopy-foraging species according to habitat vertical structure. However, number of species with different upper foraging strata (terrestrial/understory, mid-story, or canopy, following Stotz et al., 1996) did not differ among the three habitat types ($\chi^2_4 = 1.19, p = 0.88$), and as such we did not exclude canopy-dwellers from analyses.

Captured individuals were identified following the South American Classification Committee nomenclature (Remsen et al., 2010) and marked with uniquely numbered metallic bands. Neotropical migrants were identified based on Ridgely and Greenfield (2001). When categorizing species as endemic to a given biogeographic zone, we employed BirdLife International's definition of a 're-stricted range endemic species' (Stattersfield et al., 1998; Devenish et al., 2009). Species of conservation concern were classified at the global and national level following IUCN (2011) and Granizo et al. (2002), respectively. Information on degree of sensitivity to human disturbance followed Stotz et al. (1996) and on dietary guilds followed Şekercioğlu et al. (2004).

2.4. Comparison of bird assemblages across habitat and landscape types

We compared bird assemblages in different habitat and land-scapes types in terms of capture rates, species richness, and species composition. To take full advantage of the more extensive sampling undertaken in contiguous forest, we first looked at effects of habitat disturbance in contiguous forest alone, and then at effects of habitat disturbance vs. habitat loss by comparing habitat types in contiguous and fragmented forests.

Capture rates were expressed as number of individuals captured per 100 net-hours in each sampling session. We tested for the effect of habitat disturbance in capture rates among contiguous forest habitats with an ANOVA, with netting station as a random factor (unless stated otherwise, all analyses were conducted in JMP 9, SAS Institute Inc.). To test for the relative effects of habitat disturbance vs. habitat loss, capture rates were compared across habitat/landscape type combinations with a full-factorial two-way ANOVA; due to differences in sampling regimes in the two landscape types, here we included only the first sampling session for each contiguous forest site; using all contiguous forest sampling occasions or only the first one resulted in highly correlated capture rates ($r = 0.71$, $p = 0.003$).

To compare richness while controlling for differences in sample size, we computed expected species accumulation curves ('sample-based rarefaction curves'; samples randomized with replacement), with 95% confidence intervals, in EstimateS v. 8.2 (Colwell, 2006). Rarefied richness was then compared at the minimum sample size obtained across sites based on the 95% confidence intervals. We tested for the effect of habitat disturbance on richness by comparing rarefied richness across habitat types (for contiguous forest only and for contiguous forest and fragments combined). We tested for the effect of habitat loss by comparing rarefied richness between contiguous and fragmented forest. Finally, we looked for the interactive effects of habitat disturbance and habitat loss by comparing habitat/landscape type combinations; we took this approach because a formal full-factorial ANOVA is not possible with rarefied richness values. As an estimation of the total number of

species present in each habitat type given the sampling data (estimated richness), we provide the mean of four commonly employed abundance-based estimators (ACE, Chao1, Jack1 and Bootstrap), calculated using EstimateS v. 8.2 and based on 100 randomizations. Estimated richness was strongly biased by capture numbers, and as such we provide these estimates but do not compare them statistically across sites. We used linear models to investigate the relationship between capture rates or observed richness and three predictor variables: fragment size, distance to the nearest BBS border, and habitat type.

Community composition was compared across habitat and landscape types with a nonmetric multidimensional scaling (MDS) ordination based on a Bray-Curtis similarity matrix, with data square-root transformed to reduce the contribution of the most common species, using Primer-E v.5 (Clarke and Warwick, 2001). Using presence-absence data or only including the first sampling occasion for contiguous forest sites produced qualitatively similar results but increased stress values, so we included all available data (see Supplementary material Fig. 1). Analyses of similarity (ANOSIM) combined with permutation tests were used to test for significant differences in community composition across habitat/landscape types. We conducted an indicator species analysis (Dufrêne and Legendre, 1997) in PC-Ord v. 4.41 (McCune and Mefford, 1999), in which information both on species presence and abundance was combined to identify species especially associated with particular habitat/landscape types clustered together by the ANOSIM tests; significance of these associations was estimated using 1000 randomizations.

3. Results

3.1. Habitat characterization

The DA habitat model based on structural variables produced two significant functions (Wilks' λ = 0.279 and 0.866, p < 0.001 and p = 0.019). Model habitat classification was concordant with visual classification for 81% (64/79) of the habitat sampling points. Eleven of the 15 misclassified points were sites visually classified as OG but assigned by the model as SL, or vice versa. When applied to contiguous forest netting stations, this model classified five points as OG, five as SL, and five as CC (Fig. 1, Table 1). The model classified habitat in four fragments as OG, five as SL, and four as CC (Fig. 1, Table 1). Differences in habitat structure across habitat types were qualitatively similar for contiguous or fragmented forest bird sampling sites: canopy height was similar for OG and SL,

but lower in CC forests; number of medium and large trees and canopy cover decreased from OG to SL to CC; elevation did not differ (Table 1).

3.2. Species richness and capture rates

A total of 5398 individuals from 165 species and 807 individuals from 89 species were captured in contiguous and fragmented forests, respectively, for a total of 175 species (133 species if only the first sampling occasions in each site are considered; Table 2).

3.2.1. Effect of habitat disturbance in contiguous forest
In contiguous forest, capture rates did not differ among habitats ($F_{2,11.13}$ = 1.08, p = 0.37, Table 2), and richness gradually increased from OG to SL to CC sites (rarefied richness estimated for N = 1490 individuals, Table 2).

3.2.2. Relative effects of habitat disturbance vs. habitat loss
Capture rates did not differ across habitat or landscape types ($F_{5,22}$ = 0.90, p = 0.50, Table 2). Richness increased from OG to SL to CC sites [rarefied richness estimated for N = 1769 individuals; OG = 95 species (95% CI = 86–104), SL = 104 (95–113), CC = 113 (103–123)], and was lower in fragments compared to contiguous forest [rarefied richness estimated for N = 807 individuals; contiguous forest = 91 species (95% CI = 81–101), fragmented forest = 76 (63–89)]. Habitat disturbance and habitat loss had an interactive effect on richness: CC sites in fragmented forest had significantly less species than CC sites in contiguous forest. There was a non-significant trend in this same direction for OG forests, and no indication of an effect of habitat loss on richness for SL forests (Fig. 2). Models with fragment size, isolation from BBS, and habitat type as predictor variables could not explain either capture rates ($F_{4,8}$ = 0.62, p = 0.66) or observed richness ($F_{4,8}$ = 0.14, p = 0.96) in fragments.

3.3. Community composition

Species composition differed both among habitat and landscape types (Fig. 3; ANOSIM's global r = 0.602, p = 0.001). Three distinct groups were recognized: (1) OG and SL contiguous forest (p = 0.56; p-values when compared to other site types: 0.008–0.04), (2) CC contiguous forest (p-values when compared to other site types: 0.008–0.05), (3) all fragments, irrespective of habitat type (OG vs. SL, p = 0.60; OG vs. CC, p = 0.06; SL vs. CC, p = 0.64; all p-values when compared to contiguous forest habitat

Table 1
Habitat structure of avian sampling points in three different habitat types in contiguous forest and forest fragments in NW Ecuador; OG = old-growth, SL = regenerating selectively-logged, CC = regenerating clear-cut (secondary) forest. Values represent means ± 1 SD; significant ANOVA p-values are shown in bold; different letters indicate pairs of habitat types significantly different, as evaluated by Tukey–Kramer honestly significant difference post hoc tests.

|	Habitat type			ANOVA results	
	OG	SL	CC	F	p
(A) Contiguous forest	(n = 5)	(n = 5)	(n = 5)		
Canopy height (m)	26.2 ± 2.0[a]	24.9 ± 2.6[a]	14.0 ± 2.4[b]	25.18	**<0.0001**
No. medium trees[a]	25.0 ± 4.2	20.4 ± 11.1	15.1 ± 7.9	1.76	0.24
No. large trees[b]	6.5 ± 1.2[a]	2.3 ± 1.4[b]	1.8 ± 0.3[b]	27.41	**<0.0001**
Canopy cover (%)	90.9 ± 2.8[a]	82.6 ± 4.3[b]	79.5 ± 5.7[b]	10.27	**0.004**
Elevation (m)	536.2 ± 30.0	532.9 ± 37.1	516.0 ± 45.4	0.50	0.70
(A) Forest fragments	(n = 4)	(n = 5)	(n = 4)		
Canopy height (m)	26.7 ± 3.2	27.6 ± 2.9	19.4 ± 3.2	2.07	0.18
No. medium trees[a]	21.0 ± 1.0[a]	19.5 ± 3.8[a,b]	15.2 ± 2.8[b]	4.42	**0.04**
No. large trees[b]	2.2 ± 1.0[a]	1.6 ± 0.8[a]	0.2 ± 0.2[b]	7.31	**0.01**
Canopy cover (%)	92.9 ± 1.8	89.5 ± 1.6	86.3 ± 1.8	3.47	0.07
Elevation (m)	408.9 ± 52.3	426.5 ± 46.8	330.9 ± 52.3	1.00	0.40

[a] Number of trees with DBH = 10–50 cm within a 10-m radius circular plot.
[b] Number of trees with DBH > 50 cm within a 20-m radius circular plot.

Table 2
Results of avian mist-netting sampling in (A) contiguous forest (15 netting sites) and (B) forest fragments (13 sites) in NW Ecuador. Habitat types are old-growth (OG), selectively-logged (SL) or secondary (CC) forests. Capture rates are mean number of individuals (±1 SD) per 100 net-hours. S_{obs} is the number of species observed in each habitat type. S_{est} is the estimated richness given the sampling data, reported as the mean (±1 SD) of four abundance-based estimators (Chao1, Jack1, ACE and Bootstrap). S_{raref} is the number of species (and 95% confidence intervals) expected (A) in contiguous forest, if 1490 (all sessions) or 434 (first session only) individuals had been captured; or in (B) fragments, if 193 individuals had been captured.
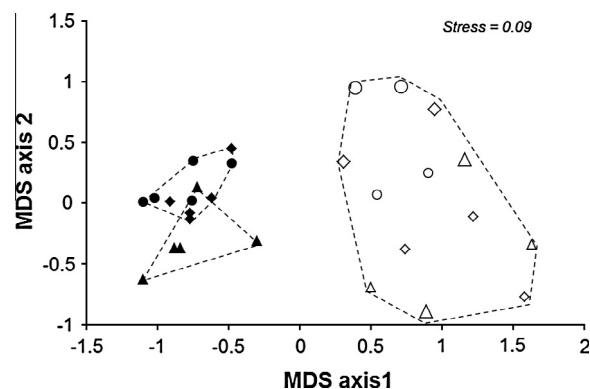
	Habitat type			Total
	OG	SL	CC	
(A) Contiguous forest				
Total individuals				
All sessions	1715	1490	2193	5398
First session only	459	434	500	1393
Capture rates				
All sessions	55.4 ± 40.5	51.4 ± 30.4	67.0 ± 34.8	
First session only	77.8 ± 51.7	71.2 ± 36.4	73.6 ± 37.6	
S_{obs}				
All sessions	105	108	137	165
First session only	60	62	72	104
S_{est} (all sessions)	104 ± 4.3	105 ± 3.5	134 ± 5.7	
S_{raref} (all sessions)	88 (80–96)	96 (88–104)	109 (97–121)	
(B) Forest fragments				
Total individuals	193	277	337	807
Capture rates	38.5 ± 13.9	49.8 ± 13.8	61.5 ± 30.3	
S_{obs}	45	67	57	89
S_{est}	45 ± 1.7	67 ± 5.1	56 ± 2.5	
S_{raref}	37 (32–42)	53 (46–60)	36 (30–42)	
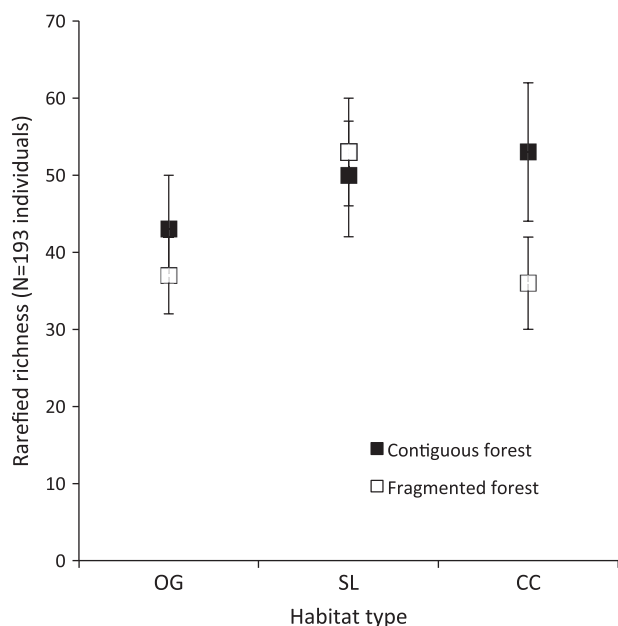
Fig. 2. Habitat disturbance and habitat loss act synergistically to reduce richness of understory birds in NW Ecuador. Shown are the effects of habitat disturbance (OG: old-growth forest, SL: selectively-logged forest, CC: clear-cut forest) and habitat loss (contiguous forest, fragmented forest) on rarefied richness. Bars represent 95% confidence intervals.

Fig. 3. Habitat loss and habitat disturbance both impact community composition of understory birds in NW Ecuador. Shown is a non-metric multidimensional scaling (MDS) plot comparing bird community composition among two forest types (contiguous forest, solid symbols; forest fragments, open symbols) and three habitat types (old-growth forest, circles; selectively-logged forest, diamonds; clear-cut forest, triangles). Among forest fragment sites, smaller and larger symbols represent fragments smaller or larger than 20 ha, respectively. Groups significantly different in terms of species composition, according to ANOSIM tests, are delimited within hatched lines.

types = 0.008). Interestingly, the one CC contiguous forest site that behaved as OG/SL was CC3, a particularly small patch of CC forest surrounded by OG forest (Fig. 1); exclusion of CC3 from this analysis amplifies differences between contiguous CC and OG/SL. Comparing fragments according to habitat × size classes (small or large OG, SL, or CC fragments, see Supplementary material Table 1) did not result in detection of significant differences in species composition among fragments (ANOSIM's global $r = 0.121$, $p = 0.25$).

We combined sites within the three distinct groups identified above to conduct an indicator species analysis, which identified 17 species indicative for combined OG/SL contiguous forest, 36 species for CC contiguous forest; there were no indicator species identified for fragments (Supplementary material Table 2). Most (59%) OG/SL contiguous forest indicator species are considered highly sensitive to human disturbance and none are considered of low sensitivity; in contrast, most CC contiguous forest indicator species have either low (44%) or medium (42%) sensitivity (Stotz et al. 1996; Supplementary material Table 2). Contiguous forest presented a higher proportion of unique species than fragments ($\chi_1^2 = 39.4$, $p < 0.001$), including several that are endemic, of conservation concern, or migratory (Fig. 4). However, proportion of endemic species ($\chi_1^2 = 1.1$, $p = 0.31$), species of conservation concern ($\chi_1^2 = 3.4$, $p = 0.06$), and migrants ($\chi_1^2 = 0.2$, $p = 0.67$) did not differ significantly between contiguous forest and fragments (Fig. 4).
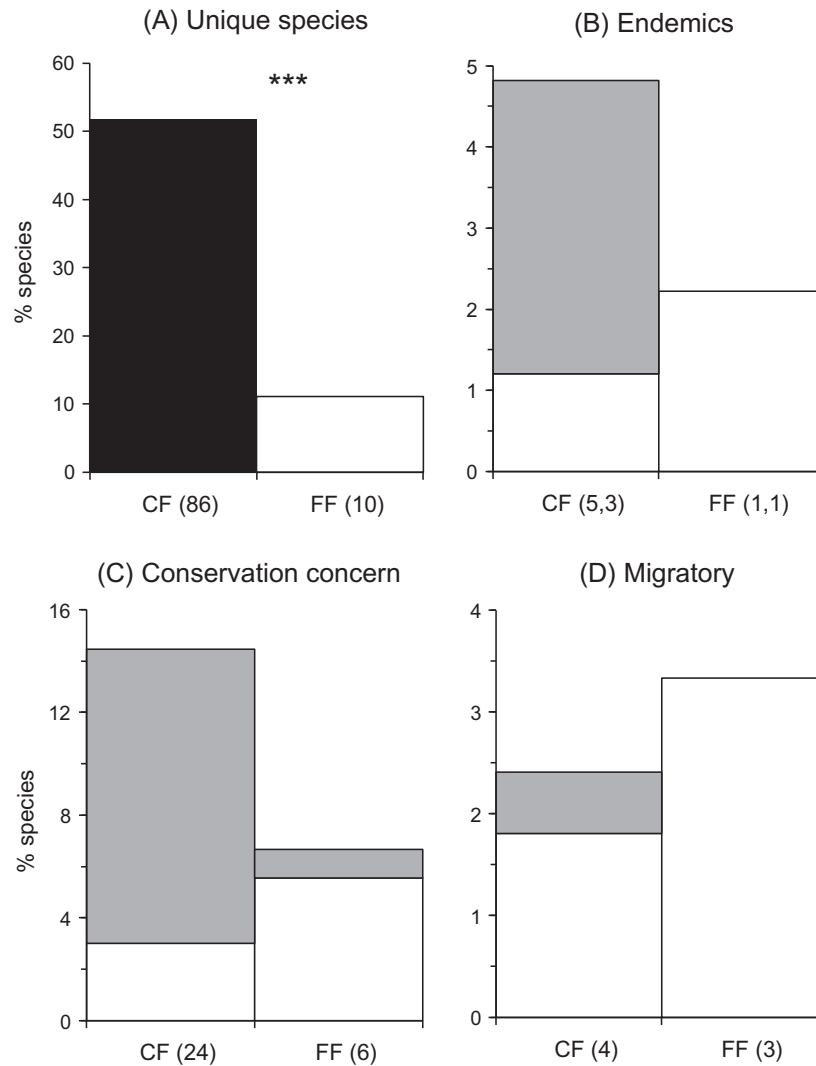
Fig. 4. Contiguous forests in NW Ecuador are important reservoirs for rare and endangered bird species. Proportion of (A) unique bird species, (B) endemics, (C) species of conservation concern, and (D) migratory species captured in contiguous forest (CF; total species observed: 165) or forest fragments (FF; 89 species in total). Number of species in each category shown between parentheses; for endemic species, the first number corresponds to Chocó endemics, the second to Tumbesian endemics; in (B–D), the gray and white portions of the columns indicate species in each category that are unique and non-unique, respectively, to contiguous forest or fragments; ***$p < 0.001$.

Proportion of species in the four main dietary guilds observed (frugivores, insectivores, nectarivores, and granivores) did not differ among habitat types in contiguous forest ($\chi^2_6 = 1.9, p = 0.93$) or fragments ($\chi^2_6 = 2.0, p = 0.92$), or between contiguous forest and forest fragments ($\chi^2_3 = 1.3, p = 0.73$). Guilds did differ in terms of their relative abundance in response to habitat loss (percent of individuals captured per guild, contiguous vs. fragmented forest, ($\chi^2_3 = 62.8, p < 0.0001$): frugivores and insectivores increased in abundance in fragments, while nectarivores decreased (Fig. 5). Guild abundance also changed in response to habitat disturbance in contiguous forest ($\chi^2_6 = 117.9, p < 0.0001$), with frugivores and nectarivores being less abundant, and insectivores and granivores more abundant in disturbed sites compared to OG forest (Fig. 5); there was no equivalent pattern in fragments ($\chi^2_6 = 8.3, p = 0.22$).

4. Discussion

Disturbed forests are increasingly common in tropical landscapes and have been advocated as focal areas for conservation (Wright, 2005; Edwards and Lawrance, 2013). Barlow et al. (2007b) point out several issues that have clouded the debate over the conservation value of disturbed tropical forests, including lack of large and undisturbed control sites, replication, and multiple metrics of biodiversity. In addition, variation in landscape context and extent of disturbance makes comparisons across studies challenging (Chazdon, 2008; Dent and Wright, 2009). To avoid these pitfalls when evaluating the conservation value of disturbed forests in an understudied tropical biodiversity hotspot, we used a factorial design with replicated sites, a control treatment (contiguous OG forest), and objective habitat characterization criteria to assess the separate effects of habitat loss and degree of habitat disturbance on multiple metrics of understory bird community integrity. OG, SL, and CC forests differed in several structural aspects but not in elevation, suggesting that different land use practices were applied regardless of topography, and that any differences found in bird communities across sites may be attributable to anthropogenic practices rather than to natural environmental variation (although we did not measure other variables such as slope and soil type).

The response of understory birds to forest changes depended on the metric considered. Species richness was affected by both habitat disturbance and habitat loss in complex ways: it increased with habitat disturbance (OG < SL < CC) and decreased with habitat loss (contiguous forest > fragmented forest). In addition, these two
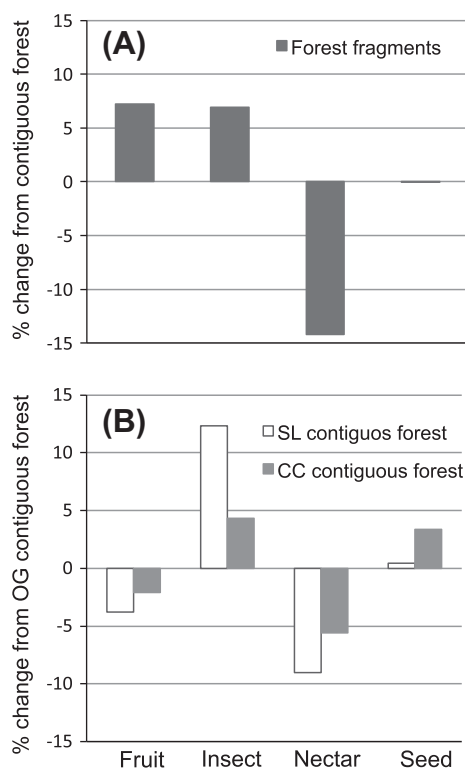
Fig. 5. Habitat loss and habitat disturbance both affect relative abundance of major guilds of understory birds in NW Ecuador. Shown is the percent change in abundance of four main dietary guilds of understory birds in response to (A) habitat loss and (B) habitat disturbance (SL: selectively-logged forest, CC: clear-cut forest).

factors had an interactive effect on richness, in that the reduction in number of species due to habitat loss was pronounced in the most disturbed (CC) forests, but not in the less disturbed (OG, SL) habitat types.

Focusing first on the effect of habitat disturbance per se on richness, the positive relationship we observed was contrary to our expectations, and underscores the fact that few if any general conclusions can be drawn from the body of research conducted to date on this relationship. Recent meta-analyses report a general richness decline with increasing disturbance (i.e., more modest for selectively-logged and more extreme for secondary forests; Barlow et al., 2007a; Gibson et al., 2011; Putz et al., 2012). In contrast, and in concordance with our own study, higher avian richness in early-successional forests was observed in studies employing visual-auditory sampling (Johns, 1991; Blake and Loiselle, 2001), perhaps due to increased productivity in the lower vegetation strata promoted by the broken canopy in disturbed forests (Blake and Loiselle, 1991, 2001). Finally, several other studies using a variety of sampling methods failed to detect any changes in richness with habitat disturbance (Edwards et al., 2011; Schleuning et al., 2011; seven of 21 studies reviewed by Barlow et al., 2007b). This wide range of results suggests that the extent and direction of habitat disturbance effects on avian richness can vary widely across systems due to deterministic and stochastic processes, and highlights the need for additional empirical studies employing comparable methods.

In contrast to habitat disturbance, available evidence suggests that habitat loss has more consistently negative effects on richness (Lees and Peres, 2006; Schleuning et al., 2011). Forest fragments typically present a depauperate biota, partly because smaller patches sample fewer species and less habitat diversity than larger patches (MacArthur and Wilson, 1967). In addition, fragments usually harbor fewer species than similar-sized patches in contiguous

forest, due to many factors including extinction of organisms with large home ranges, reduced immigration, deterioration of biotic and abiotic conditions by edge effects and increased susceptibility to fire and invasive species, and cascade effects on ecosystem processes (Ewers and Didham, 2006; Laurance et al., 2002). In keeping with these expectations, we observed a reduction in richness in fragments relative to contiguous forest.

However, we found that the interaction between habitat disturbance and loss had a strong effect on richness, in that species loss was most pronounced in the most disturbed fragments. Some fragments in this study may still owe an "extinction-debt" (Tilman et al., 1994) because habitat loss is recent (the last 40 years), but this time frame should have been sufficient to cause drastic reductions in number of species in these small fragments (<50 ha, see Supplementary material Table 1; Ferraz et al., 2003). Our findings suggest that habitat disturbance interacts in important ways with habitat loss to modulate rates of extinction and/or species recolonization following natural forest expansion. Better knowledge of fragment age and landscape-level isolation measures would be useful to make more inferences, as both of these variables have been identified as important predictors of species richness, along with patch size and habitat quality (Lees and Peres, 2006). To the extent that our data allowed us, however, we did not detect relationships between observed number of species and fragment size or distance from contiguous forest.

Capture rates were relatively stable across treatments. A full model comparing across forest and habitat types was non-significant, despite the fact that all habitat types suffered a reduction in capture rates in fragmented forest (Table 2), with less disturbed habitats being more affected (contiguous vs. fragmented forest, OG: 51% reduction in capture rates; SL: −30%; CC: −16%). Our results thus suggest that fragmentation reduced overall abundance of understory birds, especially in assemblages dominated by closed-forest species.

Changes in abundance did not affect all species similarly; rather, habitat disturbance and habitat loss interacted in complex ways to affect guild abundances. Different guilds were negatively impacted by both disturbance and habitat loss (nectarivores), favored by habitat loss but impacted by disturbance (frugivores), unaffected by habitat loss but favored by disturbance (granivores), or favored by both processes (insectivores). The positive response of insectivores to both habitat loss and disturbance is surprising, given that these are recognized as a group particularly sensitive to forest deterioration (Stouffer and Bierregaard, 1995; Sigel et al., 2006; Gray et al., 2007; Newbold et al., 2012). This finding must be interpreted with caution, however. First, the increased abundance of insectivores relative to other guilds may be more a result of the decrease in the importance of nectarivores, as these are especially represented in mature forest communities in this region; e.g., the four most-abundant species in the contiguous OG forest were understory hummingbirds (in order of importance, *Phaethornis yaruqui*, *Threnetes ruckeri*, *Thalurania fannyi*, and *Eutoxeres aquila*), which responded for 30% of all captures and suffered reductions both with habitat loss and habitat disturbance (with the exception of *T. ruckeri*, which increased in abundance with disturbance). Second, the increase in insectivore abundance in fragments was driven by a minority of the species, as most insectivores (65 out of 101 species) were more abundant in contiguous forest. Finally, the proportion of indicative species that have an insectivorous diet dropped from 76% in OG or SL contiguous forest to 61% in CC contiguous forest (Supplementary material Table 2).

The strongest effects on bird communities were related to species composition, which was affected by both habitat disturbance and habitat loss. Species composition in contiguous forest was markedly different from that of forest fragments, implying that habitat loss caused extirpation of forest specialists. To a lesser

extent (given the lack of indicator species and low proportion of unique species in fragments), habitat loss may also have promoted colonization by open-habitat specialists and/or habitat generalists. Species of conservation importance were heavily affected by habitat loss, as fragments suffered a 75% reduction in both the proportion of endemics and of threatened species, a substantial impact, even though not significant, given the small sample sizes. Conversely, contiguous forest and fragments presented similar numbers of migratory species, which often favor edge habitats (Petit et al., 1995; Blake and Loiselle, 2001).

The effect of habitat disturbance on species composition was stronger in contiguous forest than in fragments. In contiguous forest, OG and SL sites were very similar to each other and distinct from CC sites. In particular, OG and SL sites were characterized by several forest-specialist, disturbance-sensitive indicator species (e.g., *Schiffornis turdina*, *Phaenostictus mcleannani*, *Microbates cinereiventris*, among others in Supplementary material Table 2), while CC sites were characterized by many that favor regenerating habitats and have medium-to-low sensitivity to anthropogenic disturbance (e.g., granivores and/or edge-specialists such as *Arremon aurantiirostris*, *Cantorchilus nigricapillus*, *Thamnophilus atrinucha*, *Manacus manacus*, *Oryzoborus angolensis*, *Sporophila* ssp., among others, Supplementary material Table 2). In fragments, there was a non-significant but general gradient in species composition from OG to SL to CC fragments (Fig. 3). This, along with the larger spread observed among these sites (Fig. 3), highlights the idiosyncratic nature of biotic responses often observed in forest fragments (Ewers and Didham, 2006; Peters et al., 2008; Prugh et al., 2008). Although we did not detect an effect of fragment size on species composition, other unknown or unmeasured variables likely to locally influence animal communities are fragment age, shape, and connectivity, as well as more fine-scale characteristics of the habitat, such as fire history and frequency of understory grazing/trampling (Laurance et al., 2002; Ewers and Didham, 2006; Prugh et al., 2008; Dent and Wright, 2009). In addition, the patchy distribution of species commonly observed in tropical forests could cause even fairly similar fragments to sample different assemblages by chance (Laurance et al., 2002).

The similarities in species composition, species richness and forest structure between OG and SL sites highlights the comparatively benign effect of a selective-logging treatment in relation to clear-cutting, as shown by other studies (Edwards et al., 2011; Gibson et al., 2011). These results also underscore the need for long-term studies that reveal whether or not effects on the community composition of secondary forests are permanent, or how long they take to revert (Dunn, 2004).

Regenerating disturbed forests increasingly dominate tropical landscapes. While protecting remaining primary tropical forests is paramount, there is growing demand for research evaluating costs and benefits of protecting disturbed forests in different landscape contexts (e.g., Fisher et al., 2011). Our study shows that regenerating patches surrounded by contiguous forest sustain high levels of avian biodiversity and, given that past habitat disturbance has been relatively mild (i.e., selective logging), present communities that closely resemble those in primary forest. In contrast, when qualitatively similar forests occur in a fragmented landscape, we observed reductions in richness and profound changes in community composition characterized by loss of endemic, disturbance-sensitive, and endangered species. Further, there was a synergistic effect between habitat loss and disturbance, in that the most pronounced effects on richness occurred in the most disturbed forest fragments. These findings underscore the importance of considering both landscape context and the nature of habitat disturbance when evaluating the conservation value of non-pristine forests. They also reinforce the critical importance of BBS and the Mache-Chindul Reserve, which are strongholds of biodiversity in the

megadiverse and highly threatened Ecuadorian Chocó-Tumbes bioregion (Sierra, 2001), and highlight the need for pro-active conservation, reforestation, and corridor establishment programs in this region.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.07.007.

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