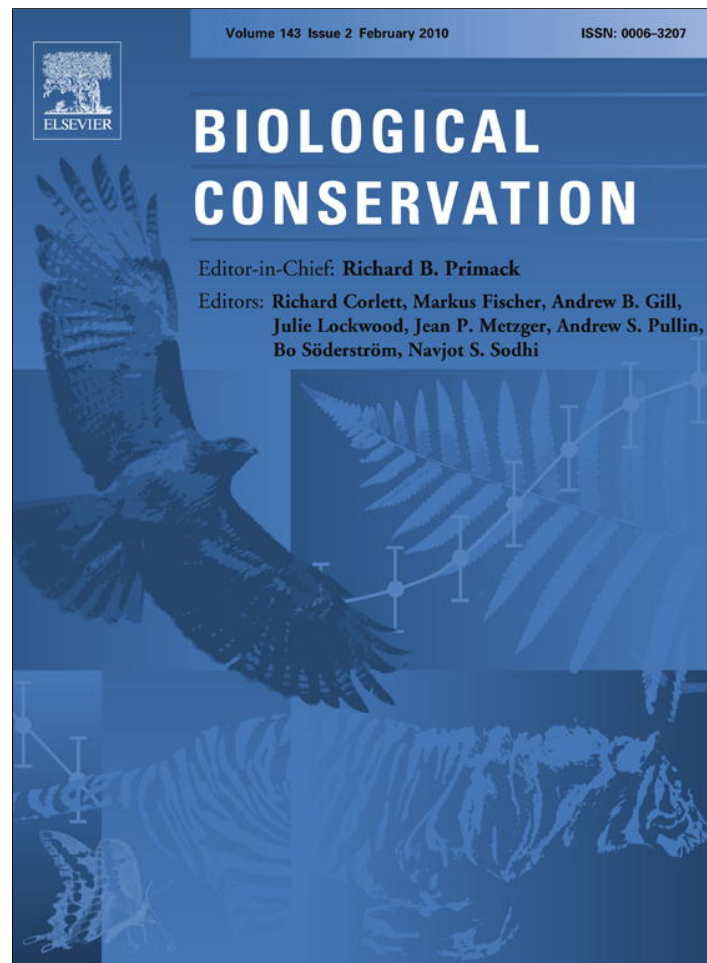


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Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Comparing bird community responses to forest fragmentation in two lowland Central American reserves

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ARTICLE INFO

Article history:

Received 13 June 2009

Received in revised form 17 October 2009

Accepted 25 October 2009

Available online 25 November 2009

Keywords:

Barro Colorado Island

Faunal relaxation

Habitat loss

Insectivore

La Selva Biological Station

Tropical forest

ABSTRACT

Habitat loss and fragmentation reduce diversity of tropical bird communities, but the predictability of how communities in fragments disintegrate over time remains unclear. We compared bird community changes of two lowland forest reserves, La Selva Biological Station (LSBS), Costa Rica and Barro Colorado Island (BCI), Panama, both approximately the same size (1500 ha) and at similar latitude (9–10°N) in Central America. Both reserves are losing bird species despite LSBS's connection to an existing large park (incomplete isolation) and BCI's favorable location within a largely forested landscape. We examined characteristics of guilds and species lost from the sites to determine whether patterns were similar, and thus predictable. Some of the same guilds declined at both reserves, particularly insectivores and ground/understory nesters. At LSBS mixed-species flock participants, forest species, and burrow-nesters also declined or became extirpated disproportionately. At BCI edge species became extirpated. Body mass was a poor predictor of species and guild loss at both sites, except for carnivores at La Selva. Thus, fragmentation appears to influence some guilds more than others, but which species decline or disappear in tropical forest fragments is also influenced by site-specific factors, mostly yet to be determined. We need to understand such idiosyncratic effects of fragmentation better, rather than rely on one-size-fits-all management plans to conserve bird communities in tropical forest fragments.

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1. Introduction

Habitat loss and forest fragmentation are the primary causes of extinction in tropical forests (Pimm and Raven, 2000; Davies et al., 2001; Raffaelli, 2004). Responses of Neotropical forest birds to habitat fragmentation have been especially well-documented relative to responses of other tropical taxa (Sodhi et al., 2004; Stratford and Robinson, 2005). Bird communities consistently lose species after isolation of forest patches, but whether particular species are consistently more likely to disappear after fragmentation and isolation remains unclear (Şekercioğlu and Sodhi, 2007). Determining whether community changes occur in predictable patterns requires long-term data because species losses after isolation, or faunal relaxation, can continue for many decades post-isolation (Brooks et al., 1999; Robinson, 1999; Ferraz et al., 2003; Feeley and Terborgh, 2008).

The Biological Dynamics of Forest Fragments Project (BDFFP), the world's largest and longest running fragmentation experiment has yielded many important results on vulnerability to habitat fragmentation (Bierregaard et al., 2001; Laurance et al., 2002).

For example, forest understory insectivores and mixed-species flocks are more likely to decline and disappear after fragmentation than are other guilds (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995; Stratford and Stouffer, 1999). Persistence of particular species is influenced by the size of fragments and the degree of isolation from nearby forests (Ferraz et al., 2007; Van Houtan et al., 2007). The degree of isolation is influenced by both the characteristics of intervening matrix habitats and the degree to which different species use the matrix (Gascon et al., 1999; Develey and Stouffer, 2001; Laurance et al., 2004). Although the BDFFP has greatly advanced our knowledge of the effects of tropical fragmentation, two issues raise concerns about the generalizability of results. First, the largest fragment in the experiment is 100 ha, an area at least an order of magnitude smaller than demonstrably vulnerable tropical sites (e.g., Matlock et al., 2002; Şekercioğlu et al., 2002; Ribon et al., 2003). Species loss takes much longer the larger the fragment (Ferraz et al., 2007), making patterns more difficult to detect. Second, characteristics of declining species after fragmentation appear to depend on the site. For example, in some landscapes large frugivores are sensitive (Levey and Stiles, 1994; Christiansen and Pitter, 1997; Peres, 2001; Ribon et al., 2003); and relatively rare species are sensitive in some studies (Pimm et al., 1988; Goerck, 1997) but not others (Karr, 1982a). Such results highlight

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the question of whether patterns of species losses from tropical fragments are predictable.

Two large forest reserves in Central America with a long history of bird community inventories provide a unique opportunity to compare patterns of species loss. La Selva Biological Station, Costa Rica and Barro Colorado Island (BCI), Panama have both experienced long-term changes in bird communities as a result of human-induced landscape changes surrounding the reserves, and are much larger (~1500 ha) than fragments in most other studies (Robinson, 1999; Sigel et al., 2006). Both sites are in lowland rainforest with far more similarities (Karr et al., 1990) than differences (Table 1).

Although both La Selva and BCI have experienced long-term avian declines and extirpations (Robinson, 2001; Sigel et al., 2006), the two sites' avian communities have never been compared formally to assess whether isolation has caused similar changes in community composition. Here we examined whether these two bird communities experienced similar avifaunal changes by comparing historical and current bird communities. The two sites share many species, but not all, so we also used ecological characterizations of all species (body mass, diet, habitat, mixed-species flock participation, nest height and nest type) to facilitate comparisons. Similar community changes would support the importance of deterministic mechanisms. Alternatively, stochasticity or local site-specific factors might play a predominant role in patterns of change. Understanding both the common and site-specific avifaunal changes in detail is a critical step in evaluating mechanisms of avifaunal change on the way to informed management.

2. Methods

2.1. Study sites

La Selva Biological Station (LSBS), Costa Rica (10°26'N, 83°59'W, 35–137 masl), located on the Caribbean Slope of the Cordillera Central, is owned and operated by the Organization for Tropical Studies (OTS) since they purchased 800 ha of old-growth forest and abandoned plantations in 1968. Today, LSBS contains approximately 1611 ha of diverse habitats, including old-growth forest (73%), swamp forest, selectively logged forest, different stages of secondary forest, abandoned cacao and *Cordia alliodora* plantations, abandoned pastures, maintained successional plots, an arboretum, and small developed areas for living and laboratory space. Vegetation is multilayered and diverse, typical of lowland tropical rainforest. Old-growth forest at La Selva is unusual in its domination by a single tree species, *Pentaclethra macroloba*, comprising ~40% of total timber volume. However, other tree species augment richness levels comparable to other Central American lowland forests (Hartshorn and Hammel, 1994).

Table 1

Characteristics of La Selva Biological Station, Costa Rica, and Barro Colorado Island (BCI), Panama.

Characteristics	La Selva	BCI
Latitude	10°N	9°N
Geographic position	Caribbean slope	Caribbean slope
Habitat	Lowland rainforest	Lowland rainforest
Fragment size (ha)	1611*	1562
Time since isolation/ disturbance	15–45 years	85 years
Life zone	Tropical wet forest	Tropical moist forest
Annual precipitation (mm)	3962	2960
Surrounding matrix	Pastures, plantations, human residences	Lake Gatun
Resident bird species	250	248

* La Selva remains connected by a forested corridor to montane forests of Braulio Carrillo National Park along its southern boundary.

Average annual precipitation at LSBS is 3962 mm, and mean monthly temperature ranges from 24.7 °C in January to 27.1 °C in August, consistent with a tropical wet-forest life zone (Holdridge, 1967; McDade and Hartshorn, 1994; Hartshorn and Hammel, 1994).

Land cover in the region surrounding LSBS was approximately 70% forest in 1963, but had declined to less than 35% by 1983, and has since continued to decline (Butterfield, 1994; Read et al., 2001). Most of the regional deforestation resulted from conversion to pasture between 1960 and 1983, fueled by the beef export market (Read et al., 2001). The rate of deforestation slowed between 1983 and 1992, but clearing continued with an increased emphasis on plantations such as heart of palm, banana, pineapple, and oil palm. Since 1992 the trend towards plantations continued, only interrupted by some small-scale reforestation projects resulting from government incentives (Read et al., 2001). Unlike the relatively rapid isolation of Barro Colorado Island by water, LSBS became isolated gradually, mostly 1960–1992.

La Selva remains connected along its southern boundary to Braulio Carrillo National Park, an approximately 44,000 ha area of old-growth forest that extends up to 3000 masl. Elevation increases abruptly in the 5–10 km wide corridor that connects LSBS to Braulio Carrillo. This corridor was officially established in 1986 to prevent complete isolation (McDade and Hartshorn, 1994). Some deforestation along this southern border and the western edge of the corridor (Fig. 2b in Read et al., 2001) may have contributed to the isolation of lowland forest species. This is compounded by the steep elevation change, which may isolate those lowland species whose upper range lies between 500 and 1000 masl (Stiles and Skutch, 1989; Blake and Loiselle, 2000). However, the corridor potentially increases the amount of old-growth forest accessible to lowland species.

Barro Colorado Island (BCI), Panama (9°09'N, 79°51'W, 26–164 masl) was formerly a hilltop in lowland forest along the Chagres River on the Caribbean slope of Panama. The area was flooded between 1911 and 1914, creating Gatun Lake as part of the Panama Canal. The nearest mainland is less than 300 m from BCI, and aside from the lake, the surrounding region is almost completely forested within 4 km and largely protected as National Park or canal watershed. The nearest forest on the mainland comprises 1900 ha and connects to other areas that constitute 12,000 ha of forest. On the opposite side of the lake is a 22,000 ha National Park. However, the lowlands of central Panama have been isolated from montane forests since the 1960s (Robinson et al., 2000). BCI was declared a biological reserve in 1923 (Chapman, 1929), but had previously been disturbed by settlers (Willis, 1974). Most of its eastern half contains relatively younger forest, while the western half contains more mature forest, but has probably also experienced minor historical disturbance (Willis, 1974; see Leigh, 1999 for details on the flora and climate).

Average annual precipitation at BCI is approximately 2670 mm with a pronounced dry season from January to April. The maximum temperature ranges between 21° and 32 °C with little seasonal variation. The life zone is classified as tropical moist forest (Holdridge, 1967; Knight, 1975).

2.2. History of ornithological surveys

The avifauna of LSBS was first described by Slud (1960), who assigned qualitative abundance to each species. More recent qualitative surveys (Stiles, 1983; Levey and Stiles, 1994; Zook et al., 1999) provided information with which Sigel et al. (2006) described population trends, one of the first analyses based on categorical abundance data. In 1976–78 T.W.S. also used 50 × 50 m square quadrats to quantify the relative abundances of LSBS bird species, a procedure repeated in 1996 (Sigel et al., 2006). Avifaunal comparisons

over this time period indicate that LSBS's bird community underwent significant changes, including declines in forest understory insectivores and mixed-species flocking species. Other surveys of its avifauna include mist-netting and point count data from the mid-1980s to the mid-1990s that demonstrate rapid changes in bird community composition along a transect from LSBS up in elevation into adjacent Braulio Carrillo National Park (Blake and Loiselle, 2000) and a comparison of old-growth and second growth bird communities using data from the same period (Blake and Loiselle, 2001). Matlock et al. (2002) compared the LSBS avifauna to that of small forest fragments associated with nearby banana plantations to demonstrate the ability of these patches to support some forest species.

Barro Colorado Island (BCI), Panama is the longest studied single fragment in the tropics (Robinson, 1999). Since it was designated a biological reserve in 1923, several ornithologists have monitored its bird community (Sieving and Karr, 1997; Robinson, 1999). Chapman (1929) and Eisenmann (1952) were the first to create lists of bird species for BCI; and Willis (1974) and Willis and Eisenmann (1979) documented 51 resident and four recent immigrant species extirpations, 34 of which were hypothesized to result from forest maturation. In a comparison of BCI with nearby Soberania National Park, Karr (1982b) identified 50–60 forest bird extirpations, not including the 34 associated with forest-maturation. He attributed the identification of additional extirpated species, beyond those recognized by Willis and Eisenmann (1979), to insufficient knowledge of the BCI bird community before and immediately after isolation (Karr, 1982b). The most recent study, consisting of censuses performed through 2006, shows that since the creation of the island, 65 species of birds have disappeared, and several others declined to near extirpation (Robinson 1999, 2001, unpublished data).

2.3. Species characterizations

To facilitate comparing avifaunal changes in the two reserves, species assignments to ecological categories were based on information from several sources including Ridgely and Gwynne (1992), volumes 1–11 of the Handbook of the Birds of the World (del Hoyo et al., 1992–2006), Sigel et al. (2006; and references therein), and the authors' own expertise (see Appendix for the entire list of species with both ecological and population trend categorizations). Each species found at either site, historically and presently, was assigned to one category for migration status at each site (BCI and LSBS); and to one, mutually exclusive category with respect to five ecological characteristics: diet, flocking behavior, habitat, nest type, and nest height. We then assigned each species to a population status (each site) and population change status (LSBS only). Migratory status consisted of four discrete categories: (1) permanent resident (P) lives at the site year round; (2) winter resident (W) spends the winter (non-breeding) months at the site; (3) migrant (M) passes through the site during migration and (4) visitant (V) occurs accidentally or visits occasionally (e.g., higher elevation birds that visit La Selva during periods of inclement weather). Dietary guilds consisted of six categories: (1) carnivores eat vertebrates, carrion, snails; and may take large arthropods; (2) insectivores eat entirely or mostly insects and other arthropods; (3) nectarivores eat floral nectar; (4) granivores eat mostly seeds; (5) frugivores eat mostly fruit and (6) omnivores are generalists and frequently use food from more than one category (e.g., arthropods and fruit), and this category also includes dabbling ducks. Flocking guilds consisted of four categories: (1) nonflockers do not flock with any species, including their own; (2) monospecific flock participants flock only with their own species; (3) mixed-species flock participants regularly travel and feed with other species and (4) ant-followers follow army ant swarms to feed on flushed

arthropod prey. Habitat guilds consisted of five categories: (1) forest species are typically associated with old-growth forest and tall secondary growth, but include species associated with streams and small rivers within forest; (2) edge species are associated with forest edge and canopy; (3) open species are found in open habitats (e.g., young second growth, pasture, plantations, suburban and urban areas); (4) aerial species spend most of their time soaring or foraging on the wing and (5) aquatic species are associated with large rivers, lakes, and marsh habitat. Nest type consisted of six categories: (1) scrape nests are found directly on the ground; (2) cup nests are cups or bowls either on the ground (with some nest construction) or off the ground; (3) platform nests are platforms typically built of sticks; (4) cavity nesters build their nests inside trees or termitaries and include both primary (construct the cavity) and secondary cavity nesters (adopt cavities formed by other species); (5) pouch nests are suspended (pendulous or pyriform) and (6) enclosed nests have a roof and typically a side entrance. Nest height consisted of four categories: (1) ground nests are found below 1 m; (2) understory nests are typically constructed between 1 and 4 m above the ground; (3) subcanopy nests are constructed below the canopy but above 4 m height and (4) canopy nests are found in the canopy, placed within or on the top level of vegetation regardless of height. Population status consisted of three categories: (1) extant species (x) are found presently at the site; (2) extirpated species (e) were observed at the site at one time, but have since disappeared and (3) old records (o) are species that may have visited the site but their presence had not been well established and so they could not be considered extirpated. For the population change status at La Selva five categories were recognized based on data from Sigel et al. (2006) and Christmas Bird Count data from 1985–2005 (available online at <http://www.ots.ac.cr/en/laselva/species/birdcounts/index.shtml>): (1) increasing species (i) have significantly increased in abundance; (2) unchanged species (u) have maintained relatively constant abundance; (3) moderately declining species (mod) have decreased in abundance but are still present in numbers; (4) severely declining species (sev) have almost disappeared or may have disappeared but their extirpation cannot be confirmed and (5) extirpated species (e) have disappeared entirely from La Selva. These additional categories were necessary to detect trends since few species are extirpated from this site. Body mass data were taken from Dunning (2008). Female mass was used where information for both sexes was given, and the nearest geographical location was used where entries were given for multiple sites. The average of the minimum and maximum values was used where a range was given without a mean.

2.4. Analyses

Aquatic species, aerial species, and old vagrant records (o) were removed from all analyses, as were visitants (V), migrants (M), and winter residents (W), although these are retained in Appendix. We created contingency tables with the number of species in each category within each of the five ecological guilds that are extant (x) versus extirpated (e) at each site; and with the BCI data we used a chi-squared test of independence, comparing population condition versus ecological characteristics (Table 2). This test was not justified with the La Selva data due to the small number of extirpations (see Section 3). We thus performed two additional analyses for La Selva data, with decreasingly conservative classes of extirpation or decline: (1) "severe decline" refers to extirpated species pooled with species showing severe declines and (2) "moderate decline" refers to extirpated species pooled with species showing both moderate and severe declines. Since only two granivores were retained we pooled them with frugivores. We also pooled platform-nesting species with scrape nesting species because both nest types are functionally similar, and pooling was needed to increase

Table 2

Changes in species richness at BCI and La Selva across guilds. Counts represent number of species in each guild category. Expected values are in parentheses. See Section 2 for definition of “severe decline” and “moderate decline” categories for La Selva species.

	BCI			La Selva			La Selva		
	Extant	Extirpated	Total	Extant	Severe decline	Total	Extant	Moderate decline	Total
<i>Diet</i>									
Omnivore	70 (63.2)	18 (24.8)	88	76 (73.2)	5 (7.8)	81	69 (64.5)	12 (16.5)	81
Carnivore	25 (25.1)	10 (9.9)	35	36 (35.3)	3 (3.7)	39	33 (31.0)	6 (8.0)	39
Insectivore	49 (61.7)	37 (24.3)	86	77 (84.1)	16 (8.9)	93	60 (74.0)	33 (19.0)	93
Nectarivore	15 (12.2)	2 (4.8)	17	15 (13.6)	0 (1.4)	15	15 (11.9)	0 (3.1)	15
Frugivore + granivore	19 (15.8)	3 (6.2)	22	22 (19.9)	0 (2.1)	22	22 (17.5)	0 (4.5)	22
Total	178	70	248	226	24	250	199	51	250
Chi-squared	$\chi^2 = 16.51, df = 4, p = 0.002$			$\chi^2 = 11.39, df = 4, p = 0.023$			$\chi^2 = 24.67, df = 4, p < 0.001$		
<i>Flock</i>									
No	118 (122.0)	52 (48.0)	170	158 (152.8)	11 (16.2)	169	144 (134.5)	25 (34.5)	169
Single	15 (14.4)	5 (5.7)	20	18 (18.1)	2 (1.9)	20	15 (15.9)	5 (4.1)	20
Mixed	39 (35.9)	11 (14.1)	50	43 (47.9)	10 (5.1)	53	35 (42.2)	18 (10.8)	53
Ant	6 (5.7)	2 (2.3)	8	7 (7.2)	1 (0.8)	8	5 (6.4)	3 (1.6)	8
Total	178	70	248	226	24	250	199	51	250
Chi-squared	$\chi^2 = 1.57, df = 3, p = 0.666$			$\chi^2 = 7.19, df = 3, p = 0.062$			$\chi^2 = 10.98, df = 3, p = 0.012$		
<i>Habitat</i>									
Forest	73 (73.2)	29 (28.8)	102	90 (102.2)	23 (10.9)	113	72 (90.0)	41 (23.1)	113
Edge	29 (34.5)	19 (13.6)	48	37 (34.4)	1 (3.7)	38	31 (30.3)	7 (7.8)	38
Open	48 (47.4)	18 (18.6)	66	67 (60.6)	0 (6.4)	67	66 (53.3)	1 (13.7)	67
Generalist	28 (23.0)	4 (9.0)	32	32 (28.9)	0 (3.1)	32	30 (25.5)	2 (6.5)	32
Total	178	70	248	226	24	250	199	51	250
Chi-squared	$\chi^2 = 6.99, df = 3, p = 0.072$			$\chi^2 = 27.70, df = 3, p < 0.001$			$\chi^2 = 36.34, df = 3, p < 0.001$		
<i>Nest</i>									
Cup	73 (73.0)	28 (28.0)	101	84 (85.8)	11 (9.2)	95	74 (75.4)	21 (19.6)	95
Platform + scrape	31 (29.6)	10 (11.4)	41	41 (39.7)	3 (4.3)	44	36 (34.9)	8 (9.1)	44
Burrow	7 (8.0)	4 (3.1)	11	7 (9.9)	4 (1.1)	11	5 (8.7)	6 (2.3)	11
Cavity	39 (34.7)	9 (13.3)	48	51 (47.9)	2 (5.2)	53	46 (42.1)	7 (10.9)	53
Pouch	14 (15.2)	7 (5.8)	21	18 (19.0)	3 (2.0)	21	14 (16.7)	7 (4.3)	21
Enclosed	13 (16.6)	10 (6.4)	23	22 (20.8)	1 (2.2)	23	21 (18.3)	2 (4.8)	23
Total	177	68	245	223	24	247	196	51	247
Chi-squared	$\chi^2 = 5.74, df = 5, p = 0.332$			$\chi^2 = 13.09, df = 5, p = 0.023$			$\chi^2 = 13.86, df = 5, p = 0.017$		
<i>Nest height</i>									
Ground	15 (17.2)	9 (6.8)	24	20 (21.7)	4 (2.3)	24	17 (19.1)	7 (4.9)	24
Understory	55 (65.3)	36 (25.7)	91	78 (82.3)	13 (8.7)	91	67 (72.4)	24 (18.6)	91
Subcanopy	87 (78.2)	22 (30.8)	109	112 (104.9)	4 (11.1)	116	101 (92.3)	15 (23.7)	116
Canopy	21 (17.2)	3 (6.8)	24	16 (17.2)	3 (1.8)	19	14 (15.1)	5 (3.9)	19
Total	178	70	248	226	24	250	199	51	250
Chi-squared	$\chi^2 = 13.20, df = 3, p = 0.004$			$\chi^2 = 9.58, df = 3, p = 0.022$			$\chi^2 = 7.53, df = 3, p = 0.057$		

cell frequencies (original categories are maintained in Appendix to increase its potential utility). Brood parasites were excluded from the nest type and nest height analyses.

We constructed a guild-by-site matrix by counting species in each guild at each site (Table 2). We also constructed three species-by-site matrices: one with all species from both sites, one with only forest-dwelling species, and one with only edge species. The sites we used are Old BCI and Old LSBS (Old LS), which are the original bird communities before any known extirpations or community changes occurred; New BCI and New LS, which are the communities today; and for La Selva “severe decline” and “moderate decline”, representing those communities that would result if severely declining and moderately declining species, respectively, were to become extirpated (Appendix).

To allow visualization of changes in community composition dissimilarity matrices (Table 3) were computed to create non-metric multidimensional scaling (NMDS) plots using all six sites (Fig. 1) with SAS 9.0. The first dissimilarity matrix contains all pair-wise combinations of sites using the Bray-Curtis overlap index, which calculates overlap between two sites based on the relative abundance of species in each guild. Subtracting the overlap index from 1 generates the dissimilarity index on a scale of 0–1, in which larger values represent a greater dissimilarity in bird communities between sites. We created three additional dissimilarity matrices for all pair-wise combinations of sites: using all species, only

forest-dwelling species, and only edge species, in all three cases using the Jaccard overlap index, which calculates overlap between sites using presence-absence data.

Binomial logistic regression (SPSS 11.5) was used to test whether body mass was a predictor of population decline for all species, and for each dietary and habitat guild for: (1) species at both sites, (2) species at BCI, and (3) species at La Selva. No nectarivore or frugivore species declined at LSBS, precluding analysis of these guilds at LSBS.

3. Results

Although the avifaunal composition of the two sites was not identical prior to their isolation, they possessed striking similarities. A total of 248 permanent resident species from BCI and 250 permanent residents from LSBS were included in the analyses here (Appendix). The two sites share approximately 70% of all species historically (old LSBS compared to old BCI). Of the 250 permanent resident species at LSBS, 75 (30.0%) are not permanent residents at BCI (a few are known from accidental or old records). Of the 248 permanent residents at BCI, 73 (29.4%) are not permanent residents at LSBS. At BCI, 70 species (28.2%) are extirpated, contrasted with only 8 of 250 (3.2%) at LSBS. Sixteen LSBS species (6.4%)

Table 3
Dissimilarity matrices for BCI and La Selva calculated from the Bray–Curtis overlap index at the guild level (a) and Jaccard overlap index at the species level for all species, forest-based species, and edge species (b, c and d respectively). See Section 2 for definition of “severe decline” and “moderate decline” categories for La Selva species.

	Old BCI	Old La Selva	New BCI	New La Selva	New La Selva severe decline species	New La Selva moderate decline species
<i>Guilds (a)</i>						
Old BCI	0.00000					
Old La Selva	0.02891	0.00000				
New BCI	0.16431	0.17009	0.00000			
New La Selva	0.03020	0.01626	0.15714	0.00000		
SevLS	0.05400	0.05042	0.12376	0.03418	0.00000	
ModLS	0.10961	0.11358	0.07267	0.09750	0.06352	0.00000
<i>All species (b)</i>						
Old BCI	0.00000					
Old La Selva	0.45820	0.00000				
New BCI	0.28226	0.28800	0.00000			
New La Selva	0.46395	0.03200	0.53147	0.00000		
SevLS	0.49045	0.09600	0.53623	0.06612	0.00000	
ModLS	0.51987	0.20400	0.55000	0.17769	0.11947	0.00000
<i>Forest-based species (c)</i>						
Old BCI	0.00000					
Old La Selva	0.40741	0.00000				
New BCI	0.28431	0.50000	0.00000			
New La Selva	0.42424	0.06195	0.48305	0.00000		
SevLS	0.48819	0.20354	0.49074	0.15094	0.00000	
ModLS	0.53782	0.36283	0.53535	0.32075	0.20000	0.00000
<i>Edge species (d)</i>						
Old BCI	0.00000					
Old La Selva	0.59016	0.00000				
New BCI	0.39583	0.68627	0.00000			
New La Selva	0.58333	0.02632	0.68000	0.00000		
SevLS	0.58333	0.02632	0.68000	0.00000	0.00000	
ModLS	0.61404	0.18421	0.66667	0.16216	0.16216	0.00000

declined severely in abundance, and another 17 (6.8%) declined moderately (Appendix).

Diet and nest height are two factors significantly associated with extirpated species on BCI (Table 2). Among the dietary guilds, more insectivores are extirpated than would be expected by chance alone. Among nest height categories, species that nest lower (ground and understory) are extirpated more than expected. Flocking behavior, habitat preference, and nest type are not significantly associated with patterns of extirpation on BCI.

Due to the low number of extirpations and thus low expected cell frequencies based on the LSBS data, the same tests as done with the BCI data are not meaningful. However, by looking at not just the extirpated, but also the near-extirpated species (severe decline), and the more inclusive class of these plus declining species (moderate decline), some patterns emerge. Diet is strongly associated with moderately declining species, with insectivores declining more than expected (Table 2), just as at BCI. Among the flocking guilds, mixed-species flock participation is significantly associated with moderate declines. Habitat association is also important, with more forest species associated with moderate declines at LSBS than expected. With respect to nest type, species with burrow nests are significantly associated with moderate declines. Nest height also shows a clear trend, with lower nesters (ground and understory) significantly associated with the moderate decline category, although the chi-squared test for the severely declining species was not quite significant ($p = 0.057$).

The distributions of species among guilds in the original bird communities of BCI and LSBS (OldBCI, OldLS) were similar before isolation. This is shown not only in the relative proximity of the sites in multi-dimensional community space (Fig. 1a), but also by the numbers of species originally in each guild (Table 4). Considering dietary guilds, BCI had a few more omnivores, and fewer insectivores. Moreover, these were the two most species-rich guilds at both sites. The number of species in each flocking guild was almost

identical originally, with LSBS having only three more mixed-species flocking species and only one fewer non-flocking species. Considering habitat guilds, LSBS began with more forest species and BCI more edge species prior to isolation. Among nest guilds, BCI had a few more cup nesters, LSBS a few more cavity nesters. Nest height was also very similar, although BCI had slightly fewer sub-canopy nesters and slightly more canopy nesters (Table 4).

Similar changes in community structure at BCI and LSBS are shown by the parallel change across communities on the guild-level NMDS plot (Fig. 1a). Present day BCI is most similar to modern LSBS, based on treating the declining and near-extirpated species at LSBS as extirpated, shown by the low pairwise dissimilarity index between New BCI and LSBS moderately decline category (ModLS, Table 3a). This indicates that LSBS may be following a similar pattern of guild loss to that experienced by BCI, assuming that present-day declines accurately predict future extirpations at LSBS.

The species-level NMDS analyses reveal site-specific patterns of community change. The species-level analysis revealed the two communities were moving apart (Fig. 1b). However, when only forest birds were analyzed, the communities once again showed a parallel trend, even though the Old LSBS and Old BCI communities began differently (Fig. 1c), which suggests the different patterns in Fig. 1b are caused by declines of edge-dwelling species at BCI. Edge species at BCI had the highest proportion of extirpations among habitat types (Table 4), which is reflected in the largest dissimilarity index between Old BCI and New BCI in all four analyses (Table 3) and correspondingly greatest distance between Old BCI and New BCI on the NMDS plots (Fig. 1d). At LSBS, by contrast, only a single edge species (*Aphanotriccus capitalis*) was extirpated, while six species experienced moderate declines (none severely; Table 2). These latter changes are reflected in the close proximity of all the LSBS points in the NMDS analysis using only edge species (Fig. 1d).

Body mass was not significantly associated with population status in any of the logistic regression analyses except for the

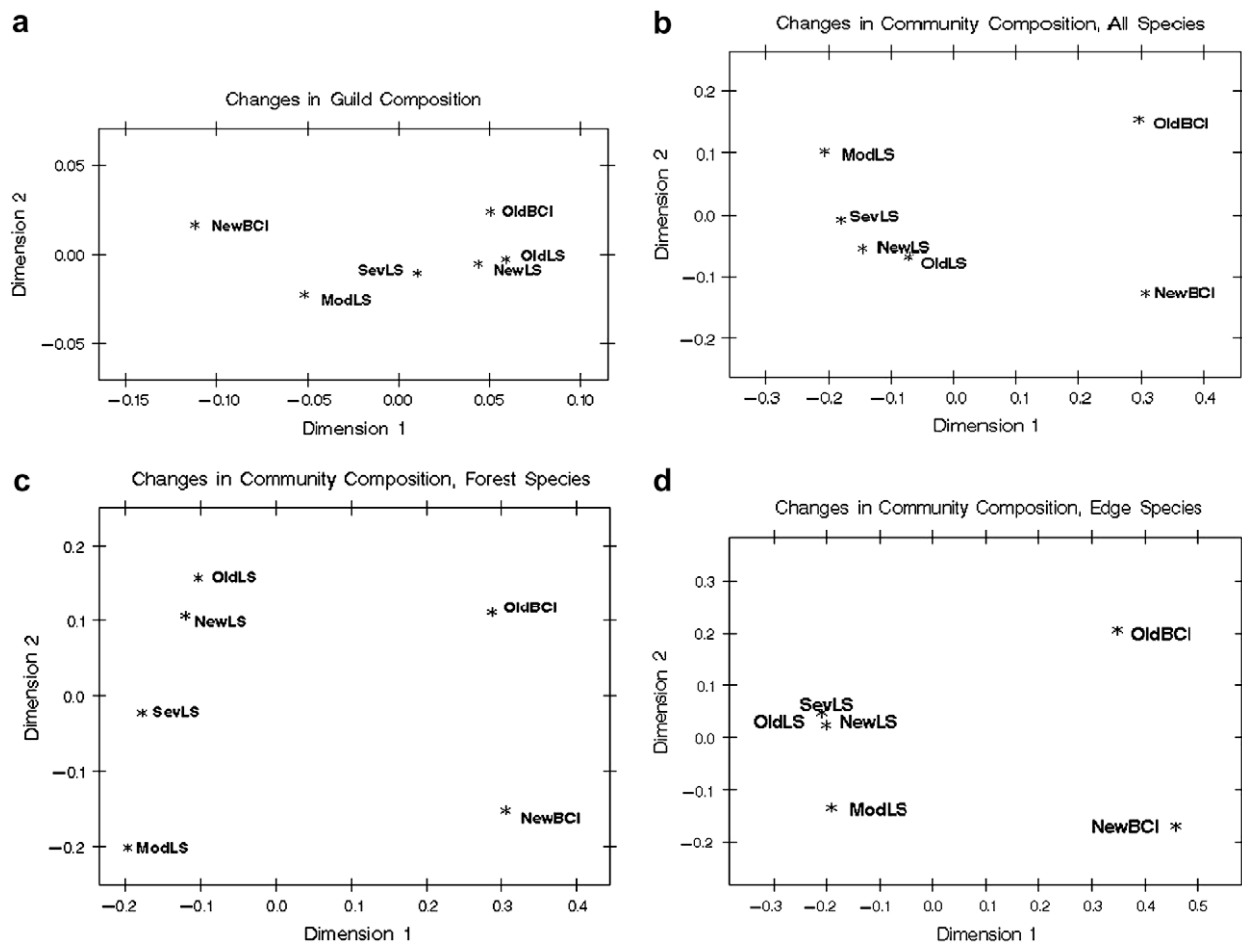


Fig. 1. Non-metric multidimensional scaling plot of BCI and La Selva bird community changes using : (a) the number of species categorized by guild, (b) all species, (c) forest-based species, and (d) edge species. The SevLS community treats “severely decline” species as extirpated while the ModLS community treats “moderate decline” species as extirpated.

carnivore guild at La Selva (Wald = 4.417, $df = 1$, $p = 0.036$), where four of the five declining or extirpated species were among the largest of the guild.

4. Discussion

Temporal dynamics of the BCI and LSBS bird communities after isolation include concordant declines as well as idiosyncratic changes. Although this may not be a surprising result, both kinds of change are instructive by highlighting ecological characteristics making birds generally vulnerable to fragmentation, and identifying site idiosyncrasies requiring explanation. Both communities initially shared 70% of their permanent resident species and nearly identical guild structures (Table 4, Fig. 1a), and both share non-random extirpations or declines, especially insectivores (Tables 2 and 4). Declining or extirpated species were also disproportionately represented by ground and understory nest height guilds at both sites. Considering idiosyncratic changes, LSBS lost a higher percentage of canopy and burrow nesters, mixed-species flockers, and forest-dwelling species (Table 4). This lack of concordance could result from stochastic species extirpations, but differences between the two sites suggest that some site-specific processes are driving species losses deterministically, and the specific guilds of species involved help identify plausible mechanisms. Detecting idiosyncratic species declines among otherwise similar sites is a strength of the kind of comparative study conducted here. Such patterns beg explanation, and we offer some potential hypotheses below, where we discuss the patterns observed by ecological guild,

the results of analyses at the species level, the limitations of our methods, and implications for tropical conservation. Both the concordant and idiosyncratic declines identify important questions for future research.

4.1. Insectivores

Insectivores responded negatively to fragmentation at both sites, a widespread tropical pattern (e.g., Thiollay 1997; Stratford and Stouffer, 1999; Şekercioğlu et al., 2002; Sodhi et al. 2004). This pattern remains to be explained convincingly, despite considerable effort. Several ecological attributes associated with tropical insectivory may be operating individually or synergistically to increase their vulnerability. For example, many forest understory insectivores occur at low population density in the tropics even without human impacts (Terborgh et al., 1990; Robinson et al., 2000). Taking into account pre-isolation population sizes, their density within isolated fragments may not be sufficient to support viable populations (Sigel et al., 2006; Sigel, 2007). Small populations are generally vulnerable to extirpation due to demographic and ecological stochasticity, genetic drift, and inbreeding (Pimm et al., 1988; Westemeier et al., 1998).

The isolation of many remnant insectivore populations in fragmented tropical landscapes is exacerbated by their reluctance to cross unsuitable habitat, even as narrow as a small road or trail (Stouffer and Bierregaard, 1995; Develey and Stouffer, 2001; Laurance et al., 2004). Another factor that may increase the vulnerability of insectivores is dietary specialization (Sherry, 1984;

Table 4

Number of species by site within each guild category in the initial BCI and La Selva bird communities and the percent loss experienced at both sites.

Guild	Old BCI/Old LS	New BCI% extirpated	New LS% extirpated	SevLS% extirpated and severely declining	ModLS% extirpated, severely and moderately declining
<i>Diet</i>					
Omnivore	88/81	20.5	2.5	6.2	14.8
Carnivore	35/39	28.6	7.7	7.7	15.4
Insectivore	86/93	43.0	3.2	17.2	35.5
Granivore	1/1	0.0	0.0	0.0	0.0
Nectarivore	17/15	11.8	0.0	0.0	0.0
Frugivore	21/21	14.3	0.0	0.0	0.0
<i>Flock</i>					
None	170/169	30.6	3.6	6.5	14.8
Single	20/20	25.0	0.0	10.0	25.0
Mixed	50/53	22.0	1.9	18.9	34.0
Ant	8/8	25.0	12.5	12.5	37.5
<i>Habitat</i>					
Forest	102/113	28.4	6.2	20.4	36.3
Edge	48/38	39.6	2.6	2.6	18.4
Open	66/67	27.3	0.0	0.0	1.5
Generalist	32/32	12.5	0.0	0.0	6.3
<i>Nest</i>					
Scrape	6/7	0.0	0.0	0.0	14.3
Cup	101/95	27.7	2.1	11.6	22.1
Platform	35/37	28.6	8.1	8.1	18.9
Burrow	11/11	36.4	9.1	36.4	54.5
Cavity	48/53	18.8	3.8	3.8	13.2
Pouch	21/21	33.3	0.0	14.3	33.3
Enclosed	23/23	43.5	0.0	4.3	8.7
Parasitic	3/3	66.7	0.0	0.0	0.0
<i>Nest height</i>					
Ground	24/24	37.5	4.2	16.7	29.2
Understory	91/91	39.6	3.3	14.3	26.4
Subcanopy	109/116	20.2	0.9	3.4	12.9
Canopy	24/19	12.5	15.8	15.8	26.3

Rosenberg, 1990; Marra and Remsen, 1997; Şekercioğlu, 2007), making them particularly sensitive to fluctuating resource distribution (Karr, 1982b). For example, specialist army ant-following insectivores are more vulnerable than generalists to forest fragmentation in Africa (Peters et al., 2008; Peters and Okalo, 2009). Both reluctance to cross unsuitable habitat and dietary specialization may contribute to relatively large home range size (Terborgh et al., 1990), and consequent low population density.

Şekercioğlu et al. (2002) found too little difference in arthropod availability or prey-consumption patterns among fragments to explain sensitivity of insectivores. One possible explanation for this negative result is that arthropod sampling (pit traps, sticky traps, and timed searches) was random, rather than focused specifically at foraging microhabitats to which tropical insectivores are adapted (Blake and Loiselle, 2009). Moreover, the Şekercioğlu et al. (2002) control site (227 ha) was itself an isolated forested area smaller than fragments in the present study, which are themselves experiencing insectivore declines over time. Thus, it is plausible that arthropod community changes occur in areas even larger than their control site. Şekercioğlu et al. (2002) did find a positive correlation between the ability of an insectivore to use non-forest habitat and their persistence in small fragments, indicating that dispersal ability may be an important factor in determining the persistence of tropical insectivores in small fragments (see also Lees and Peres, 2008). In summary, tropical rainforest interior insectivorous birds appear to be sensitive to forest fragmentation in general, but more research is needed to resolve the mechanism(s).

4.2. Nest height

Nest predation contributes to the decline of bird species in fragmented temperate forest landscapes (Robinson et al., 1995), and

has also been implicated as a mechanism responsible for the declines of bird species in fragmented tropical forests (Sieving, 1992; Githiru et al., 2005; Stratford and Robinson, 2005; Young et al., 2008). However, too little rigorous study of nest predation rates exists for tropical fragments, mostly due to the difficulty of finding and monitoring enough real nests (Stratford and Robinson, 2005; Young et al., 2008; Robinson, 2009). Much of what we do know comes from studies of artificial nests (e.g., Gibbs, 1991; Sieving, 1992), but these may not indicate predation risk at real nests (Moore and Robinson, 2004; Thompson and Burhans, 2004; Robinson et al., 2005a). The traditional explanation for an increase in nest predation in fragmented tropical forests is “mesopredator release” (Sieving, 1992), in which forest fragments lose the top predators that control the populations of many mesopredators that are opportunistic nest predators (e.g., medium-sized omnivorous vertebrates). However, this hypothesis may not apply in the tropics (e.g., Spanhove et al., 2009) for a variety of reasons (Lahti, 2009). For example, video monitoring of real nests on BCI shows that almost all of the predation was attributable to a single species of colubrid snake (*Pseustes poecilonotus*), not a traditional “mesopredator” (Robinson et al., 2005b). We know little about *P. poecilonotus* except that it is a diurnal, primarily terrestrial, occasionally arboreal, forest species (Martins and Oliveira, 1999), which also occurs at LSBS.

Our result that ground- and low-nesting birds are declining and becoming extirpated disproportionately at both LSBS and BCI suggests that some deterministic mechanism is operating, such as the persistence of terrestrial or terrestrial-based predators in tropical forest fragments. The bird-eating snake *P. poecilonotus* is certainly a candidate in Central American forests based on the Robinson et al. (2005b) BCI results, but more information is needed on the abundance of this and other potential nest-predator species in tropical fragments and the surrounding

matrix, not to mention intact tropical forest (Lahti, 2009; Robinson, 2009).

4.3. Mixed-species flocks

Mixed-species flocks are known to be vulnerable to fragmentation across the tropics (Sodhi et al., 2004; Lee et al., 2005). One of the most puzzling findings of the present study is that mixed-species flocking species declined significantly at LSBS, but not BCI (Table 2). Two factors that have been suggested to explain the vulnerability of mixed-species flock participants to fragmentation impacts are: (1) large home ranges and thus large forest area requirements (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995; Maldonado-Coelho and Marini, 2000), and (2) reluctance to cross open areas and roads, increasing susceptibility to isolation (Develey and Stouffer, 2001; Ferraz et al., 2007). Mixed-species flocks in the tropics typically form around one or a few “nuclear” species attended by several facultative flocking species (Buskirk, 1976; Munn and Terborgh, 1979; Levey and Stiles, 1994). At LSBS, two previously common forest understory flock assemblages have all but disappeared (Sigel et al., 2006; Appendix), whose nuclear species are: (1) tanagers *Chlorothraupis carmioli* and *Tachyphonus delatrii*, and (2) antwrens *Myrmotherula fulviventris*, *M. axillaris*, and *Microrhopias quixensis*. The loss of nuclear species at LSBS could contribute to the decline and extirpation of species that depend heavily on flocking for food. Facultative flocking species *Lanio leucothorax* and *Myiobius sulphureipygius*, which associate with tanager flocks and antwren flocks, respectively, also declined severely, possibly to the point of extirpation at La Selva (Appendix). The loss of these nuclear and attendant flocking species has left the old-growth forest of LSBS depauperate of bird activity compared to other tropical sites (e.g., Refugio Bartola, Nicaragua – B. Sigel, pers. obs.).

The persistence of antwren flocks at relatively high density on BCI (Robinson, 2001) contrasts sharply with their near disappearance at LSBS. One possibility is that Barro Colorado Island has a greater degree of rainfall seasonality, with a relatively stronger dry season than LSBS, which could increase the abundance of dead leaf clusters and aerial leaf litter, a preferred foraging substrate of the antwrens (Greenberg and Gradwohl, 1980; Gradwohl and Greenberg 1982, 1984). Another possibility, under investigation, involves changes in peccary abundance at LSBS (N. Michel, unpublished data). Clearly the identification of the mechanism(s) underlying such dramatically different avifaunal changes at LSBS versus BCI require further investigation, if only because of their implications for management (see below).

4.4. Habitat

LSBS and BCI experienced some similar patterns of species loss related to habitat, but also exhibited some important differences. One difference identified here is that forest birds declined at LSBS, whereas habitat was nearly, but not significantly associated with extirpation at BCI (Table 2). All but the generalist guild at BCI experienced relatively similar percent losses, but LSBS forest birds experienced a higher percent loss than the other habitat guilds (Table 4). We suggest that the most parsimonious explanation is differences in landscape: BCI is a true island isolated by Lake Gatun, while LSBS is almost completely surrounded by pasture and plantation. As the forest regenerated at BCI, many open and edge species became extirpated due to loss of their preferred habitat (Robinson, 1999, 2001) coupled with effective isolation from other such habitat in the landscape. At LSBS a greater diversity of habitat types remains accessible, especially since OTS purchased several annexes that consisted mostly of secondary forest and regenerating pasture, and since the habitat surrounding LSBS likely supports

large numbers of open country and edge species. Supporting this idea, some open and edge species have increased in abundance at LSBS as a result of the deforestation in the region (Sigel et al., 2006). In general, subtle site differences in terms of habitat and microhabitat can explain significant changes in avian species composition of tropical forests, even among “replicate” sites in close proximity (Blake and Loiselle, 2009).

The opposing trend of avifaunal community changes at BCI and LSBS suggested by Fig. 1b is at least partly due to proportionately greater loss of second growth and open-country species at BCI. Once this is controlled for by removing non-forest species (Fig. 1c), the two communities show parallel changes in community composition, indicating similar processes operating in the forest as indicated by the guild-level analysis (Fig. 1a). The implication of the similar community trends in just the forest species, not seen when non-forest species are included, is that once landscape differences are controlled, the reduction and isolation of forest has had similar effects on both bird communities. Despite a net increase in regenerating forest, LSBS, and to some extent BCI, are still losing forest-based species. These species are probably lost due to landscape-level effects of fragmentation and isolation. At BCI many forest species do not recolonize readily (Robinson, 1999; Moore et al., 2008), and therefore those species that become extirpated usually do not return despite the net increase of mature forest. La Selva is connected along its southern boundary to the nearly continuously forested Braulio Carrillo National Park. However, the history of disturbance along this corridor combined with the steep elevational gradient from LSBS into the higher elevation park may have effectively isolated many lowland forest species at LSBS. According to data collected from 1985 to 1989, many lowland species were abundant in the corridor but dropped out quickly between 500 and 1000 m in elevation (Blake and Loiselle, 2000), where their present status is unknown. Further investigation of dispersal and usage of secondary and non-forested habitat by old-growth tropical forest species, especially in corridors such as La Selva-Braulio Carrillo, are necessary to determine population isolating factors (e.g., Holderegger and Wagner, 2008).

4.5. Nest type

LSBS and BCI also differed with respect to declines and extirpations in nest type. Specifically, certain types were associated with declining species at LSBS, but not at BCI (Table 2). The nest type that had the greatest proportion of declines at La Selva was burrow nesters, six of which (~55%) were either extirpated or declined significantly. These species include two bucconids (*Malacoptila panamensis* and *Monasa morphoeus*), three furnariids (*Hylocistetes subulatus*, *Automolus ochrolaemus*, and *Sclerurus guatemalensis*), and one troglodytid (*Microcerculus philomela*). These burrow nesters dig burrows on relatively level ground, unlike kingfishers and jacamars, which prefer to burrow into steep banks. All of these declining species are insectivores and it may be that this is an incidental result of high correlation between insectivory and burrow nesting (see Section 4.7, below). An alternative explanation is that burrow nests are indeed vulnerable at LSBS, possibly due to the high density of collared peccaries (*Tayassu tajacu*), which trample the understory to such an extent as to impact litter depth and ground-level vegetation (N. Michel, unpublished data). The abundance of a keystone herbivore such as the collared peccary is precisely the kind of idiosyncratic factor that could help explain multiple changes at LSBS not observed at BCI, and thus warrants further study. The majority of research on nest predation in the tropics focuses on open cup nests (e.g., Sieving, 1992), leaving burrow nesters poorly studied. Further research is necessary to explore the relative abundance of potential nest predators, and both their direct and indirect impacts on different nest types.

4.6. Body mass

Although large body size is widely claimed to be an important predictor of extinction vulnerability in birds (Gaston and Blackburn, 1995; Sodhi et al., 2004) and large-bodied species in general (Pimm et al., 1988), it was not significantly associated with declining or extirpated species in our analysis, except LSBS raptors. Owens and Bennett (2000) found that extinction risk from habitat loss affected birds with smaller body size, whereas extinction risk from human persecution and/or introduced predators was higher in larger-bodied species. This result implicates habitat change as the most important factor in our two study sites, which is consistent with the fact that both BCI and LSBS are protected from hunting. Because many tropical bird species are longer-lived and have lower population densities than their temperate counterparts (traits often associated with larger-bodied species), it may mitigate the overall effect of larger-bodied species being more vulnerable to extinction in the tropics. That is, many small-bodied tropical species may be vulnerable to extinction for the same reason that larger-bodied species are more vulnerable globally, i.e., low population density and slow life histories. An important goal of future research should thus be to discern the relative importance of body size *per se* versus life-history and habitat loss/degradation for species vulnerability to fragmentation.

4.7. Methodological issues

Lack of statistical independence of the ecological guilds confounded our ability to pinpoint which guild characteristics make forest birds vulnerable to extirpation. For example, there was complete correlation between burrow nests and the “ground” nest category. A significant association between burrow nests and extirpation may also cause a significant association between ground nests and extirpation. However, either result implicates increased nest predation from a low-foraging predator, or at least increased understory disturbance of some kind.

Our study incorporated historical data to reveal generalizations about guild and species declines both shared, and site-specific between two large, long-term forest isolates that are also important tropical biological research stations. A major drawback was that we only had two large Neotropical sites with appropriate historical data, which limited our ability to generalize further. Unfortunately, few reserves of comparable area remain on the Caribbean slope of Central America to allow further comparisons.

4.8. Implications

We have documented significant changes in the bird communities of two reserves at least an order of magnitude larger than 100 ha. The fact that such large reserves, one connected to a large park and the other situated in a largely forested landscape, are still losing species many years after isolation, suggests that the effects of fragmentation on tropical bird communities will be extensive and long-lasting. Our data also call into question conservation plans based on the assumption that particular guilds known to be sensitive in one region will also be sensitive elsewhere. Conservationists should expect some degree of site-specific responses to fragmentation, and future research should be directed at identifying such responses. This implies that the minimum critical size to preserve an intact bird community in the tropics may be much larger than previously recognized. According to pre-isolation insectivore densities at La Selva, we estimate that its area would need to be at least an order of magnitude larger (i.e., 10s of thousands of ha) to maintain viable populations of some tropical insectivores (Sigel, 2007; see also Thiollay, 2002).

We compared declining species at LSBS with extirpated species at BCI because relatively few species at La Selva (only 8 of 250) have disappeared. Part of the discrepancy in the number of extirpations between the two sites stems from our conservative approach of placing some species that may have been lost into the “severely declining” category because their extirpation remains to be confirmed. Another factor may be the ability of species to persist at LSBS due to its connection with Braulio Carrillo National Park. Even if particular species persist at a site such as LSBS, their low abundance makes them “functionally extinct” (Şekercioğlu et al., 2004). Another important difference between the two sites is time since isolation. La Selva has experienced some form of isolation for considerably less time than BCI (Table 1). We suspect that many of the declining species at LSBS are on their way to disappearing as faunal relaxation and site-specific disturbances take their course.

Species declined or were lost non-randomly from guilds at both LSBS and BCI. This suggests that deterministic models incorporating autecological factors should be important in predicting the biodiversity and community composition of fragments post-isolation (see also Blake and Loiselle, 2009). Insectivores and species that nest on the ground and in the understory appear to be particularly susceptible to the effects of habitat fragmentation across the region. However, which species are lost in a fragment is also affected by its landscape context. The landscape differences between BCI and LSBS were responsible for many, but not all of the declines that were unique to each site, especially the greater loss of open and edge species at BCI. Climatic and geographic factors such as the more intense seasonality of BCI may also have contributed to the differences (e.g., in antwren flocks), although alternative hypotheses for site-specific declines are plausible, as discussed above. It is therefore important to examine general patterns of vulnerability to fragmentation as well as the individual context of each fragment when predicting the impacts of fragmentation on tropical bird communities.

Despite our ability to identify a variety of patterns of avian guild susceptibility to forest fragmentation, and both similarities and differences between LSBS and BCI, we remain far from identifying the relevant mechanisms. Many hypotheses suggested by this study clearly require further investigation, including the role of nest predators, prey composition and abundance, dispersal barriers, indirect effects of herbivores such as peccaries, and small population size. Since some of the factors that put tropical forest birds at risk are correlated statistically in studies such as ours (many species are simultaneously forest understory, flocking, and insectivorous species!), we need experimentation and other means to tease apart cause-and-effect. Understanding the mechanisms responsible for bird community changes identified will both advance our understanding of tropical community response to fragmentation and improve our ability to design reserve systems that can maximize the preservation of the remaining tropical biodiversity.

Acknowledgements

We gratefully acknowledge funding for this study from an A.W. Mellon Research Exploration Award in Tropical Biology administered by the Organization for Tropical Studies (T.W.S. and B.J.S.) and from the Center for Tropical Forest Science (W.D.R.). Anonymous reviewers made several valuable suggestions for improvement of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.10.020.

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