REVISTA DE
Biología Tropical

Effect of a major highway on the spatial and temporal variation in the structure and diversity of the avifauna of a tropical premontane rain forest

Gerardo Avalos[1,2]* & Esteban Bermúdez[1]

1. Escuela de Biología, Universidad de Costa Rica, 11501-2060 San Pedro, San José, Costa Rica; tbermudez@deppat.com
2. The School for Field Studies, Center for Sustainable Development Studies, 100 Cummings Center, Suite 534-G, Beverly, MA 01915-6239 USA; avalos@fieldstudies.org

* Correspondence

Received 21-X-2015. Corrected 14-VI-2016. Accepted 15-VII-2016.

Abstract: Roads immersed in conservation areas will increase in number, size, and traffic over the next decade, and thus, understanding their effects on forest-dependent wildlife is crucial for improving current management practices and reducing the negative impacts of roads on sensitive species. We examined the influence of route 32 (a.k.a. Guápiles Highway) on temporal and spatial changes in the structure of the avifauna of Braulio Carrillo National Park, Costa Rica, a site crossed by this road along 25 km. The highway connects the capital city of San José with the Harbor of Limón in the Caribbean Sea (142 km). Although the road is narrow (12 m in width and comprised by two lanes along most of the route) it services over 1.5 million motor vehicles per year, 12 % are heavy trucks and trailers. We expected the highway to divide the avifauna, and thus to observe significant differences in species structure on opposite sides of the road. We described changes in bird diversity between wet and dry seasons at Las Palmas and Ceibo trails located on opposite sides of the highway (14 point counts per trail), and evaluated how abundance and diversity varied with road distance. Censuses took place during wet and dry seasons from 2002 to 2005. We listed 245 species and 6 035 observations during the 4-yr survey. Rare species dominated the avifauna (65 % of species < 5 observations), and species overlap between trails was high (Sorensen= 71 %; Morisita= 0.96). Species accumulation curves varied little among trails, yielding 190 species. Resident species represented 70 % of observations, followed by elevational (15 %) and long-distance migrants (1-2 %). Understory species were the most abundant (60 %) followed by canopy birds (30 %). Species turnover rate was 55 % between seasons, but species composition between trails remained homogeneous. Overall, birds were avoiding the road (abundance increased away from the road) although other diversity parameters (richness, dominance, Shannon index, and equitability) were not influenced by road proximity. Although the avifauna remained homogeneous on both sides of the road, which did not support the fragmentation hypothesis, the highway reduced the abundance and diversity of specialized understory insectivores associated with primary forests near the road. This highway will expand outside the National Park (from 2 to 4 lanes along 107 km from Río Frío to Limón) in the next years, which will increase traffic volume and road impacts within the Park. Roads are increasing across highly diverse tropical areas justifying the need for management practices based on the identification of sensitive groups. Rev. Biol. Trop. 64 (4): 1383-1399. Epub 2016 December 01.

Key words: species turnover, biodiversity monitoring, road ecology, road avoidance, understory insectivores.

Roads have multiple effects on the ecology of terrestrial communities and are increasingly dominating features in continental landscapes (Laurance et al., 2014). Roads are responsible for direct habitat loss, increased fragmentation and isolation of the original habitat, and the modification of landscape topography (Coffin, 2007; Laurance et al., 2014). Roads change microclimate conditions, increase edge penetration, favor extremes in temperature and radiation, intensify exposure to gas emissions, augment litter accumulation and noise pollution, and favor the establishment of exotic, disturbance-tolerant species (Coffin, 2007; Brown et al., 2006, Prasad, 2009). In addition, roads intensify plant mortality (Prasad, 2009) and increase the likelihood of roadkills and forest fires (Pinowski, 2005; Laurance, Goosem, & Laurance, 2009). Roads provide access to illegal hunting and extraction (Young, 1994) by making fragile areas more accessible (Rajvanshi & Mathur, 2015). In response to road disturbances a significant portion of the original biota moves away from the road, extending the impacts of fragmentation beyond the immediate road vicinity (Goosem, 2000; Benítez-López, Alkemade, & Verweij, 2010). The negative ecological effects of roads are ubiquitous, but they are more severe in tropical forests, where the high degree of niche specialization, typical of tropical species, translates into rapid biodiversity loss closer to the roads (Laurance, 2004).

One of the main immediate impacts of roads is the reduction of bird density and diversity (Benítez-López et al., 2010; Arévalo & Newhard, 2011). Forest interior, understory, and canopy species are particularly sensitive to road fragmentation (Develey & Stouffer, 2001; Laurance et al., 2009), while short-distance migrants and edge species could benefit from increased disturbance (Laurance et al., 2002). The vast majority of tropical species are edge avoiders (Laurance et al., 2002; Lindell et al., 2007), and thus, are likely to be negatively affected by fragmentation. The impacts of roads on biodiversity are linked to the dispersal ability of the organisms involved, their behavioral and physiological constraints and habitat requirements; this is not necessarily reflected in decreased species diversity. Sensitive groups, such as terrestrial insectivores, are usually the most heavily impacted, being behaviorally limited to move between gaps and forest fragments separated by short distances (Stratford & Stouffer, 1999). For instance, obligated ant-followers require extensive foraging grounds, and have difficulty crossing open spaces, being restricted to move between fragments using the remaining vegetation connecting forest patches (Stratford & Stouffer, 1999; Lees & Peres, 2008). Large body size, low dispersal ability, high feeding specialization, low population density, high dependence on a complex forest matrix, and low reproductive output are all factors associated with a decreased capacity to survive fragmentation (Sodhi, Liow, & Bazzaz, 2004). Many of these characteristics are typical of forest-interior bird species, especially, understory insectivores (Lees & Peres, 2008; Sánchez, Vargas-Castro, Ávalos, & Paniagua, 2014).

Monitoring programs would help to differentiate road impacts from the regular spatio-temporal variation in the abundance of different avian groups. Describing spatio-temporal changes in the structure of the avifauna is a mandatory step, essential to discriminate regular changes in the dynamics of the avifauna from anthropogenic disturbances. However, most studies on road impacts are based on one-time surveys (i.e., Develey & Stouffer, 2001). Instead, long-term monitoring is necessary considering the complexity of tropical avifaunas, which are subject to a constant species turnover involving long-distance and elevational migrants (Blake, Stiles & Loiselle, 1990) and highly mobile resident species with different sensitivities to environmental impacts. Monitoring programs should facilitate the analysis of road impacts by establishing a baseline, characterizing changes in species composition over time, identifying sensitive groups, and separating anthropogenic impacts from the background changes in species turnover (Lindenmayer, 1999; Beaudrot et al., 2016).

In this study, we analyzed the influence of route 32 (also known as the Guápiles Highway) on seasonal changes in the diversity of the avifauna of Braulio Carrillo National Park in Costa Rica. Route 32 is a mass-transit highway bisecting this mountainous protected area along 25 km. The road runs from the capital city of San José to the Harbor of Limón on the Caribbean Sea (142 km), representing the fifth road in importance in terms of traffic volume (more than 1.5 million motor vehicles use this road per year, 12 % are heavy trucks and trailers). The highway is narrow (12 m) and has 2 lanes along most of its route, but the Costa Rican government plans to expand it to 4 lanes along the Río Frío-Limón section (107 km) outside the National Park, which will certainly increase traffic volume throughout the whole highway. Until now, there has been no formal assessment of road impacts on any vertebrate group. First, we describe the structure of the avian community and the species turnover, and then we assessed if the road influences bird distribution by examining changes in species composition, abundance, species richness and diversity relative to distance from the road, focusing on the most disturbance-sensitive group: understory insectivores. Braulio Carrillo National Park is one of the most biologically and topographically diverse areas in Costa Rica (Blake & Loiselle, 2000). Understanding seasonal changes in avian diversity and how they are affected by human impacts is crucial to improve management alternatives capable of ameliorating the ecological effects of roads in tropical regions. The extent of the road network and traffic volume are expected to increase in the next decade across the Tropics (Laurance, 2015), and thus, it is critical to understand the impacts of roads on sensitive species, especially in regions bordering and bisecting protected areas. The results of this study are relevant to increase our knowledge on turnover rates of tropical birds, establish a baseline for future studies, and identify groups sensitive to road disturbances.

MATERIALS AND METHODS

Study site and data collection: Our study was conducted in Quebrada González, Braulio Carrillo National Park (BCNP), Costa Rica (47 500 ha, 10°13’ N - 84°37’ W, 400-500 m in elevation, Fig. 1). The forest at this site receives an average of 4 095 mm of rain per year and is considered a tropical premontane rain forest (Holdridge & Grencke, 1971). The temperature ranges between 25-28 ºC. The elevational gradient throughout the Caribbean side of Braulio Carrillo varies between lowland tropical rainforests (30 m) to tropical montane forests (2 906 m), representing one of the last protected elevation gradients still covered by continuous forests in Central America. These conditions support dense, evergreen forests, complex in structure and highly diverse in bird species composition. The whole Park supports nearly 500 bird species, which represent 80 % of the resident and 40 % of all bird species in Costa Rica (including long-distance migrants,

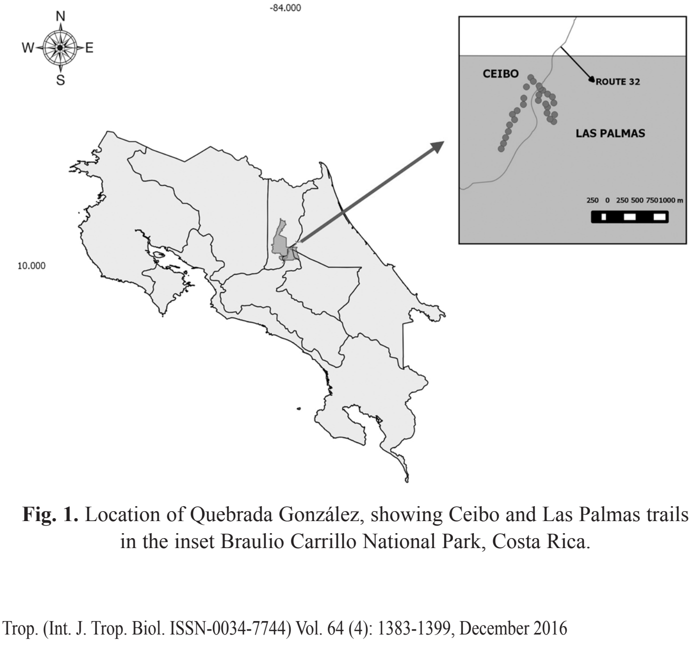

Fig. 1. Location of Quebrada González, showing Ceibo and Las Palmas trails in the inset Braulio Carrillo National Park, Costa Rica.

Blake & Loiselle, 1992). This National Park is bisected by Route 32, one of the busiest roads in the country, accounting for an average of about 4 000 vehicles per day. The Park was created in 1978, whereas the highway was initiated in the same year and was officially opened in 1987. We used Ceibo-Botarrama (hereafter, Ceibo) and Las Palmas trails, which face one another on the West and East sides of the road, respectively (Fig. 1). At this site, the road had two lanes and a width of 12 m. Though very near one another (the first census point for each trail were located on the edge of the road), the forest structure of each trail is different. Las Palmas loops for 1.6 km going almost entirely through primary forest, though some old secondary growth is found near the end of the trail. The 1 km loop of El Ceibo spans old second growth, but transitions into a primary forest on the portion of the trail extending off from Ceibo into Botarrama at the farthest point of the trail. Primary forest is found at the farthest points of the El Ceibo and throughout all of Botarrama.

Bird censuses: A handheld Global Positioning System (GPS) unit (Magellan model no. 315) was used to determine geographic coordinates in 14 census points separated by 120 m following the outline of both trails (Fig. 1). Four groups of 2-3 ornithologists hiked in alternating directions starting on opposite ends of the trails, and we randomly alternated trails and teammates to homogenize error. Each point was observed for 10 min and every bird that could be seen, heard and identified within a radius of 30 m was registered. When necessary, bird calls were recorded on tape and identified later. Censuses were done for 5 days in a row in April, as well as in November (starting in 2002 and ending in 2005). Data collection went from 5:30-9:30 am and from 2:30-5:30 pm.

Characterization of the general structure of the avifauna: We first provided an overall description of the structure of the avifauna. We measured similarity in species and family composition among trails using the classic Sorensen index, which is based on incidence data. Additionally, we used the Morisita index to measure overlap in species composition among trails using abundance data (Jost, Chao, & Chazdon, 2011). Species were separated into four categories of foraging strata (above the canopy, canopy, understory and near the water) following Stiles and Skutch (1989), Blake et al. (1990), and personal observations within the study area. Migrant status consisted of altitudinal migrants (AM), latitudinal migrants (M) and residents (R) following the criteria of Obando-Calderón et al., (2014) and Stiles and Skutch (1989). The body weight values of specialized understory insectivores including army ant followers (families Formicariidae, Furnariidae, Thamnophilidae and Troglodytidae) follow Stiles and Skutch (1989).

Temporal variation in diversity and species turnover: We compared the temporal variation in species diversity using two-way ANOVA (corrected for multiple comparisons using the Bonferroni approach), where season and trail were the predictor variables, and species richness, number of observations, Shannon index of diversity, dominance and equitability were the response variables. We compared species composition among census dates and trails using non-metric multidimensional scaling (MDS) and cluster analyses based on the Morisita index similarity matrix. Average turnover rates in bird species composition were also calculated using this similarity matrix.

Effect of distance on diversity: We used ordinary least squares regression to measure the relationship between road distance and bird diversity. Distance to the road was measured from the geographic location of each census point to the nearest road edge using ArcGIS 10 (ESRI, 2011). We quantified diversity for the overall avifauna as well as for specialized understory insectivores using species richness, the Shannon Diversity Index (H´) based on natural logarithms, equitability (H´/lnS, where S= number of species), evenness ($e^{H'}/S$), and species dominance denoted as 1-Simpson index, or 1-D, where:

$$D = \sum_{i}^{S} \left(\frac{ni}{N}\right)^2$$

D varies from 0 (all taxa are equally abundant) to 1 (one taxon dominates the sample), n_i= number of observations of species *i*, and N= total number of observations. These measures of diversity are intuitive and provide a representative value of the number of species as well as their relative abundance or evenness. We also examined the trend between distance to the road and the body weight distribution of specialized understory insectivores using OLS regression. Large insectivores occur at lower densities and require larger territories to satisfy food requirements, and are the first ones to disappear under altered environmental conditions (Sodhi et al., 2004). All statistical analyses were performed using JMP Pro 10.0.0 (SAS, 2012). Species diversity indices were calculated using PAST 1.94b (Hammer, Harper, & Ryan, 2001) and EstimateS version 8.2.0 (Colwell, 2005) following the recommendations of Jost et al. (2011) and Legendre and Legendre (2012).

RESULTS

General structure of the avifauna: similarity in species composition: A total of 245 species from 38 families and 6035 observations were registered during the 4-year survey. We observed 190 species in Ceibo and 191 at Las Palmas. The trajectories of the species accumulation curves varied little among Ceibo and Las Palmas and approached 190 species in both cases. Rarefaction analyses showed no differences in species richness between trails. Thus, the sampling protocol was sufficient to estimate species richness, and both sides of the road had about the same number of species, although Las Palmas had 683 more observations (Fig. 2B). The avifauna was dominated by rare species since 65 % of all species had less than 5 observations.

One hundred thirty-six species were common to both sides (Ceibo had 189 species and Las Palmas had 191). This results in a Sorensen index of 71 %. The magnitude of the Morisita index was 0.96 (Table 1). Of the species with 5 or more occurrences (61 and 70 for Ceibo and Las Palmas, respectively) 61 were common to both sides, resulting in a Sorensen index of 93 % (Morisita index= 0.96). Therefore, both sides showed great similarity in species composition, even after correcting for abundance. Species composition was thus homogeneous, and that the road was not separating the avifauna.

The characteristics of species diversity (richness and equitability) were similar for Ceibo and Las Palmas (Table 1). Dominance was low for both sides of the road, being close to 5 %. This was associated with high levels of evenness which approached the maximum value given the observed number of species. Quebrada González showed a high level of bird diversity characterized by high evenness (low dominance), high richness, and high

TABLE 1

Bird species diversity and species similarity at Ceibo and Las Palmas, showing the two most abundant species (and their percentage of total observations in bold-face). Braulio Carrillo National Park, Costa Rica

	Ceibo	Las Palmas
Species richness	189	191
Number of observations	2 676	3 359
Shannon index	3.7	3.73
Equitability %	70	71
Dominance %	5.3	5.1
Olive Tanager (*Chlorothraupis carmioli*)	**14 %**	**14.82 %**
Tawny-crested Tanager (*Tachyphonus delatrii*)	**8.7 %**	**8.12 %**
Sorensen index both trails %		71
Morisita index both trails		0.96

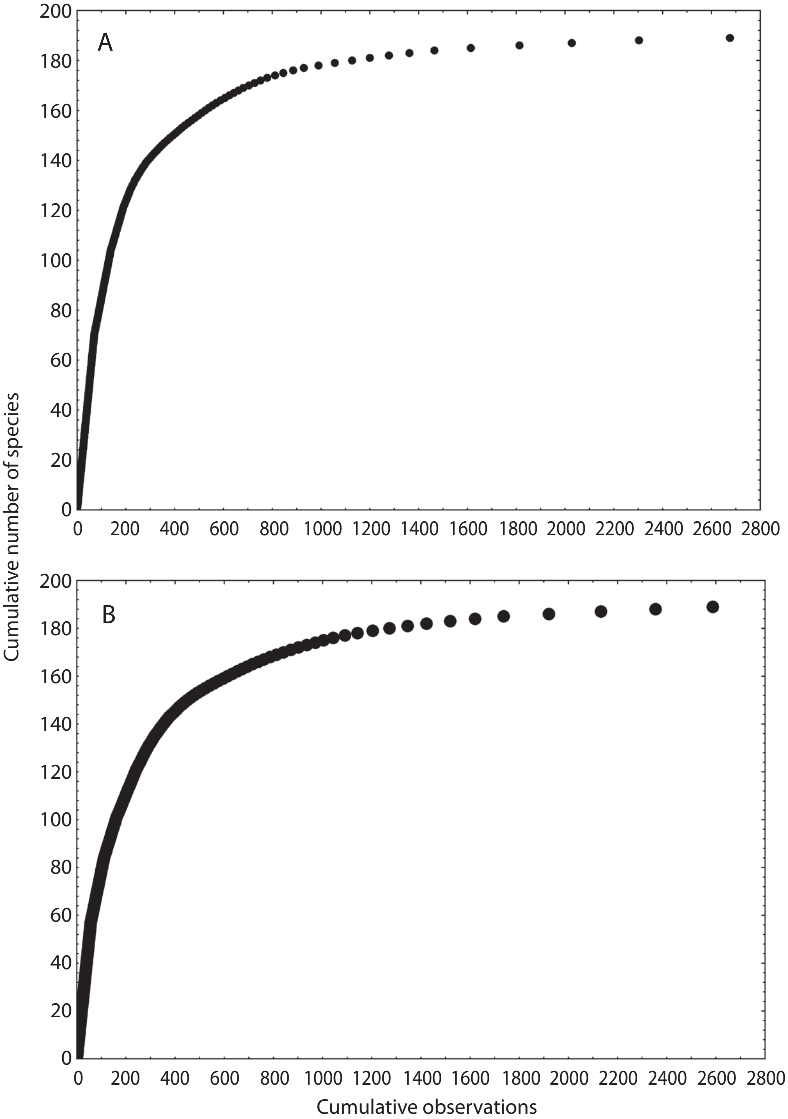

Fig. 2. Bird species accumulation curves for Ceibo (A) and Las Palmas (B), Braulio Carrillo National Park, Costa Rica.

species diversity, with both trails sharing a high number of species. The most common species, which form the core of mixed flocks, the Olive (*Chlorothraupis carmioli*) and the Tawny-crested Tanagers (*Tachyphonus delatrii*) had the same relative abundance in the two trails (Table 1).

Structure of the avifauna per foraging strata: In terms of the use of the forest profile, the avifauna was dominated by understory species, which accounted for more than 60 % of the species. These were followed by canopy birds with 30 % of all species (Table 2). Species composition per strata was almost identical for the two sites. Sixty species of understory birds were shared, out of the 87 species for Ceibo and 82 for Las Palmas, yielding a Sorensen index of 71 % (Morisita index = 0.96), showing that understory species

TABLE 2
Percentage composition of the foraging strata of the avifauna of Braulio Carrillo National Park along the Ceibo and Las Palmas trails

Strata	Ceibo	Las Palmas
Above the canopy	1.42	2.41
Canopy	28.44	32.36
Understory	67.38	62.34
Near water	2.76	2.88

differed little in overall composition. Results were similar among trails for canopy species. Ceibo had 95 and Las Palmas had 102, with 70 species in common, yielding a Sorensen index of 71 % (Morisita index = 0.87), indicating that similarity in canopy bird composition was similar between trails.

Migratory status: The Avifauna was dominated by residents, followed by elevational migrants (Table 3). The contribution of long-distance migrants was minimal in terms of abundance (2 % in Ceibo, and 1 % at Las Palmas). In terms of species richness, the contribution of long-distance migrants increased by up to 13 % in Ceibo and 6 % at Las Palmas (Table 3). Altitudinal migrants represented 15 % of the species in Ceibo and 14 % at Las Palmas, but contributed a small percentage to the total number of observations.

In terms of similarity, the Sorensen index varied little among resident species, and altitudinal and latitudinal migrants between trails (Table 3). The magnitude of this index was slightly higher for resident species. Regarding abundance data, the Morisita index was lowest for latitudinal migrants, whereas altitudinal migrants and residents showed a similar level of species overlap. In summary, the structure of the avifauna in terms of migrant status differ the most for latitudinal migrants among trails.

Temporal variation in diversity and species turnover rates: During the end of the wet season (November) we observed a consistent increase in the number of species caused partially by the influx of long-distance migrants (Table 4). Although the overall contribution of this group was low, its influence increased at the end of the wet season, coinciding with the peak of the winter migration. Altitudinal migrants also increased their contribution to the overall diversity. There was a significant effect of season in the number of species (two-way ANOVA r^2= 0.70, $F_{1,10}$= 21.36, P= 0.0009), but trails did not differ in species number ($F_{1,10}$= 2.46, P= 0.14). The rest of the diversity parameters showed no differences among seasons or trails (Table 4).

When temporal changes in species composition and abundance were examined using the Morisita index, the censuses grouped according to season, segregating April (dry season) from November (wet season; Fig. 3A, Fig. 3B). The

TABLE 3
Structure of the avifauna according to migratory status at Ceibo and Las Palmas (AM = altitudinal migrant, M = latitudinal migrant, R = resident). In parentheses, the percentage of total observations/species

	Ceibo		Las Palmas	
	N observations	N species	N observations	N species
AM	216 (8.07)	30 (15.78)	366 (10.91)	28 (14.65)
M	70 (2.61)	26 (13.68)	56 (1.67)	24 (12.57)
R	2390 (89.31)	134 (70.52)	2935 (87.42)	139 (72.77)

	Ceibo			Las Palmas		
	AM	M	R	AM	M	R
H´	2.44	2.68	3.4	2.29	2.94	3.43
Equitabillity (%)	71	83	70	68	92	70
Dominance (%)	6	11	6	16	6	6

TABLE 4
Variation in species richness and diversity over time at El Ceibo and Las Palmas trails
in Braulio Carrillo National Park, Costa Rica

	N species	N observations	Dominance (%)	H´	Equitability (%)
			Ceibo		
Dry Season					
2002	56	215	5.2	3.52	88
2003	52	259	6.2	3.28	83
2004	60	521	8.6	3.05	74
2005	56	289	8.3	3.10	77
Wet Season					
2002	84	357	4.4	3.70	83
2003	68	445	6.7	3.27	78
2004	64	602	7.8	3.10	74
			Las Palmas		
Dry Season					
2002	63	226	5	3.522	85
2003	53	192	5	3.438	86
2004	69	628	8	3.084	72
2005	51	444	8	3.076	78
Wet Season					
2002	90	537	5	3.60	80
2003	73	465	5.6	3.46	80
2004	84	882	5.6	3.45	78

cluster analysis produced three groups: one joined together censuses done during the dry season during the years 2002 and 2003, the second joined the wet season censuses of the same years, and a third one grouped the wet and dry seasons of 2004 and 2005 (Fig. 3A). In this latter group, censuses done in the dry season classified the trails together. The resulting pattern is that the avifauna changed between wet and dry seasons, but there was no segregation per trail (Fig. 3B).

Ceibo had an average Morisita value between successive census dates of 0.69 (SD= 0.11), whereas Las Palmas was 0.73 (SD= 0.14). In general, the structure of the avifauna changed 25-30 % between wet and dry seasons using abundance data. There was a significant change in species composition and abundance between seasons, although the structure of the avifauna was homogeneous among trails within a season. The mean value of the Morisita index across all possible combinations of trails and dates was 0.70 (SD= 0.11, Table 5). When the analysis was done using the Sorensen index, the overlap for Ceibo was 42 % (SD= 4.4) and 46 % (SD= 6.3) for Las Palmas. The average of all possible combinations of this index for the census dates was 44.8 % (SD= 5.8 %). When incidence data are considered, the avifauna had a turnover rate of 55 %.

Diversity vs. distance: In both trails, species abundance increased with increasing distance from the road (Fig. 4, Ceibo, r^2= 0.90, P = 0.0001, and Las Palmas, r^2= 0.54, P= 0.01). The rest of the diversity parameters (species richness, dominance, Shannon index, and equitability) did not show a significant relationship with road distance.

Diversity vs. distance for specialized understory insectivores: We examined the response of specialized understory insectivores, including army ant followers (families

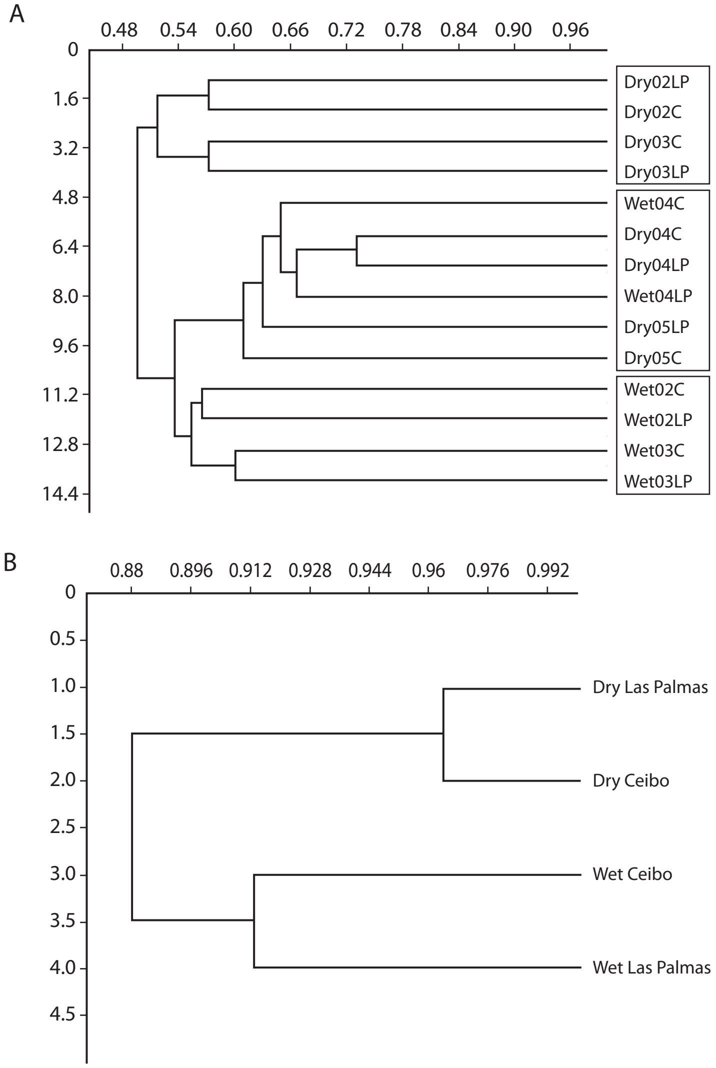

Fig. 3. (A) Classification of censuses according to trail and seasonality over a period of 4 years using cluster analysis –single linkage- based on the Morisita index of similarity. A census is designated by seasonality (dry season or wet season), year of census (the two digits after Dry or Wet) and trail (C = Ceibo, LP = Las Palmas). (B) Census groups clustered according to season using single linkage and the Morisita index of similarity.

Formicariidae, Furnariidae, Thamnophilidae and Troglodytidae) to distance from the highway. Twenty-five and 27 species of understory insectivores were observed at Ceibo and Las Palmas, respectively. Out of these species, 17 were common to both sides (Sorensen index= 65 %, Morisita= 81.64 %), showing high similarity in species composition for both trails. In Ceibo, understory insectivores did not vary their abundance, diversity, or average weight variation relative to road distance. In contrast, at Las Palmas there were positive and significant relationships for species richness (r^2= 0.47, $F_{1,9}$= 8.02, P= 0.01), the Shannon index (r^2= 0.50, $F_{1,9}$= 9.05, P= 0.01), a negative relationship for dominance (r^2= 0.38, $F_{1,9}$= 5.65, P= 0.04), and a positive trend for species with larger weight found away from the

TABLE 5

Matrix of species turnover at El Ceibo and Las Palmas trails in Braulio Carrillo National Park, Costa Rica, from 2002 to 2005, measured with the Morisita index of similarity. AP = April, NOV = November, C = Ceibo, LP = Las Palmas. Year of census is indicated by the digits in between letters. In bold-face the values of successive census dates within and between trails

	AP02C	AP03C	AP04C	AP05C	NOV02C	NOV03C	NOV04C	AP02LP	AP03LP	AP04LP	AP05LP	NOV02LP	NOV03LP
AP02C													
AP03C	0.639												
AP04C	0.726	0.783											
AP05C	0.714	0.678	0.929										
NOV02C	**0.512**	**0.719**	0.625	0.574									
NOV03C	0.479	**0.697**	**0.615**	0.581	0.573								
NOV04C	0.636	0.652	**0.823**	**0.797**	0.575	0.61							
AP02LP	0.824	0.699	0.633	0.596	0.507	0.613	0.633						
AP03LP	0.756	0.86	0.853	0.781	0.714	0.632	0.718	0.656					
AP04LP	0.818	0.78	0.945	0.879	0.631	0.59	0.781	0.695	0.876				
AP05LP	0.744	0.728	0.872	0.882	0.548	0.591	0.729	0.669	0.836	0.89			
NOV02LP	0.518	0.656	0.623	0.561	0.89	0.521	0.538	**0.474**	**0.7**	0.645	0.562		
NOV03LP	0.673	0.837	0.72	0.658	0.719	0.726	0.626	0.735	**0.838**	**0.764**	0.763	0.695	
NOV04LP	0.707	0.744	0.831	0.772	0.661	0.629	0.893	0.69	0.828	**0.843**	**0.784**	0.642	0.752

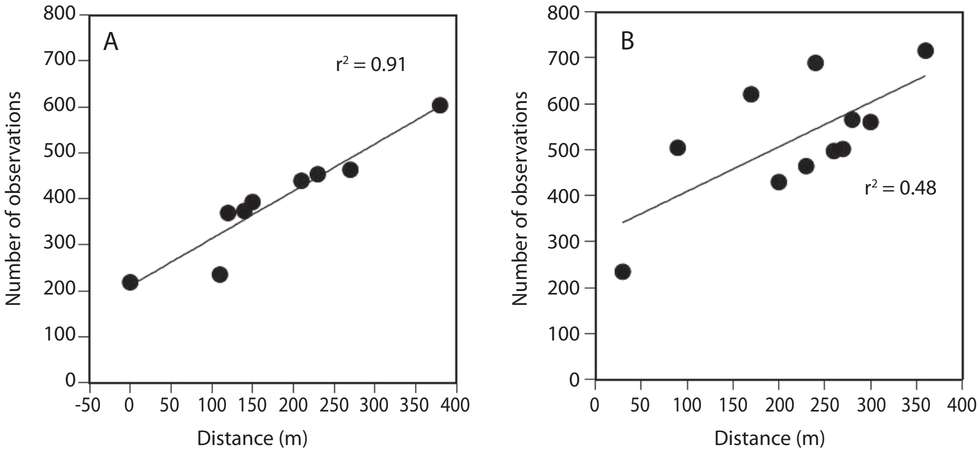

Fig. 4. Overall bird abundance vs. distance from the road in Braulio Carrillo National Park, Costa Rica at the Ceibo (A), $r^2 = 0.91$, slope = 1.02; and (B) Las Palmas trails, $r^2 = 0.54$, slope = 0.97.

road (natural OLS logarithmic regression, $r^2= 0.43$, $F_{1,9}= 6.87$, $P= 0.02$; Fig. 5). Many of the species in this guild require primary forests, which are prevalent in Las Palmas. Ceibo traverses secondary forests until it joins the Botarrama trail.

DISCUSSION

The avifauna of Quebrada González was very homogeneous in species composition and abundance when comparing opposite sides of the road resting support to the road

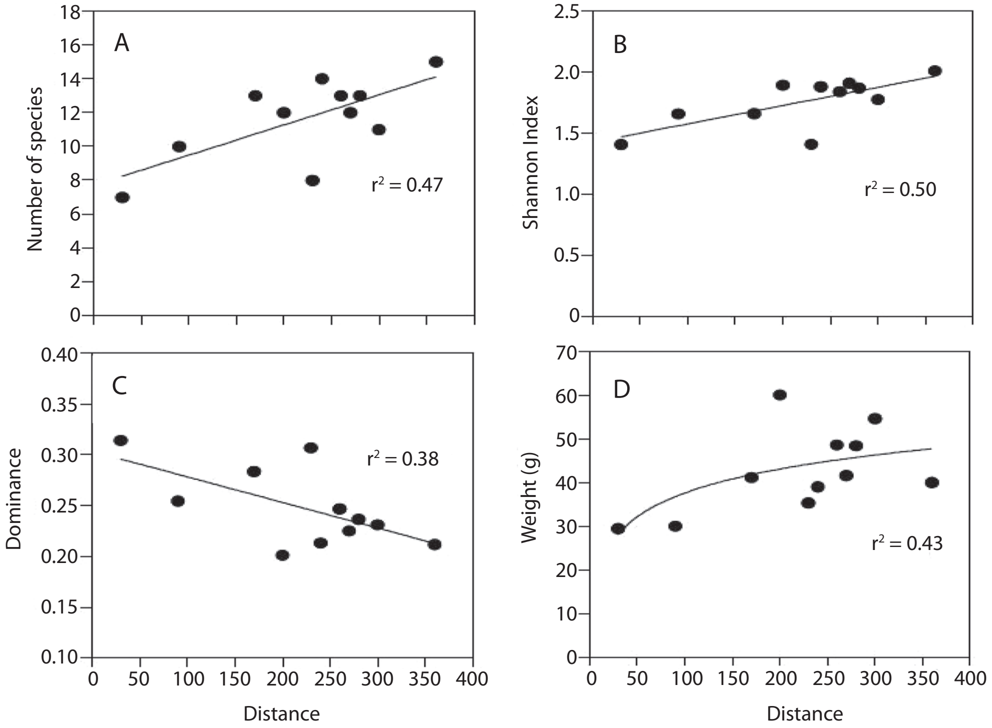

Fig. 5. Variation in (A) number of species, (B) Shannon Index of Diversity, (C) dominance and (D) average body weight of specialized understory insectivores per distance relative to the highway at Las Palmas trail measured with OLS regression in Braulio Carrillo National Park, Costa Rica.

fragmentation hypothesis. This avifauna complex, in which 65 % of all species are rare, results in high levels of diversity and evenness, and thus, some species would be observed a few times, and only on one side of the road. This could lead to a potential sampling artifact showing segregation in species composition. In contrast, there was predominant uniformity across different lines of analyses (i.e., species composition, use of forest strata, and migratory status). The results of the incidence and abundance-based analyses (Sorensen and Morisita indices) showed high overlap in species composition on opposite sides of the road. It is possible that forest areas away from the road could serve as a colonization source for birds reaching sites closer to the road, but if the road was having a fragmentation effect, species composition could have been different in areas influenced by the highway. Instead, overall abundance decreased closer to the road, showing that the predominant response from most species was road avoidance. The effect of the road fragmentation was minimal; instead, birds were avoiding the road proximity.

Does the highway affect the abundance and distribution of understory insectivores?

Establishing evidence for an anthropogenic impact, such as road disturbance, requires the use of multiple indices, multivariate statistic techniques, and an extended monitoring program. Researchers must establish a baseline to characterize the spatial and temporal dynamics of the avifauna. Species differ in dispersal ability and tolerance to disturbances, including clearings, secondary forests, and roads. If true that many life history strategies predispose some species to be negatively impacted by the road, some species may actually benefit (Coffin, 2007). Ecological studies on road impacts need to be focused on target groups such as understory insectivores, which require specialized habitat requirements, large areas, the existence of a continuous matrix of vegetation, and the availability of primary forests and specific food resources (Cintra & Cancelli, 2008; Lees & Peres, 2008; Stratford & Stouffer, 2013; Sánchez et al., 2014). Since many of these species are difficult to detect, the implementation of different sampling techniques (i.e., mist-nets, translocation studies, and radio-tracking) could help to complement point count censuses (Develey & Stouffer, 2001; Laurance, 2004; Laurance & Gomez, 2005).

The analysis of understory insectivores, and especially ant-followers did not show strong trends pointing to segregation on opposite sides of the road (species overlap, species numbers and abundance were similar). Instead, negative relationships between road distance and species richness and diversity were significant only for Las Palmas. This trail is dominated by primary forest and presents a very steep topography. In contrast, closer to the road, Ceibo is covered by secondary forest, is located on much flatter topography, and has a much thinner road edge. Forest structure (canopy height and number of strata) was more complex at Las Palmas. Many species of understory insectivores associated with primary forests require high levels of environmental complexity (Stratford & Stouffer, 2013) and thicker edges (Laurance, 2004), which influence the distribution and abundance of habitats sheltering their prey (Sánchez et al., 2014). The availability of aerial leaf litter (i.e., fallen leaves trapped in understory vegetation) is higher in more complex forests, especially primary forests (Vargas, Sánchez & Ávalos, 2011). Aerial leaf litter represents the main foraging substrate for many understory insectivores and its abundance influences the location of foraging territories. For instance, the abundance of the White-breasted Wood Wren, *Henicorhina leucosticta,* depends on increased canopy cover and leaf area index (Vargas et al., 2011; Sánchez et al., 2014), both higher in primary forests; these factors in turn are correlated with the availability of aerial leaf litter, and thus, the biomass of potential prey (which is higher in structurally complex, multilayered, primary forests). The primary forests of Las Palmas are thus associated with increased resources for understory insectivores (supporting species with larger weight, as reported here).

Many understory insectivores establish long-term territories for foraging and reproduction (i.e., Vargas et al., 2011). The quality of the territory varies with arthropod abundance (i.e., availability of aerial litter) and the complexity of forest structure (Cintra & Cancelli, 2008) influencing the distribution and density of these species (Laurance, 2004), some of which could survive fragmentation as long as small corridors connect forest patches (i.e., Sánchez et al., 2014). We noticed that some species (i.e., White-breasted Wood Wren, *H. leucosticta,* and the Spectacled Antpitta, *Hylopezus perspicillatus*) maintained well-established territories and were found predictably at specific points along the trails. For instance, we used mist-nets sparingly throughout this study, and observed that in certain areas several understory insectivores were caught at the same time (i.e., the Ocellated Antbird, *Phaenostictus mcleannani*, the Stripe-breasted Wren, *Cantorchilus thoracicus*, and the White-breasted Wood Wren, *H. leucosticta*). The distribution of understory insectivores that are ant-followers is influenced by the dispersion and habitat use of army ants (see Chaves-Campos, 2003), which tend to be more abundant in primary forests (Kumar & O'Donnell, 2009). Insectivorous birds tend to decline with increasing disturbance. Multiple studies have found two groups of insectivorous birds to be especially sensitive to human impacts in Neotropical forests: terrestrial insectivores (Canaday, 1996; Şekercioḡlu et al., 2002), and ant-following insectivores (Bierregaard & Lovejoy, 1989; Şekercioḡlu et al., 2002). Canaday (1996) lists other factors that make understory insectivores highly susceptible to habitat disturbances, such as changes in microclimatic conditions affecting the abundance and distribution of their prey species, high ecological specialization, fluctuations in predation rates as mortality source for these birds, and competition from opportunistic, disturbance-tolerant omnivores, and general patchy distribution (Robinson, Brawn & Robinson, 2000). Although speculative, some other factors could influence the distribution of insectivores relative to road distance observed at Las Palmas, including road noise, and fine changes in microclimatic conditions affecting habitat use, as well as insect distribution and abundance, which could have been different between Ceibo and Las Palmas. Develey and Stouffer (2001) found that insectivores reluctantly crossed narrow roads in Amazonia after being attracted using playbacks. Their analysis of territory distribution found evidence indicating that the road formed the limit of many territories, and that this group consistently avoided road areas.

Congruent with our results, a few studies have shown that roads decrease bird abundance in general in the immediate vicinity of the road (Laurance, Stouffer & Laurance, 2004; Fahrig & Rytwinski, 2009; Benítez-López et al., 2010; Arévalo & Newhard, 2011). This has been associated with increased noise, but it is likely that other variables come into play. The relationship between road noise and species richness was weak but statistically significant in the Arévalo and Newhard (2011) study, although a high level of variation in species richness per noise level was prevalent. Tropical rainforests have comparable levels of natural noise coming from the dawn chorus, or from streams and rivers. Since many factors affect sound transmission in topographically and spatially heterogeneous rainforest, the pattern of decreasing noise with increasing distance from the road is not necessarily linear.

Comparative studies of species turnover in similar areas of Costa Rica are scarce. Blake and Loiselle (2000) analyzed changes in avian structure along an elevational gradient (from 50 to 2 000 m) in the Caribbean slope of Braulio Carrillo and La Selva Biological Station over one year. Their estimate of the contribution of elevational migrants is congruent with our results (14-15 % of the total). A similar study, done by Young, DeRosier and Powell (1998) using mist-nets, analyzed changes in species diversity following an elevation gradient from the Caribbean to the Pacific slope of the Tilarán Mountains. The authors found that different life zones shared only 15 out of 235 species capable of moving across the gradient. Understory insectivores showed high exclusivity to a life zone, whereas altitudinal migrants traversed ample ranges in elevation and needed continuous vegetation cover. The lower portion of this gradient was unprotected but had the highest diversity. Both studies measured turnover rates between sites, rather than over time. Similarly, Jankowski, Ciecka, Meyer and Rabenold (2009) measured species turnover along the Pacific side of the Tilarán Mountains, between 1 000-1 700 masl, and found distinct species structure separated by changes in moisture associated with the location of cloud forests and rain-shadowed forests. In general, small-ranged species could be responsible for the segregation between sites (Fjeldså, Bowie, & Rahbek, 2012). Tropical avifaunas are very dynamic, and species composition varies across space and time, being influenced by competitive interactions, dispersal ability, population dynamics, changes in the physical structure of the habitat, level of resources, the area of the habitat and its degree of isolation, and migration patterns (Terborgh, 1977; Develey & Peres, 2000; Fjeldså et al., 2012).

Turnover rates are measured within the context of colonization of island habitats and species extinction in forest fragments (Laurance et al., 2002; Sodhi et al., 2004; Sodhi, Lee, Koh, & Dunn, 2005) rather than as part of regular long-term monitoring projects (Boulinier et al., 2001). The paucity of comparative data as well as the lack of uniformity in methods and objectives makes it difficult to compare turnover rates. The nearby La Selva Biological Station (22-146 masl) had a higher average Sorensen index (84 %), but a similar Morisitia index (0.75) over a period of 20 years (1983-2003) of Christmas counts (which includes winter migrants), showing a relatively lower turnover rate of just 25 %. As Blake and Loiselle (2000) and Young et al., (1998) showed, elevation is of crucial importance determining turnover rates, although species from opposite sides of the gradient may move along the gradient (Ávalos, 2005; 2015). The analysis of the effect of elevational gradients on diversity is controversial since multiple factors come into play (i.e., ecological, evolutionary, and biogeographic processes acting on multiple species). Rahbek (1997) demonstrates the importance of including the area of the habitat to explain species distribution across gradients. Thus, it is uncommon that only one factor could be the only, overriding explanatory force (Lomolino, 2001; Rahbek & Graves, 2001).

The presence of a mass transit highway through Braulio Carrillo National Park decreases bird abundance close to the road and negatively affects insectivorous bird populations associated with primary forests. The anthropogenic disturbances resulting from the presence of this highway increased the degree of edge effects, and although is not fragmenting the avifauna, is certainly decreasing their general abundance close to the road. The general pattern of overall decreased abundance close to the road and of negative effects, especially on understory insectivores, begs for more detailed studies using focal species to finally determine if the road is fragmenting the populations of sensitive groups. Mitigation alternatives such as overpasses and underpasses are not feasible due to the significant costs involved and the potential ineffectiveness of some options (i.e., underpasses could be too dark for birds to use them). Simpler alternatives to decrease the multiple effects of the road should be focused on designing buffer areas separating roads from protected areas, imposing honking and speed limits, installing speed bumps, and more importantly, educating the population on the negative effects of roads on wildlife. Since roads will increase in number, size and volume of traffic in the next decade (Laurance et al., 2014), it is imperative to understanding their impacts on sensitive groups of species, especially in areas bordering national parks.

ACKNOWLEDGMENTS

We thank the park rangers of Quebrada González for significant logistic support. This study was supported by the Directorate of Research of the University of Costa Rica project number 111-A3-128, and by The School for Field Studies. Willy Alfaro, Katya Barrantes, César Sánchez, and volunteers and students from UCR and SFS helped during data collection. Ideawild provided important field equipment. Luis Sandoval and four anonymous reviewers provided feedback that improved the manuscript.

RESUMEN

Efecto de una carretera principal en la variación espacial y temporal en la estructura y la diversidad de la avifauna de un bosque lluvioso tropical premontano. Las carreteras inmersas en áreas de conservación van a aumentar en número, tamaño, y volumen de tráfico en la próxima década, por lo que comprender los efectos de las mismas sobre la fauna dependiente de bosque es crucial para mejorar las prácticas de manejo y reducir los impactos negativos de los caminos sobre las especies más frágiles. Examinamos la influencia de la ruta 32 (conocida como la carretera a Guápiles) sobre los cambios temporales y espaciales en la estructura de la avifauna del Parque Nacional Braulio Carrillo, Costa Rica, el cual es atravesado por esta carretera a lo largo de 25 km. La carretera conecta la ciudad capital de San José con el puerto de Limón en el Caribe (142 km). Aunque la calle es estrecha (12 m de ancho en dos carriles en la mayor parte de la ruta) da servicio a más de 1.5 millones de vehículos por año, 12 % de los cuales es transporte pesado. Esperábamos que la carretera fragmentara a la avifauna, y por lo tanto que hubieran diferencias significativas en la estructura de las especies en lados opuestos de la ruta. Describimos los cambios en la diversidad de aves entre las estaciones secas y húmedas en los senderos Las Palmas y Ceibo situados en lados opuestos de la carretera (14 puntos de conteo por sendero), y evaluamos cómo la abundancia y la diversidad variaron con la distancia hacia la carretera. Los censos se realizaron durante las estaciones húmedas y secas desde el 2002 al 2005. Encontramos 245 especies y 6 035 observaciones durante el período de 4 años. Las especies raras dominaron la avifauna (65 % de las especies < 5 observaciones), y mostraron un alto traslape entre senderos (Sorensen= 71 %; Morisita= 0.96). Las curvas de acumulación de especies variaron poco entre senderos, generando 190 especies. Las especies residentes representaron el 70 % de las observaciones, seguidas migrantes de elevación (15 %) y especies migratorias latitudinales (1-2 %). Las especies de sotobosque fueron las más abundantes (60 %), seguidas por las aves de dosel (30 %). La tasa de recambio de especies fue del 55 % entre estaciones, pero la composición de especies entre senderos permaneció homogénea. El patrón general consistió en que las aves evitaron la carretera (la abundancia aumentó lejos de la carretera), aunque otros parámetros de diversidad (riqueza, dominancia, el índice de Shannon y la equidad) no fueron influenciados por la proximidad de la calle. Si bien los resultados no apoyaron la hipótesis de la fragmentación, la carretera redujo la abundancia y diversidad de insectívoros especializados de sotobosque asociados a bosque primario. Esta carretera se expandirá fuera del Parque Nacional (de 2 a 4 carriles a lo largo de 107 km de Río Frío a Limón) en los próximos años, lo que aumentará el impacto del volumen de tráfico dentro del parque. Las carreteras cercanas a zonas protegidas están aumentando en los trópicos, por lo que es crucial desarrollar alternativas de manejo basadas en la respuesta de los grupos sensibles a estos impactos.

Palabras clave: recambio de especies, monitoreo de la biodiversidad, ecología de carreteras, evitación de caminos, insectívoros de sotobosque.

REFERENCES

Arévalo, J. E., & Newhard, K. (2011). Traffic noise affects forest bird species in a protected tropical forest. *Revista de Biología Tropical,* 59(2), 969-980.

Ávalos, G. (2005). Banded-tailed Pigeon (*Columba fasciata*) at low elevations in Braulio Carrillo National Park, Costa Rica. *Ornitologia Neotropical, 16*, 1-2.

Ávalos, G. (2015). Highest elevational record of the Long-billed Hummingbird (*Phaethornis longirostris* Delattre, 19843, Aves: Trochilidae) in Costa Rica. *Brenesia, 83-84*, 89-90.

Bierregaard, Jr. R. O., & Lovejoy, T. E. (1989). Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonica, 19*, 215-241.

Blake, J. G., & Loiselle, B. A. (2000). Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *The Auk, 117(3),* 663-686.

Blake, J. G., Stiles, F. G., & Loiselle, B. A. (1990). Birds of La Selva Biological Station: Habitat Use, Trophic Composition and Migrants. In A. H. Gentry (Ed.), *Four Neotropical Rainforests* (pp. 161-182). Yale, CT: University Press.

Beaudrot, L., Ahumada, J., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., … Hurtado, J. (2016). Standardized Assessment of Biodiversity Trends in Tropical Forest Protected Areas: The End Is Not in Sight. *PLOS Biology, 14*(1), 1-21. doi:10.1371/journal.pbio.1002357

Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation, 143(6),* 1307-1316.

Boulinier, T., Nichols, J. D., Hines, J. E., Sauer, J. R., Flather, C. H., & Pollock, K. H. (2001). Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology, 82(4),* 1159-1169.

Brown, G. P., Phillips, B. L., Webb, J. K., & Shine, R. (2006). Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation, 133(1),* 88-94.

Canaday, C. (1996). Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation, 77*(1), 63-77.

Chaves-Campos, J. (2003). Localization of army-ant swarms by ant-following birds on the Caribbean slope of Costa Rica: following the vocalization of antbirds to find the swarms. *Ornitologia Neotropical, 14*, 289-294.

Cintra, R., & Cancelli, J. (2008). Effects of forest heterogeneity on occurrence and abundance of the scale-backed antbird, *Hylophylax poecilinotus* (Aves: Thamnophilidae), in the Amazon forest. *Revista Brasileira de Zoologia, 25*(4), 630-639.

Coffin, A. W. (2007). From roadkill to road ecology: a review of the ecological effects of roads. *Journal of transport Geography, 15*(5), 396-406.

Colwell, R. K. (2005). *ESTIMATES: Statistical Estimation of Species Richness and Shared Species from Samples*. Version 7·5. User's Guide and Application. Rtrieved from http://purl.oclc.org/estimates

Develey, P. F., & Peres, C. A. (2000). Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology, 16*(01), 33-53.

Develey, P. F., & Stouffer, P. C. (2001). Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology, 15*(5), 1416-1422.

ESRI. (2011). *ArcGIS Desktop: Release 10. Redlands.* CA, USA: ESRI.

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and society, 14*(1), 21.

Fjeldså, J., Bowie, R. C., & Rahbek, C. (2012). The role of mountain ranges in the diversification of birds.

Annual Review of Ecology, Evolution, and Systematics, 43, 249-265.

Goosem, M. (2000). Effects of tropical rainforest roads on small mammals: edge changes in community composition. *Wildlife Research, 27*(2), 151-163.

Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica, 4*, 1-9.

Holdridge, L. R., & Grencke, W. C. (1971). *Forest environments in tropical life zones: A pilot study*. New York: Oxford.

Jankowski, J. E., Ciecka, A. L., Meyer, N. L., & Rabenold, K. N. (2009). Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. *Journal of Animal Ecology, 78*, 315-327.

Jost, L., Chao, A. & Chazdon, R. L. (2011). Compositional similarity and β (beta) diversity. In A. E. Magurran & B. J. McGill (Eds.), *Biological diversity: frontiers in measurement and assessment* (pp. 66-84). Oxford: University Press.

Kumar, A., & O'Donnell, S. (2009). Elevation and forest clearing effects on foraging differ between surface –and subterranean– foraging army ants (Formicidae: Ecitoninae). *Journal of Animal Ecology, 78*(1), 91-97.

Laurance, S. G. (2004). Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications, 14*(5), 1344-1357.

Laurance, S. G., Stouffer, P. C., & Laurance, W. F. (2004). Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology, 18*(4), 1099-1109.

Laurance, S. G., & Gomez, M. S. (2005). Clearing Width and Movements of Understory Rainforest Birds. *Biotropica, 37*(1), 149-152.

Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., … Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology, 16*(3), 605-618.

Laurance, W. F., Goosem, M., & Laurance, S. G. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution, 24*(12), 659-669.

Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Goosem, M., … Burgues-Arrea, I. (2014). A global strategy for road building. *Nature, 513*, 229-232.

Laurance, W. F. (2015). Bad Roads, Good Roads. In R. van der Ree, C. Grilo & D. J. Smith (Eds.), *Handbook of Road Ecology* (pp. 10-15), USA: Wiley.

Lees, A. C., & Peres, C. A. (2008). Avian life-history determinants of local extinction risk in a hyper-fragmented neotropical forest landscape. *Animal Conservation, 11*, 128-137.

Legendre, P., & Legendre, L. F. (2012). *Numerical ecology* (Third Edition). USA: Oxford.

Lindell, C. A., Riffell, S. K., Kaiser, S. A., Battin, A. L., Smith, M. L., & Sisk, T. D. (2007). Edge responses of tropical and temperate birds. *The Wilson journal of ornithology, 119*(2), 205-220.

Lindenmayer, D. B. (1999). Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management, 115*(2), 277-287.

Loiselle, B. A., & Blake, J. G. (1992). Population variation in a tropical bird community. *BioScience, 42*(11), 838-845.

Lomolino, M. A. R. K. (2001). Elevation gradients of species-density: historical and prospective views. *Global Ecology and biogeography, 10*(1), 3-13.

Obando-Calderón, G., Camacho-Varela, P., Chaves-Campos, J., Garrigues, R., Montoya, M., Ramírez-Alán, O., & Zook, J. (2014). Lista Oficial de las Aves de Costa Rica. *Zeledonia, 17*, 44-59.

Pinowski, J. (2005). Roadkills of vertebrates in Venezuela. *Revista Brasileira de Zoologia, 22*(1), 191-196.

Prasad, A. E. (2009). Tree community change in a tropical dry forest: the role of roads and exotic plant invasion. *Environmental Conservation, 36*(03), 201-207.

Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist, 149*(5), 875-902.

Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences, 98*(8), 4534-4539.

Rajvanshi, A., & Mathur, V. B. (2015). Planning Roads through Sensitive Asian Landscapes. In R. van der Ree, C. Grilo, & D. J. Smith (Eds.), *Handbook of Road Ecology* (pp. 430-438). USA: Wiley.

Robinson, W. D., Brawn, J. D., & Robinson, S. K. (2000). Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs, 70*(2), 209-235.

Sánchez, N. V., Vargas-Castro, L. E., Ávalos, G., & Paniagua, F. (2014). Effect of prey availability on the abundance of White-breasted Wood-Wrens, insectivorous birds of tropical lowland forests. *Journal of Field Ornithology, 85*(4), 347-354.

SAS. (2012). *JMP Pro 10.0.0*. Cary, North Carolina, USA: SAS Institute.

Şekercioğlu, Ç. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D., & Sandí, R. F. (2002). Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences, 99*(1), 263-267.

Sodhi, N. S., Liow, L. H., & Bazzaz, F. A. (2004). Avian extinctions from tropical and subtropical forests. *Annual Review of Ecology, Evolution, and Systematics, 35*, 323-345.

Sodhi, N. S., Lee, T. M., Koh, L. P., & Dunn, R. R. (2005). A century of avifaunal turnover in a small tropical rainforest fragment. *Animal Conservation, 8*(2), 217-222.

Stiles, F. G., & Skutch, A. F. (1989). *Guide to the birds of Costa Rica*. Ithaca, NY: Cornell.

Stratford, J. A., & Stouffer, P. C. (1999). Local extinctions of Terrestrial Insectivorous Birds in a Fragmented Landscape near Manaus, Brazil. *Conservation Biology, 13*, 1416-1423.

Stratford, J. A., & Stouffer, P. C. (2013). Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *Journal of Field Ornithology, 84*(1), 1-12.

Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. *Ecology, 58*, 1007-1019.

Vargas, L. E., Sánchez, N. V., & Ávalos, G. (2011). Forest structure and territory size relationship in the neotropical understory insectivore *Henicorhina leucosticta*. *Journal of Tropical Ecology, 27*(01), 65-72.

Young, K. R. (1994). Roads and the environmental degradation of tropical montane forests. *Conservation Biology, 8*(4), 972-976.

Young, B. E., DeRosier, D., & Powell, G. V. (1998). Diversity and conservation of understory birds in the Tilarán Mountains, Costa Rica. *The Auk, 115*(4), 998-1016.