ARTICLE

SPATIAL AND TEMPORAL CHANGES IN THE STRUCTURE AND DIVERSITY OF THE AVIFAUNA OF CARARA NATIONAL PARK, COSTA RICA, IN RESPONSE TO ROAD PROXIMITY

Gerardo Avalos[1,2]* J. Edgardo Arévalo[1,2] and César Sánchez[3]

[a1] Escuela de Biología, Universidad de Costa Rica, 11501-2060 San Pedro, San José, Costa Rica; gerardo.avalos@ucr.ac.cr

[a2] The School for Field Studies, Center for Sustainable Development Studies, PO BOX 150-4013 Atenas, Alajuela, Costa Rica

[3] Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

* Corresponding Author: *gerardo.avalos@ucr.ac.cr*

Abstract. Documenting changes in species distribution is critical to understanding bird diversity, establishing a baseline for comparative studies, quantifying bird turnover rates, and identifying groups sensitive to anthropogenic disturbances. We examined changes in diversity of the avifauna of Carara National Park (Costa Rica), a transitional forest bordered by a busily trafficked road, between the wet and dry seasons of 2007. We established count points in two sectors of the Park (Carara trails, twelve points, and the Meandric Lagoon, eight points), and did censuses twice a day for five consecutive days in July and August (wet season), and in November (dry season). We measured species similarity among trails and seasons using the Sørensen and Morisita indices, and used principal component analysis to consolidate species numbers, the number of observations, and the Shannon diversity index. The first component (96 % of the variation) served to measure road influence on bird abundance and diversity. We applied these analyses to specialized understory insectivores (Formicariidae, Furnariidae, Troglodytidae and Thamnophilidae), expecting a negative effect of the road on diversity and abundance closer to the road. We observed 178 species (1 690 observations) combining wet and dry seasons. Species numbers varied little between sites and seasons (estimated number of species = 100). Species similarity between sites was higher during the wet season (Sørensen index = 71.9 %). The trails clustered according to season rather than location. The avifauna was dominated by resident species during wet and dry seasons (94 % and 85 % of observations, respectively). The road affected bird distribution within the first 100 m, showing a significant effect on specialized insectivores. Roads bordering conservation areas will increase in number and traffic in the next decades. It is critical to understand their effects on wildlife to improve management practices and reduce impacts on sensitive species.

Keywords: *Beta diversity, fragmentation, species turnover rate*

Resumen. Documentar cambios en la distribución de las especies es fundamental para comprender la diversidad de las aves, establecer una línea base para estudios comparativos, cuantificar tasas de recambio, e identificar grupos sensibles a perturbaciones antropogénicas. Examinamos los cambios en la diversidad de la avifauna del Parque Nacional Carara (Costa Rica), un bosque de transición bordeado por una carretera de tráfico denso, entre las estaciones húmeda y seca del 2007. Establecimos puntos de conteo el sendero Carara (doce puntos) y Laguna Meándrica (ocho puntos), e hicimos censos dos veces al día durante cinco días consecutivos en julio y agosto (temporada húmeda), y en noviembre (temporada seca). Medimos la similitud de especies entre senderos y estaciones utilizando Sørensen y Morisita, y utilizamos componentes principales para consolidar el número de especies, el número de observaciones, y el índice de diversidad de Shannon. El primer componente (96% de la variación) sirvió para medir la influencia de la carretera en la abundancia y diversidad de aves. Aplicamos estos análisis a insectívoros especializados de sotobosque (Formicariidae, Furnariidae, Troglodytidae y Thamnophilidae), esperando un efecto negativo de la carretera en la diversidad y la abundancia. Observamos 178 especies (1 690 observaciones) entre las estaciones húmeda y seca. El número de especies varió poco entre sitios y estaciones (número estimado de especies = 100). La similitud de especies entre los sitios fue mayor durante la estación húmeda (índice de Sørensen = 71.9%). Los senderos se agrupan según la temporada en lugar de la ubicación. La avifauna estuvo dominada por especies residentes durante las estaciones húmeda y seca (94% y 85% de las observaciones, respectivamente). La carretera

afectó la distribución de aves dentro de los primeros 100 m, mostrando un efecto significativo en insectívoros especializados. Los caminos que bordean las áreas de conservación aumentarán en número y tráfico en las próximas décadas, por lo que es fundamental comprender sus efectos sobre la vida silvestre para mejorar las prácticas de manejo y reducir los impactos en los grupos más sensibles.

Palabras clave: Diversidad beta, fragmentación, tasa de recambio de especies.

INTRODUCTION

The dynamism of spatial and temporal changes in the composition of tropical avifaunas is determined by habitat structure (Sigel et al. 2006), environmental gradients (Jankowski et al. 2009, Blake & Loiselle 2001), variation in food resources (i.e., plant reproductive phenology and insect seasonality, Blake & Loiselle 1991, Loiselle & Blake 1994), population dynamics (Jetz & Rahbek 2002), competitive interactions (Jankowski et al. 2010), and migration patterns (Wiens 1989). Tropical avifaunae are highly diverse and are composed of species with different ecological requirements and levels of abundance, whose distributions change across space and time (Loiselle & Blake 1994). Knowledge of patterns of distribution and abundance of bird species has direct management and conservation implications. We know relatively little, however, of how compositional changes take place over space and time in the same area, especially in highly diverse tropical communities (Kattan et al. 2006, Biamonte et al. 2011, Avalos & Bermudez 2016, Sandoval et al. 2018). Most of the information on tropical environments is restricted to elevational gradients (Young et al. 1998, Blake & Loiselle 2000, Jankowski et al. 2009). Studies looking at turnover rates and compositional changes over time at one location (Blake & Loiselle 2001) are lacking for most tropical sites. Seasonal and spatial changes within the same geographic area projected over time represent a poorly explored aspect of beta diversity (Baselga et al. 2015). Communities are open systems and do not develop in isolation but are subject to great dynamism as the physical structure and quality of the environment changes with the seasons, with faunas showing a continuous turnover of species gains and losses. This process is exacerbated by changes in land use such as forest loss and urbanization (Biamonte et al. 2011, Sandoval et al. 2018, Tucker et al. 2018). Thus, it is critical to develop monitoring programs to measure differences in the structure of avian communities, as they reflect changes in the abundance of other organisms, and could serve as baseline to measure the impacts of land cover changes, increased urbanization and road expansion, habitat fragmentation, and climate change (Jankowski et al. 2009, Gasner et al. 2010, Pereira et al. 2010).

Carara National Park, located in the Central Pacific slope of Costa Rica, is one of the most ecologically heterogeneous protected areas, characterized by a mosaic of habitats (i.e. coastal environments including mangroves and wetlands, and seasonal forests) representing the transition between tropical rain and tropical dry forests. In addition to local habitat heterogeneity, Carara forms part of an altitudinal gradient, which is under strong pressure for agricultural and urban development and road disturbance. The eastern border of the park runs for 3.6 km parallel to the coastal highway, a road which carries heavy traffic. Roads change microclimate conditions, increase noise and air pollution, and favor exotic and disturbance-tolerant species (Coffin 2007, Prasad 2009). The overall abundance and diversity of vertebrates decrease closer to roads (Goosem 2000, Trombulak & Frissell 2000). In the immediate vicinity of Carara, the road reduces bird density and diversity (Benítez-López et al. 2010, Arévalo & Newhard 2011). Typical forest interior, understory, and canopy species are very sensitive to road disturbances and edge effects (Develey & Stouffer 2001, Laurance et al. 2009). In contrast, short-distance migrants and edge species benefit from fragmentation and the increased habitat heterogeneity close to roads (Laurance et al. 2002). Since the vast majority of tropical birds avoid edges (Lindell et al. 2007), it is likely that bird abundance and diversity will decrease closer to the road. Our objective here is to compare spatial and temporal changes in the avian assemblage structure of Carara National Park at two opposite ends of the annual cycle of this community in relation to road proximity. We expect forest interior species and understory insectivores to decrease in abundance closer to the road, and bird diversity to be higher during the wet-to-dry season transition due to the addition of long-distance migratory species. Road networks and traffic volume are expected to increase globally in the next decade (Laurance et al. 2014) and, accordingly, it is crucial to create the baseline for understanding road impacts on sensitive species, especially in areas bordering national parks. Results of this study are

relevant to understanding the ecological conditions determining abundance and diversity patterns in transitional forests, establishing a baseline for future studies, increasing our knowledge on turnover rates of tropical birds, and identifying bird groups that are particularly susceptible to disturbance by roads.

MATERIAL AND METHODS

Study site: This research was conducted in Carara National Park (9°46´85´´N, 84°36´83´´ W, 5 242 Ha, 26 masl, 25ºC, 2 500-3 300 mm) from July to August, and during late November 2007. The site presents distinct wet (May-November) and dry (December-April) seasons (Herrera 1986). Carara is located in the Central Pacific lowlands of Costa Rica, protecting a transitional forest between the strongly seasonal tropical dry forests of the Pacific North West and the very humid tropical rainforests of the Osa Peninsula further south. No other park in Costa Rica maintains such a large area of protected transitional forests, including an altitudinal gradient from sea level to 600 m, and even higher as significant forest tracts connect Carara with Fernando Castro Cervantes Wildlife Refuge and Turrubares Protected Zone, encompassing seven life zones (Holdridge & Grenke 1971). The park maintains swamps, lagoons, and gallery forests, as well as secondary and primary forests, representing a habitat island surrounded by a landscape dominated by cattle pastures and urban development projects. Coastal Highway 34 borders the eastern side of the park for four kilometers with a traffic volume of 400 vehicles per hour and has proved to influence bird distribution and abundance (Arévalo & Newhard 2011, Arévalo & Blau 2018). Carara has approximately 360-400 bird species (including aquatic species as well as the second largest population of Scarlet Macaws in Costa Rica after the one in Osa Peninsula, Dear et al. 2010). Our research comprised the trails around the Visitor Center and Ranger Station (hereafter, Carara trails), as well as the Laguna Meándrica trail (hereafter, ML) located on the NW limit of the Park (Fig. 1).

Forest structure: We used the proportion of canopy cover as a measure of forest structure using a spherical densiometer (Model-C) operated at each census point. We also recorded canopy height measured with a laser rangefinder at each census point.

Bird monitoring and identification: following the outline of the trails, we established twelve locations for point counts in Carara and eight along the ML trail, all separated linearly by 120 m. Along each trail we classified these points into three categories of distance from the road:
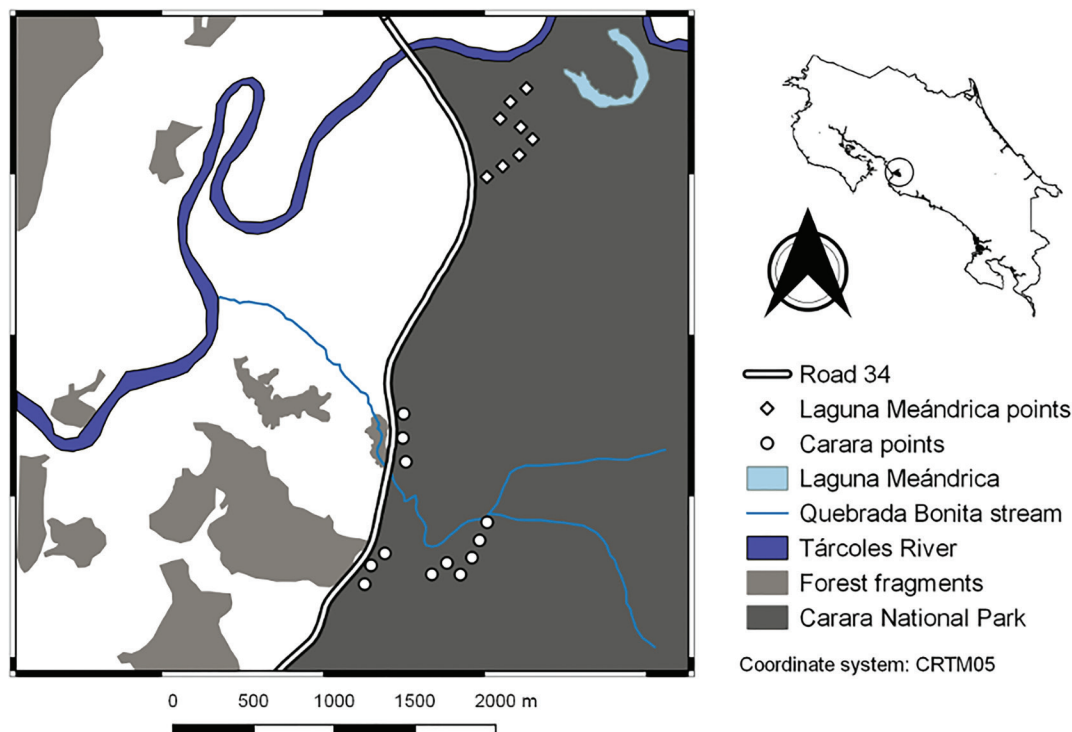

Figure 1. Study area showing landscape composition including Carara National Park, the sampled points, as well as streams, lagoons, the road, and forest fragments embedded in pasture fields.

close (0-100 m), intermediate (>100 m to 300 m), and far (> 300 to 690 m). Two groups of two to three ornithologists walked in alternate directions twice a day starting at opposite ends of the trails, constantly alternating locations, trails, and teammates to homogenize error. Every point was observed for 10 min and any bird that could be seen or heard within a radius of 30 m was identified to species level. When necessary, bird calls were recorded and identified afterwards. Censuses were done twice a day for five consecutive days in July and in August (wet season), as well as in November 2007 (transition to the dry season, hereafter termed "dry season"), with data collection taking place from 5:30-9:30 and from 14:30-17:30.

Measurement of temporal and spatial changes in avian structure: Species diversity and abundance were measured using PAST 1.94b (Hammer et al. 2001) and EstimateS version 8.2.0 (Colwell 2005) applying the indices recommended by Jost et al. (2011) and Legendre & Legendre (2012). Rarefaction analyses were done using Ecosim (Gotelli & Entsminger 2013). Species numbers were compared among sites and seasons using species accumulation curves. Similarity in species composition between trails and seasons (beta diversity) was measured with the Sørensen (incidence-based) and Morisita-Horn (abundance-based) indices. A cluster analysis was applied to the similarity matrix of the Morisita-Horn index between sites and seasons. One-way ANOVA was used to test for differences in species richness and abundance across categories of distance from the road. We analyzed the distribution of specialized understory insectivores within the families Formicariidae, Furnariidae, Troglodytidae and Thamnophilidae relative to distance categories from the road. Migrant status consisted of altitudinal (AM) and latitudinal migrants (M) and residents (R) following Obando-Calderón et al. (2014).

Diversity measures: We quantified diversity using species richness and the Shannon Diversity index (H´) calculated using natural logarithms. To measure similarity

in species overlap we used the classic Sørensen index based on species incidence. In addition, to measure species overlap we used the Morisita index for abundance data (Jost et al. 2011). Both indices provide simple, intuitive measures of species turnover, or beta diversity, across space and time. Since there were significant differences in number of observations across censuses (see Table 1), we adjusted the species richness values and the Shannon diversity index using rarefaction analyses based on the smallest number of observations, which was recorded during the wet season in Carara (n = 344). After standardizing for sample size, the number of species was affected by sampling effort during the dry season in Carara, and during the wet season at the ML site (observed values fell outside the 95 % confidence interval relative to rarified values, Table 1). The Shannon index, however, was not affected by sample size (Table 1). Since the differences in species richness and Shannon diversity indices were small between sites and seasons with respect to rarified values, we performed the rest of the analyses without adjusting the sample size.

Bird distribution relative to distance from the road: The number of species, the number of observations, and the Shannon index were highly correlated (average Pearson correlation = 0.90). To consolidate richness and diversity we calculated a principal component factor, which explained 96 % of the variation. We used the scores of this principal component as a response variable in a nested analysis of variance using distance category (close, intermediate, and far) nested within trail to measure the influence of the road on bird abundance and diversity. All analyses were done using JMP 10 statistical software (SAS Institute, Cary, North Carolina).

RESULTS

The Carara trails were located in more mature forests relative to those at Meandric Lagoon. In Carara, average tree height around count points was 28.33 m (± 11.94 SD),

Table 1. Number of species and observations per site and season at Carara National Park, 2007

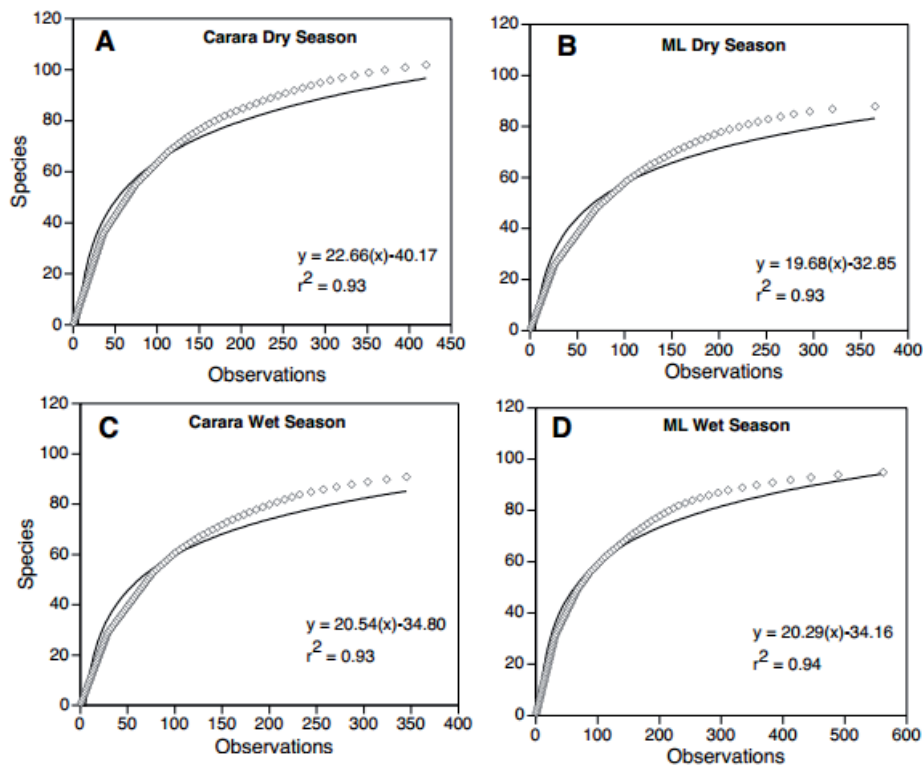| | Carara | | ML | |
	Wet	Dry	Wet	Dry
Number of species	86	102	89	87
Number of observations	333	420	543	364
Rarefied Number of species 95 % CI		89-98	72-84	84-88
Shannon Diversity Index H´	4.02	4.14	3.72	3.94
Rarefied H´ 95 % CI		4.05-4.12	3.63-3.80	3.94-3.96

Figure 2. Species accumulation curves for Carara (A, C) and the Meandric Lagoon (B, D) during wet and dry season, respectively. Open circles refer to the observed number of species and the continuous line, to the logarithmic models.

compared with the 20.62 m (± 8.46 SD) of ML. Further, average canopy cover of the Carara trails was 92.62 % (± 5.23 SD) as compared with ML (84.12 % ± 16.60 SD), which was also more variable. Carara and ML were structurally different and highly heterogeneous, favoring the accumulation of a wide range of species.

We observed a total of 171 species distributed into 1 660 observations combining wet and dry season censuses. Number of species showed little variation between sites and seasons. ML yielded the highest number of observations (543) during the wet season (Table 1). In all cases (Fig. 2), the estimated number of species was close to 100, since all curves became asymptotic close to this number. The shape of the curve shows that the sampling effort in all cases was sufficient to account for most of the species at these two sites and seasons. The slope value (the rate of new species accumulation relative to cumulative sampling effort) ranged between 19.68 and 22.66, showing small variation between sites and seasons.

Incidence-based similarity in species composition between sites was higher during the wet season (Sørensen index = 70.1 % of similarity, Table 2). The lowest value was observed for ML for the wet vs. dry season comparison, showing the highest species turnover. Overall, the avifauna

of Carara changed an average of 55.44 % (± 8 SD) between seasons.

When the analysis is done using abundance-based similarity, the lowest value of the Morisita index of similarity (0.415) was observed again for the Carara dry season vs. ML wet season comparison (Table 2). The average turnover rate of the avifauna for abundance-based data was 48.2 % (± 11 SD), close to the magnitude of the Sørensen index.

After consolidating the data for wet and dry seasons using the Morisita index as the similarity matrix (Fig. 2), the sites clustered according to trail rather than season. Differences in forest structure, therefore, had a stronger impact on patterns of similarity in bird species richness and abundance rather than seasonal differences.

Migratory status: The avifauna of Carara was clearly dominated by resident species, which represented 99 % and 86 % of the total number of observations during the wet and dry seasons, respectively. Long-distance migrants increased their abundance from less than 1 % during the wet season (we recorded a Black-throated Blue Warbler, *Setophaga caerulescens*, possibly returning late to its breeding grounds) to 13 % during the dry season. The

TABLE 2 Similarity in bird species composition using incidence (Sørensen index) and abundance data (Morisita index) per site and season at Carara National Park, 2007

	Sorensen Index		
	Dry season Carara	ML dry season	Wet season Carara
Dry season Carara			
ML dry season	0.66		
Wet season Carara	0.535	0.532	
ML-wet	0.508	0.537	0.701
	Morisita Index		
	Dry season Carara	ML dry season	Wet season Carara
Dry season Carara			
ML dry season	0.469		
Wet season Carara	0.57	0.421	
ML-wet	0.515	0.415	0.717

abundance of altitudinal migrants varied between 5-1.5 % during wet and dry seasons (Fig. 3).

Bird distribution relative to distance from the highway: The principal component analysis explained 70 % of the variation in diversity parameters ($F_{5,14}$ = 6.28, P = 0.002), with a significant effect of trail (F = 11.63, P = 0.004), but not of distance within a trail ($F_{4,4}$ = 1.69, P = 0.2). Consistently, LM showed higher diversity parameters per distance

category than the Carara trails, with a clear trend of increasing number of species and observations, as well as of increasing Shannon index values with increasing distance from the road (Fig. 4a, 4b, 4c). The road affected bird distribution and diversity within the first 100 m. After 100 m, intermediate and far distances showed similar values, with a stronger effect in the ML trail.

During the dry season intermediate distances had a higher number of species and observations (Fig. 5a, 5b). During the wet season, 19 species in the families Formicariidae, Furnariidae, Thamnophilidae and Troglodytidae showed a significant effect of distance from the road relative to diversity indicators, with intermediate distances
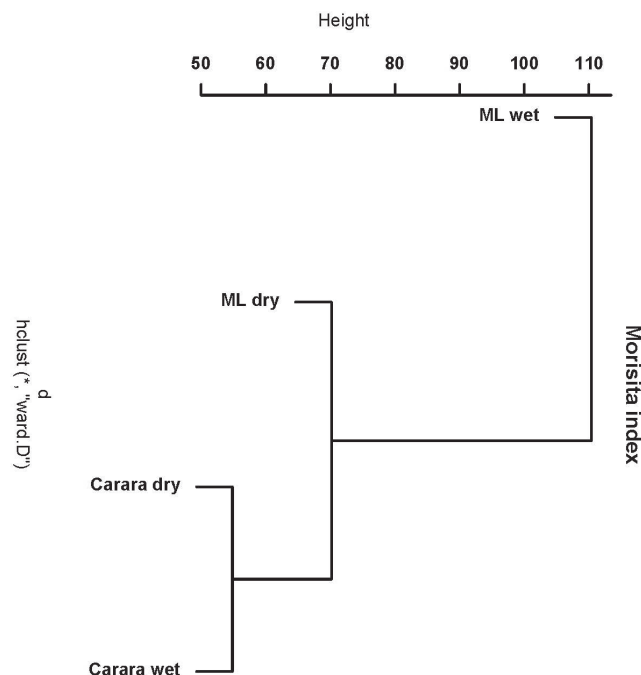

Figure 3. Classification of bird species according to trail and season using the Morisita index of similarity and the Ward method in Carara National Park, Costa Rica, 2007.
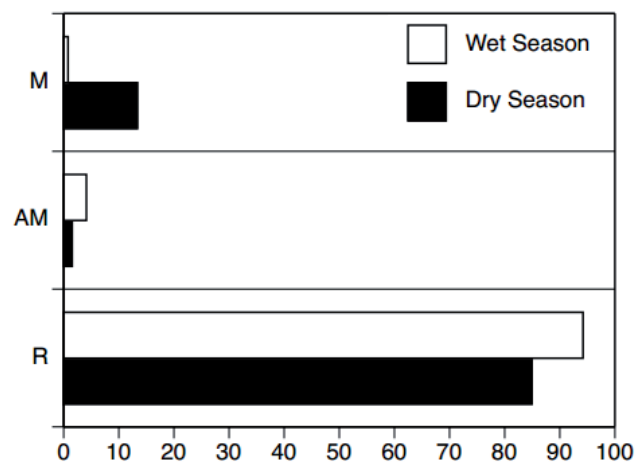

Figure 4. Percentage contribution of latitudinal migrants (M), resident species (R), and altitdinal migrants (AM) to the overall composition of the avifauna in Carara National Park between wet and dry seasons in 2007.
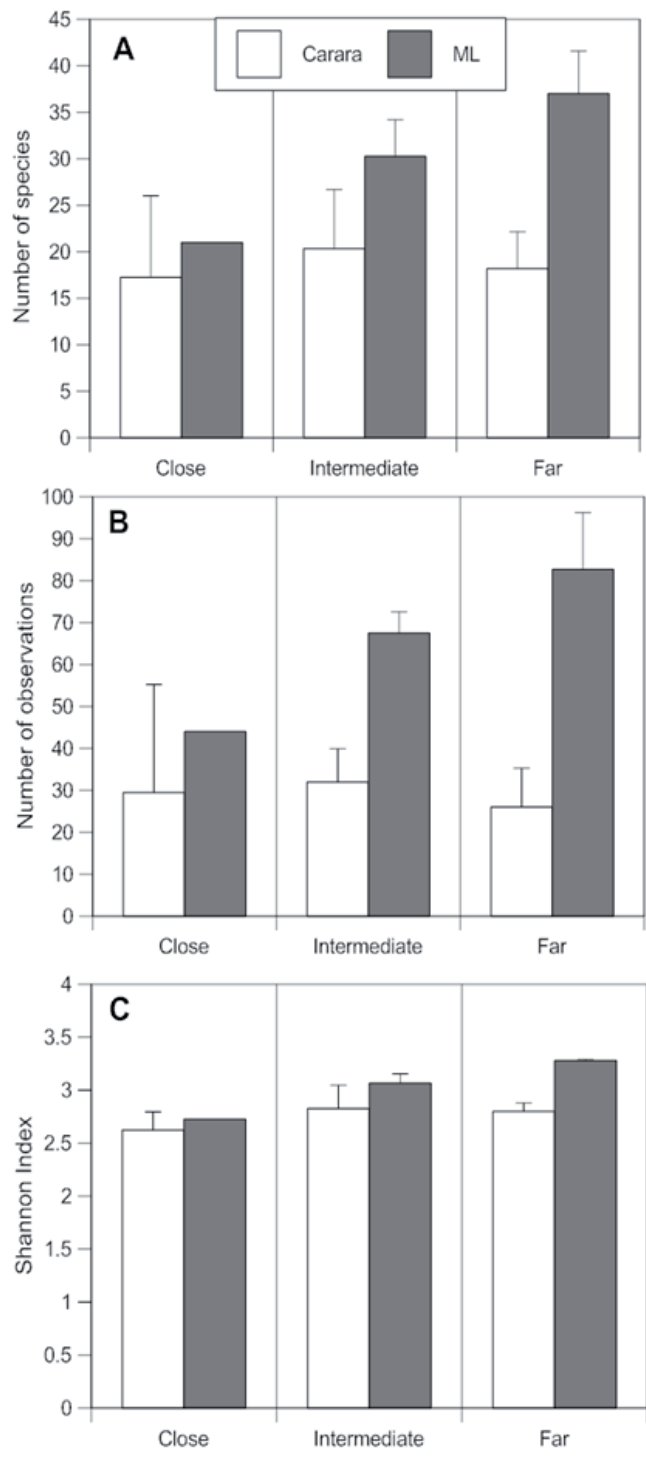
Figure 5a. Variation in average number of species, abundance, and diversity relative to distance from the road during the wet season in Carara National Park, Costa Rica, 2007. Error bars indicate ±1 S.E.
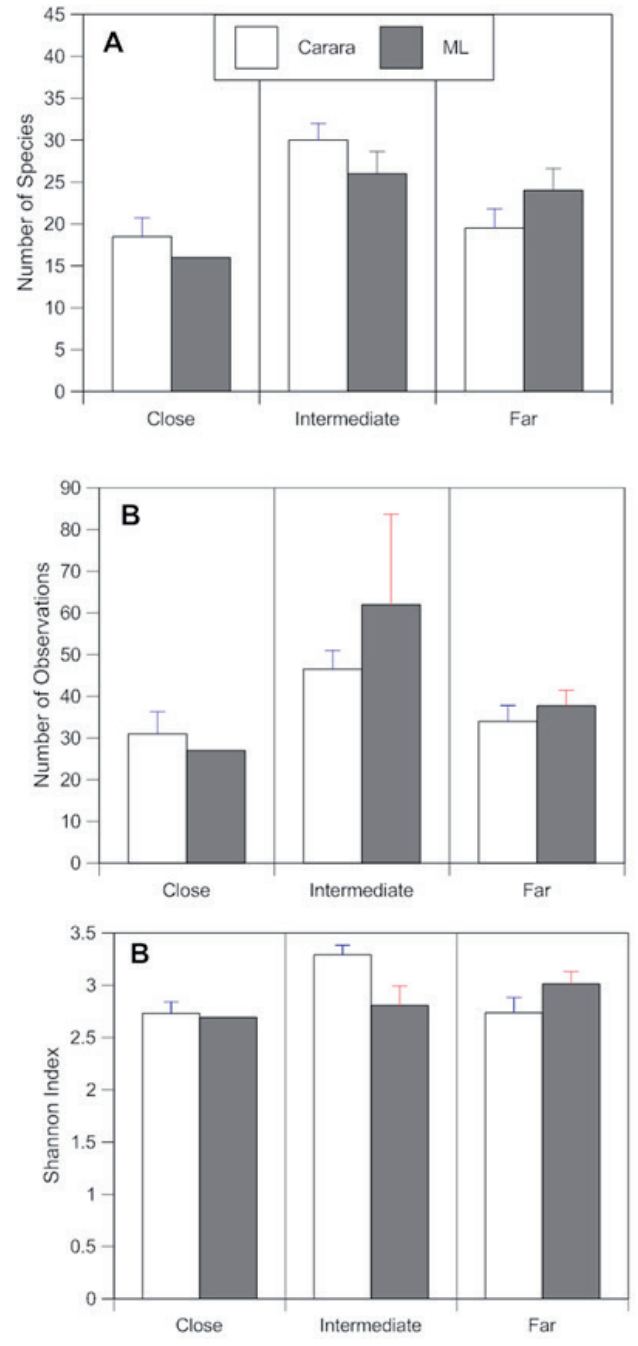
Figure 5b. Variation in average number of species, abundance, and diversity in relation to distance from the road during the dry season in Carara National Park, Costa Rica, 2007. Error bars refer to ±1 S.E.

showing the highest diversity, and the immediate vicinity of the road showing the lowest diversity ($F_{2,16}$ = 5.82, P = 0.01). During the dry season, 20 species within the specialized understory insectivore families did not vary in species richness and abundance as a function of distance from the road ($F_{2,17}$ = 2.22, P = 0.14).

DISCUSSION

In addition to being a transitional forest between tropical dry and tropical rain forests, considerable habitat heterogeneity gives Carara National Park a high level of species diversity. We found a higher and more complex canopy in the Carara trails relative to the more open conditions of ML, although Quesada-Acuña et al. (2015) described a higher similarity in forest structure and tree species composition between these sites possibly associated with the fact that their experimental sites were closer to the road. Our point counts were, instead, located at increasing distances from the road. Compared with Braulio Carrillo National Park, Monteverde, and La Selva, the number of detected species here was relatively high (Young et al. 1998, Sigel et al. 2006, Jankowski et al. 2009, Avalos & Bermúdez 2016). Between sites and seasons, there was an overall change of nearly 50 % in incidence and abundance-based diversity. Other sites for which we have data show similar species turnover (55 % in Braulio Carrillo National Park, Avalos & Bermúdez 2016) whereas the Christmas bird counts of La Selva had a turnover rate of 70 %. Carara and ML increased in similarity during the wet season and decreased during the dry due to the influence of long-distance migrants. More comparative data is needed before we can extend our conclusions to other tropical areas.

We found a decreasing pattern of abundance and diversity with increasing proximity to the road during the wet season, especially within the first 100 m and when comparing close and far sites. This pattern was not found during the dry season. During the wet season, we observed that the thickness of the forest edge in Carara increases relative to that in the dry season. A relatively thinner forest edge during the dry season allows noise to penetrate farther into the forest compared with the wet season (Arévalo & Newhard 2011). Congruent with Arévalo & Newhard (2011) this study shows that the effects of the road reached 100 m inside the forest. After this threshold, intermediate and far distances away from the road differ little in diversity parameters. Arévalo & Blau (2018) showed that Carara National Park had the highest traffic volume per hour and traffic noise levels compared with two other national parks bordering roads. Noise levels decreased from 94 dB along the forest edge to 60 dB within the first 100 m, and to 50 dB

at 650 m away from the road (Arévalo & Blau 2018). The same study found small differences in noise levels between wet and dry seasons, and no differences between weekdays and weekends. On average, however, noise levels were slightly higher (3.44 dB) in the afternoon than in the morning. We expect that our censuses were not affected by the variation in traffic and noise levels since our sampling protocols accounted for environmental changes by randomizing the order of locations, sites, and teammates during the censuses.

Consistent with the noise distribution patterns observed by Arévalo & Blau (2018), we found a general decreasing pattern in species richness and abundance with road proximity. This pattern was consistent in both seasons. Intermediate rather than far distances, however, showed the greatest difference in species richness compared with close locations in the dry season. Disturbances of infrastructure reduce bird abundance up to 1 km (Benítez-López et al. 2010), and roads in particular exacerbate plant desiccation thus lowering habitat quality (Laurance et al. 2009) and homogenizing the effect of distance beyond 100 m from the road. Here, insectivore species were less abundant closer to the road during the wet season. It is possible that insect abundance is also negatively affected by more disturbed and drier forest edges. For example, roads can alter bird spatial distribution and decrease bird foraging efficiency (Francis & Barber 2013). Another factor that could contribute to the decrease in abundance near the road is traffic noise, which interferes in vocal communication by masking acoustic signals that fall within the bird call frequency (Parris & Schneider 2009). Consequently, birds may avoid noisy areas or may adapt call structure to minimize the masking effect of the road (e.g. Goodwing & Shriver 2010, McClure et al. 2013). Arevalo and Newhard (2011) found a negative relationship between levels of noise and bird density and species richness in our study area. We cannot attribute the reduction of bird species and density near the road to a single factor but, rather, to a combination of direct road effects (noise, visual stimuli, turbulence) and edge disturbances acting negatively and in a synergistic manner.

In conclusion, our results showed a significant effect of the road on overall abundance and diversity with a seasonal effect for understory insectivores. Although differences in habitat structure were associated with differences in the composition of the avifauna, the bird assemblage shared high levels of similarity and species turnover between trails and showed a consistent response to the road. Roads will increase in number and traffic density in the near future reaching 25 million km worldwide, increasing especially in

areas of high biodiversity (Laurance et al. 2014). Mitigating the impacts of roads bordering conservation areas is difficult and expensive although some alternatives (i.e., overpasses, tunnels, and physical barriers) have shown some encouraging results (Pell & Jones, 2015). The best alternative is to avoid the first cut (Laurance et al. 2015) and concentrate major roads away from natural areas. Sensitive groups such as understory insectivores represent indicators for a wide range of negative consequences for biodiversity of the increased human dominance of natural landscapes (González-Gallina et al. 2013, Lewis et al. 2015). Significant infrastructure development should be avoided close to natural areas, as there is little window for adaptation of the local biota (Laurance et al. 2015). Increase in traffic density and speed, plus easy access to a road for hunters and poachers have shown substantial negative impacts on biodiversity protection. In less diverse and simpler, semi-open temperate environments, roads actually increase habitat heterogeneity and thus increase species diversity (Morelli et al. 2015, Wiącek et al. 2015), but roads in the tropics usually have a catastrophic effect (Laurance et al. 2009). Carara National Park is one more example of the negative consequences of roads adjacent to protected areas. Avoiding similar cases will require a clear vision from local governments, international funding institutions supporting infrastructure development, and local communities if we are to preserve key habitats such as the rare transitional forest in the face of road expansion at the global level.

REFERENCES

Arévalo JE, Newhard K (2011) Traffic noise affects forest bird species in a protected tropical forest. Revista de Biología Tropical 59:969-980

Arévalo, JE, Blau E (2018) Road encroachment near protected areas alters the natural soundscape through traffic noise pollution in Costa Rica. Revista de Ciencias Ambientales 52:27-48

Avalos G, Bermúdez E (2016) 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. Revista de Biología Tropical 64:1383-139

Baselga A, Bonthoux S, Balent G (2015) Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. PLoS One 10:e0127913

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

Biamonte E, Sandoval L, Chacón E, Barrantes G (2011) Effect of urbanization on the avifauna in a tropical metropolitan area. Landscape Ecology 26:183-194.

Blake J G, Loiselle BA (1991) Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. The Auk 108:114-130

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

Blake J G, Loiselle BA (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. The Auk 118:304-326

Coffin AW (2007) From roadkill to road ecology: A review of the ecological effects of roads. Journal of Transport Geography 15:396-406

Colwell RK (2005) ESTIMATES: Statistical Estimation of Species Richness and Shared Species from Samples. Version 7.5. User's Guide and Application. http://purl.oclc.org/estimates. Last access: 1 November 2018

Dear F, Vaughan C, Polanco AM (2010) Current status and conservation of the Scarlet Macaw (Ara macao) in the Osa Conservation Area (ACOSA), Costa Rica. Research Journal of the Costa Rican Distance Education University 2:7-21

Develey PF, Stouffer PC (2001) Effects of Roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. Conservation Biology 15:1416-1422

Francis CD, Barber JR (2013) A framework for understanding noise impacts on wildlife: an urgent conservation priority. Frontiers in Ecology and the Environment 11:305-313

Gasner MR, Jankowski JE, Ciecka AL, Kyle KO, Rabenold KN (2010) Projecting the local impacts of climate change on a Central American montane avian community. Biological Conservation 143:1250-1258

González-Gallina A, Benítez-Badillo G, Rojas-Soto OR, Hidalgo-Mihart MG (2013) The small, the forgotten and the dead: highway impact on vertebrates and its implications for mitigation strategies. Biodiversity and Conservation 22:325-342

Goodwing SE, Shriver WG (2010) Effects of traffic noise on occupancy patterns of forest birds. Conservation Biology 25:406-411

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

Gotelli NJ, Entsminger GL. (2013) EcoSimR: Null models for ecology. http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html. Last access: 1 November 2018

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:9

Herrera W (1986) Clima de Costa Rica. UNED, San José

Holdridge LR, Grenke WC (1971) Forest environments in tropical life zones: a pilot study. Oxford, New York

Jankowski JE, Ciecka AL, Meyer NY, Rabenold KN (2009) Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. Journal of Animal Ecology 78:315-327

Jankowski JE, Robinson SK, Levey DJ (2010) Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. Ecology 91:1877-1884

Jetz W, Rahbek C (2002) Geographic range size and determinants of avian species richness. Science 297:1548-1551

Jost L, Chao A, Chazdon RL (2011) Compositional similarity and b (beta) diversity. In: Magurran AE, McGill BJ (eds) Biological Diversity: Frontiers in Measurement and Assessment. Oxford, New York. pp 66-84

Kattan GH, Franco P, Saavedra-Rodríguez CA, Valderrama C, Rojas V, Osorio D, Martinez J (2006) Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. Conservation Biology 20:1203-1211

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, … Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605-618

Laurance WF, Goosem M, Laurance SG (2009) Impacts of roads and linear clearings on tropical forests. Trends in Ecology & Evolution 24:659-669

Laurance WF, Clements GR, Sloan S, O'Connell CS, Mueller ND, Goosem M, … Burgues-Arrea I (2014) A global strategy for road building. Nature 513:229-232

Laurance WF, Peletier-Jellema A, Geenen B, Koster H, Verweij P, Van Dijck P, ... Van Kuijk M (2015) Reducing the global environmental impacts of rapid infrastructure expansion. Current Biology 25:R259-R262

Legendre P, Legendre LF (2012) Numerical Ecology, 2nd edn. Elsevier, Oxford

Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. Science 349:827-832

Lindell CA, Riffell SK, Kaiser SA, Battin AL, Smith ML, Sisk TD (2007) Edge responses of tropical and temperate birds. The Wilson Journal of Ornithology 119:205-220

Loiselle BA, Blake JG (1994) Annual variation in birds and plants of a tropical second-growth woodland. The Condor 96:368-380

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR (2013) An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society B 280:1-9

Morelli F, Jerzak L, Pruscini F, Santolini R, Benedetti Y, Tryjanowski P (2015) Testing bird response to roads on a rural environment: A case study from Central Italy. Acta Oecologica 69:146-152

Obando-Calderón G, Chaves-Campos J, Garrigues R, Montoya M, Ramírez O, Zook J (2014) Lista oficial de las aves de Costa Rica. Zeledonia 18:33-83

Parris KM, Schneider A (2009) Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecology and Society 14:29

Pell S, Jones D (2015) Are wildlife overpasses of conservation value for birds? A study in Australian sub-tropical forest, with wider implications. Biological Conservation 184:300-309

Pereira HM, Belnap J, Brummitt N, Collen B, Ding H, Gonzalez-Espinosa M, ... Vieira C (2010) Global biodiversity monitoring. Frontiers in Ecology and the Environment 8:459-460

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

Quesada-Acuña SG, Valdelomar V, Morales GR, Matarrita-Herrera M, Hernández IS (2012) Caracterización del paisaje y análisis del límite oeste del Parque Nacional Carara, Costa Rica: implicaciones para la conservación de la biodiversidad. Brenesia 78:6-11

Sandoval L, Martínez D, Ocampo D, Vásquez Pizarro M, Araya HD, Carman E, Sáenz M, García-Rodríguez A (2018) Range expansion and noteworthy records of Costa Rican birds (Aves). Check List 14:141-151

Sigel BJ, Sherry TW, Young BE (2006) Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conservation Biology 20:111-121

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30

Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, ... Bartlam-Brooks H (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359:466-469

Wiącek J, Polak M, Filipiuk M, Kucharczyk M, Bohatkiewicz J (2015) Do birds avoid railroads as has been found for roads? Environmental Management 56:643-652

Wiens JA (1989) The Ecology of Bird Communities. Volume 2, Processes and Variations. Cambridge, New York

Young BE, DeRosier D, Powell GV (1998) Diversity and conservation of understory birds in the Tilarán Mountains, Costa Rica. The Auk 115:998-1016

003-Ecotropica_Article 37-V3.indd   10   07-10-2020   14:27:05