

BIRD COMMUNITY STRUCTURE AND SPECIES RESPONSES TO EDGES IN LAUREL FOREST FRAGMENTED BY NARROW ROADS (TENERIFE, CANARY ISLANDS)

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ABSTRACT

We examined interacting effects of habitat structure, topographic landscape, road edge and vehicle traffic (density and noise), on bird species composition, abundance and diversity in the laurel forest of Tenerife (Canaries). We examined multivariate habitat and landscape factors determining bird community composition and structure, and modality of specific responses by comparing road edge vs interior zones. Abundance of breeding birds in laurel forest showed slight to no increases in response to roads. Two specialized taxa, the palaeoendemic pigeon *Columba bollii* and *Regulus regulus*, revealed nearest negative reductions in abundance near roads. Higher noise levels, vegetation density, lower canopy closure and wood selective extraction characterized roadsides. Most passerines showed moderate affinity for forest edges and did not evidence decreases due to road proximity. The topographic landscape in these mountainous areas strongly interacted with road edge effects to determine bird community structure. Narrow road disturbances on the laurel forest was related to moderate increase in bird abundance and diversity near edges, but at the cost of losing presence of forest-demanding species playing important ecological roles.

KEYWORDS: *Columba bollii*, laurel forest, topographic landscape, bird modal responses, road impact.

RESPUESTA DE LA ESTRUCTURA DE LA COMUNIDAD DE AVES Y LAS ESPECIES DE BOSQUES DE LAURISILVA FRAGMENTADOS A LA TRANSICIÓN CON CARRETERAS ESTRECHAS

RESUMEN

Cuantificamos los efectos de la estructura del hábitat, la topografía, el efecto de borde viario y del tráfico de vehículos (intensidad de circulación y ruido) sobre la composición, abundancia y diversidad de aves en el bosque de laurisilva de Tenerife (Canarias). Modelizamos las respuestas de las aves comparando el borde con el interior forestal. La abundancia de aves nidificantes mostró una variación poco acusada en respuesta al efecto de borde, con dominancia de especies ampliamente tolerantes e incluso afines a estos ecotonos. Casi todos los paseriformes mostraron afinidad por los bordes viarios. Dos taxones especializados, la paloma paleoendémica *Columba bollii* y el pequeño paseriforme *Regulus regulus*, fueron menos abundantes en los bordes viarios. Los altos niveles de ruido, la mayor densidad de la vegetación, menor cobertura del dosel forestal y la extracción de madera fueron los principales factores de incidencia negativa sobre las palomas. El paisaje topográfico en estas áreas montañosas interactuó con esos efectos de borde e influyó en la estructura de la comunidad de aves. Las alteraciones del hábitat están relacionadas con un aumento de la abundancia y diversidad de la mayoría de especies orníticas en los márgenes, mientras que otros taxones importantes son menos frecuentes.

PALABRAS CLAVE: *Columba bollii*, laurisilva, paisaje topográfico, respuesta modal de las aves, impacto de las carreteras.

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INTRODUCTION

Birds in road-fragmented forests face impacts from area reduction and ecosystem division, especially near urban, heavily disturbed areas (Yahner 1988, Bierregaard and Lovejoy 1989, Reijnen *et al.* 1995, Blair 1996, Canaday 1997). Changes in forest structure, microclimate and plant species composition may lead to population losses that may be critical for vulnerable, forest-dependent and endemic species, especially for those taxa relying on foraging and nesting places affected by habitat transformation (Bierregaard and Lovejoy 1989, Santos *et al.* 1998, Rolstad 1991, Maas *et al.* 2009).

Roads induce additional fragmentation by facilitating human access to formerly remote areas, producing changes in territorial uses, facilitating dispersal and transport of alien species, and by subsequent division of already separated remnants (Forman *et al.* 2002a, Donaldson and Bennet 2004, Coffin 2007, Fahrig and Rytwinski 2009, van der Ree *et al.* 2015). Bird species composition, abundance and diversity can be affected by roads in various ways, and these alterations may propagate large distances toward the preserved forest interior (Canaday 1997, Ortega and Capen 1999, Forman and Deblinger 2000, Forman *et al.* 2002a, b). Ecological gradients may favor edge-prone or habitat-generalist species whereas negatively impacting edge-avoiders or habitat-interior taxa (Lindell *et al.* 2007). Bird species richness decreases near highways and this effect propagates several kilometers into surrounding habitat (Brotons and Herrando 2001). Narrow forest roads can cause significant reductions in richness of area-sensitive bird species (or edge-avoiding taxa) (Laurance 2004, Laurance *et al.* 2004, Rich *et al.* 1994, Arévalo and Newhard 2011).

Road edges also induce high bird population densities, especially if birds are favored by habitat supplementation at these ecotones (Havlin 1987, Meunier *et al.* 1999, D'Amico *et al.* 2013). Habitat quality in road-fragmented forests determines bird density and use of space for nesting and feeding (Reijnen and Foppen 1994, Willson *et al.* 1994, Kociolek *et al.* 2011). Šálek *et al.* (2010) found that bird richness decreased from forest edges, to low traffic road edges, to forest interior in central Europe. Forest road margins provide complementary resources that are unavailable at forest interior (Yahner 1988). However, this habitat use may involve other risks. For example, Holm and Laursen (2011) found that Great tit *Parus major* broods

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suffered greater mortality in hedgerows near roads with dense and high-speed traffic than in others of lower intensity or without any traffic.

So far, road impacts on birds have been studied mostly in continental areas of the Northern hemisphere. Road disturbances to oceanic island birds are much less studied (Delgado *et al.* 2008). A particularly poorly studied aspect is the roadkill incidence from traffic on animal populations on oceanic islands, particularly on birds and mammals (Tejera *et al.* 2018). For instance, bird roadkill in the Lanzarote Biosphere Reserve has been found to be high even under relatively low traffic intensity (Tejera *et al.* 2018). Fragmentation processes other than roads are also known to induce severe declines in island bird species (Castelleta *et al.* 2005, García-del-Rey *et al.* 2013).

Roads have increased in area and extended their effects in spatially-limited island ecosystems over the last few decades. However, their effects on oceanic island biotas are still poorly known. Most bird extinctions have been reported from oceanic islands (Steadman 2006). The role of human transport corridors in this demise is not well understood for oceanic islands. Other causes of threatening, like hunting or alien predators may interact with a developed road net to augment impact on native avifaunas on islands (Whittaker and Fernández-Palacios 2007, García-Carrasco *et al.* 2020). Ecological impacts of roads traversing orographically complex landscapes such as mountain forests on islands are scarcely studied (Gucinski *et al.* 2001). On oceanic islands and mainland mountain habitats, orography may greatly determine impacts of road fragmentation and ecological responses of birds (McGarigal and McComb 1995, Miller *et al.* 1996).

The Canarian laurel forest (or laurisilva) is a Tertiary-relict, subtropical ecosystem, which harbors exclusive bird taxa, partly due to insular conditions, as well as Palearctic elements (Báez 1992, Martín and Lorenzo 2001). These island bird assemblages are relatively poor in species diversity, forming simple communities if compared to nearest continental grounds (Iberia, North Africa). However, the laurisilva shelters interesting populations of palaeoendemic frugivore pigeons and several subspecific endemic passerines, internationally relevant, deserving efforts in basic and applied research, and which interact with the landscape structure and impacts derived from roads traversing these forests.

Apart from birds, diverse road edge effects on other biotic and abiotic aspects of the laurisilva, conferring forest interior-edge contrast which in turn may interact and affect birds have been already reported (Delgado *et al.* 2001, 2007a,b, 2013a,b). Furthermore, in a previous study comparing bird communities near road edges and at forest interior, we found a weak dependence of bird abundance on road proximity (Delgado *et al.* 2008). Road edge effects on birds may be obscured by or interact with other concurrent habitat factors such as landscape configuration and vegetation structure. Hence, there is a need to disentangle those factors likely explaining the observed pattern of bird species abundance in this road-fragmentation context. We thus performed a multifactorial approach to bird species responses to roads as linear elements integrated in the forest landscape, considering both vegetation structure and diversity and landscape type.

We aimed to answer the following questions: Does road proximity affect breeding bird community structure, i.e. in terms of abundance, species composition,



diversity, and species-specific abundance responses? We compared forest structure (habitat types and vegetation) between road edges and forest interior to assess how the bird community responds to such variation. We aimed to classify bird species regarding their responses to forest structure and road proximity. Finally, distance between natural areas and the suburban zone determines human accessibility by car, and the intensity of direct and indirect road disturbances (traffic, noise, human presence) reaching remote patches. Hence, we also aimed to assess the extent of impact on the bird species abundances along a gradient of motorized traffic and noise.

MATERIAL AND METHODS

STUDY AREA

Here we realized bird censuses along asphalt roads and at forest interior of the laurisilva in the Anaga mountains, the largest laurisilva remnants on NE Tenerife, Canaries (28-29°N, 16-17°W) (fig. 1, table 1). We performed censuses in both mature laurisilva (mainly formed by *Laurus novocanariensis*, *Morella faya*, *Ilex canariensis*, *Erica arborea*, *Persea indica*, *Prunus lusitanica* and *Apollonias barbujana*) and *Erica-Morella* formations (tree-heath-wax-myrtle thicket) (del Arco *et al.* 2010). These forests are traversed by a narrow, two-lane asphalt road mostly running along the ridge and steep ravine slopes of the massif dorsal, connecting sparse settlements by a set of minor secondary roads (fig. 1, table 1). We divided the census zones following the gradient of increasing distance from the periurban area (W of the study forest, Las Mercedes), toward the easternmost sector of Anaga (table 1). Due to road width, high frequency of curves and asphalt surface conservation and remoteness, the motorized traffic losses intensity, and human disturbance decreases along the road from W to E. General features of structure, composition and diversity of the study forests have been exposed in detail elsewhere (Delgado *et al.* 2008, Delgado 2009, Fernández-Palacios 2009).

To assess the magnitude of the gradient in traffic density between suburban and remote areas, we noted number of vehicles per hour, at every sampling point along bird count transects (table 1). We also used official traffic density data (Mean Daily Intensity, MDI; Cabildo de Tenerife 2001). To obtain a general view of motorized traffic in the study area, we used data from 5 gauging measuring stations to check for MDIs for years 2002 (that of this study), 2008, 2013 and 2017 (last year with available traffic data) (Cabildo de Tenerife, 2018). MDIs averaged 1311.3 vehicles/day (708.23, SD) for the whole period; no significant differences in traffic intensity were found between years by means of a chi-square test ($\chi^2_3 = 1.544$, $p > 0.05$).

BIRD COUNTS

We performed bird counts between april-june, 2002, encompassing the breeding season for most species (Martín and Lorenzo 2001). Censuses started early in the morning (07:00-08:00 am) and lasted for 3-4 hours depending on weather.



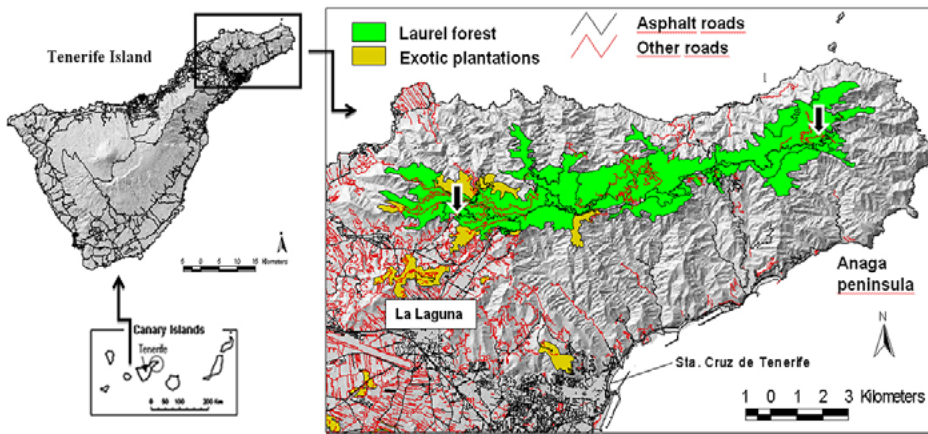


Figure 1. Map of the study area in eastern Tenerife (Canary Islands) showing the road-remoteness gradient along the Anaga peninsula. The black arrows represent the extremes of the gradient along the road transect (enclosed within the laurel forest tract longitudinally arranged along the peninsula) between the periurban area near La Laguna city (West) and the farthest road end (East). The concentrations of urban and periurban areas and vial infrastructure are depicted by the line pattern (asphalt and other roads).

We perform census only in absence of windy or rainy weather and relatively calm weather conditions.

We used linear transects which were subdivided into replicates with a fixed band of 50 m width (Bibby *et al.* 2000). Each complete transect was replicated three times, yielding a total of 36 count sessions distributed in 12 major transect units (table1), changing the order of transects between census days. We distributed transects and transect length between road edges and forest interior as homogeneously as possible according to area and topography limitations of this forest ecosystem. Forest interior was defined as areas distant ≥ 100 m from any transport or urban infrastructure, human-made clearings or forest-shrubland ecotones. We chose this distance because of the frequency and density with which in these forests there appear paths and dust tracks interrupting transects longer than such distance. We aimed to avoid influence of proximity of such linear gaps to our focal linear infrastructures. Many studies have shown that road influence reaches far into the traversed habitats (review in Forman *et al.* 2002). However, in our study area there were a higher chance of intersection with other interposed linear structures such as firebreaks, paths and roads, and other forest edges within the first 100 m from our focal road (Delgado *et al.* 2007, 2008). Hence, forest interior was defined as areas distant ≥ 100 m from any transport or urban infrastructure, human-made clearings or forest-shrubland ecotones.

We subdivided each transect in 100×50 m (0.5 ha) subunits to take bird data and traffic noise. The overall census effort was 72 and 113 sampling subunits along road edges and interior forest respectively (table 1). Different sampling size



TABLE 1. DESCRIPTIVE FEATURES OF ROAD TRANSECTS

SITE CODE	SITE NAME	TRANSECT LENGTH (KM)	N.º OF 0,5 HA CENSUS SUBUNITS	ROAD EDGE/ FOREST INTERIOR	AVERAGE DISTANCE TO NEAREST URBAN/ SUBURBAN NUCLEI (KM)	ALTITUDINAL RANGE (M A.S.L.)	AVERAGE ROAD WIDTH (M)	AVERAGE TRAFFIC DENSITY (N.º VEHICLES/H) ± 1 ET
1	Las Mercedes-1	1.5	15	Edge	0.25	660-770	9.1	106.1 ± 46.5
2A	Las Mercedes-2	1.1	11	Edge	0.5	810-855	7.5	96.5 ± 45.1
2B	Cruz del Carmen	0.6	6	Edge	0.9	880-920	8.2	133.3 ± 78.9
7	Las Yedras	1	10	Interior	1	885-835	-	-
9	Pedro Álvarez-Cruz del Carmen	1.2	12	Interior	1	700-690	-	-
6	Las Mercedes-3 (El Moquinal road)	2.5	25	Edge	1.2	800-820	11.3	18.4 ± 9.5
3	Aguirre-1	1.5	15	Interior	2	770-890	-	-
8	Las Quebradas-Pedro Álvarez	2	20	Edge	2	780-700	7.1	14.1 ± 7.5
11	Aguirre-2	1.5	15	Interior	2	750-650	-	-
10	Pijaral-Ensellada	2.1	21	Edge	8	760-785	7.4	20 ± 20.9
4	Ensellada-Pista de C. Tejo	1.5	15	Edge	9	785-810	5.4	7.3 ± 3.5
5	Chinobre-Anambro	2	20	Interior	9	810-900	-	-
Totals		18.5	185 (92.5 ha)	Interior 7.2 km Edge 11.3 km		650-920	8	51.2 ± 27.4

¹ Asphalt right-of-way plus roadsides, ditches and surfaces accessible by vehicles.

for forest edge and interior is due to limitations of accessibility and on-road safety in abrupt terrain. We also established these census subunits to facilitate collection of sound, habitat and vegetation data in order to relate these attributes with bird variables (see below).

NOISE AND TRAFFIC DENSITY

Noise recording was performed by a person walking ca. 10-20 m behind the bird observer (J.D. Delgado), along with bird census from 07:00-08:00 h and during 3-4 hours. Noise level samples were taken along roads and at forest interior. Roads were walked along the asphalt edge; interior forest was subdivided in 100-m long transect subunits running further than 100 m from the edge. At the start and the end of each subunit, we took three consecutive 1-min noise samples (3 minutes per sampling point) (Harris 1998). We recorded noise with a handheld YF-22, Type 2 sound level meter. Measures were taken within the frequency range 31.5Hz-8 KHz. Bird vocalizations are mostly produced within the 2-4 KHz range (Dooling and Popper 2007, Wright *et al.* 2010). This means that any non-wanted sound within this frequency will have the highest probability to mask bird sounds and affect song perception through changes in the sound environment of birds. Noise intensity was adjusted to the range 20-130 decibels (dB(A)), weighed logarithmic measure A, or A-weighting (Harris 1998). We used this procedure because the A-weighting mode for decibels is the most commonly used method in bird studies. A-weighting is useful to estimate overall sound pressure in a mode which maximizes similarity with bird hearing range, taking into account that there also differences between bird species and habitat structure (Dooling and Popper 2007, Wright *et al.* 2010). Resolution was 0.1 dB(A) and precision ± 1.5 dB(A). The sound level meter was used in Lmax-Lmin mode held at ~ 1.3 m above ground (probe directed to the opposite edge; the same road edge was always sampled). Minimum, maximum and average values were obtained for each 1-min sample and 3 min overall. As a noise level indicator we used a sound pressure level or *energy equivalent level* (*Leq*; Harris 1998). For a measurement period of 1 min, *Leq* expresses a continuous-value signal having the same total energy than the single sound recordings. In other words, it represents, for birds being affected by traffic noise, the level or pressure of noise which equals the energy average of sequential individual measurements taken over a sampling period. The following equation (Harris 1998) was computed:

$$Leq = 10 \log_{10} [1/T \sum t_i \cdot 10^{Li/10}] \text{ [dB(A)]}$$

where

T = recording time during which the noise level is: $Li \pm 2$ [dB(A)]

Li = single sound record (i) [dB(A)]

t_i = time duration of each single sound record



TABLE 2. DESCRIPTIVE LANDSCAPE AND HABITAT STRUCTURE VARIABLES

VARIABLE	CODE	DETAILS
<i>Road and other landscape attributes</i>		
1) Total width (m)	RW	Asphalt surfaces + accessible roadsides (with graduated tape)
2) Verge (side) width (m)	SW	On both sides of the asphalt surface
3) Average slope (°)	Slope	With hand clinometer
4) Topographic category (ridge, slope, valley)	Topo	
<i>Vegetation and substrate attributes¹</i>		
Vegetation		
5) Tree canopy cover (%) ²	CCover	With spherical forest densiometer (Lemmon, 1957).
6) Average canopy height (m)	CHeight	
7) Understory shrub cover (%)	ShrubCov	
8) Average shrub height (m)	ShrubHe	
9) Herb/grass cover (%)	GrassCov	
10) Stem (trunk) density (diameter classes ³ , in cm): <5; 5-10; 10-20; 20-30; >30	T5, T10, T20, T30, Tm30	
11) N.º vertical vegetation strata ⁴	NStra	
12) N.º fleshy-fruit producing plant species	FruitSpp	
13) N.º shrub species	ShrubSpp	
14) N.º tree canopy species	TreeSpp	
15) N.º stumps of woody plant species (selective logging)	Stump	
Ground or substrate		
16) Litter cover (%)	LittCov	
17) Rocky cover (%)	RockCov	

¹ Variables taken within 10 m-radius circles; all visual counts and visual estimates unless otherwise indicated.

² Along road transects tree canopy cover was recorded directly above the corridor center and at 5 m from the road edge toward the forest.

³ Diameter at breast height (DBH).

⁴ Number of vegetation strata between ground level and canopy above the circle center.

HABITAT STRUCTURE ASSESSMENT

We surveyed habitat structure to analyze its correlations with bird community patterns along road edges and forest interior. Two habitat surveying points were set at the beginning and the end of each 100 m transect subunits (n = 370 points overall). Each point was a circle (radius: 10 m; 314.2 m² = 0.031 ha) within which habitat variables were estimated (table 2). The pooled area of the 2 points

(0.062 ha) covered -12 % of transect area (0.5 ha). We recorded general landscape features and local habitat variables to explore their influence on bird community structure: a) road width, and b) width of both road edges combined (since birds often use such edges for foraging), c) terrain slope, d) three topographic categories (ridge, slope or hillside, and valley bottom or ravine basin) to determine if topography affects other structural variables (Miller *et al.* 1996); e) eleven descriptors of structure and composition of vegetation, and two descriptors of ground substrate at the plot scale (table 2).

STATISTICAL ANALYSIS

We estimated differences between road edge and forest interior in composition, species richness, Shannon's diversity ($H' = -\sum p_i \ln p_i$; where p_i is the frequency of species i in relation to total number of individuals in a sample of n species), equitativity or evenness ($E = H'/H'_{\max}$, where $H'_{\max} = \ln S$), Simpson's dominance index ($D = 1/\sum p_i^2$), and bird density (n° birds/10 ha) (Magurran 2004). Between (edge vs. interior) and among (ridge, slope, valley) habitat categories in community descriptors were tested for significance by the Kruskal-Wallis and Mann-Whitney's U tests (Sokal and Rohlf 1995).

Associations between distance to suburban edge, traffic density and noise levels, and the parameters of the bird community were assessed by non-parametric correlation (Spearman's Rho, r_s). To test the relationship between our two problem variables, namely noise levels (independent variable) and bird abundances (dependent variable), partial correlation analysis was used as an additional way to control for the influence of road edge proximity, and distance to suburban edge. We aimed to ascertain that any potential bird-noise relationship were not due to their association with transect location regarding road edges, or transect proximity to urban areas. We thus fixed the effect of transect location (road edge vs. forest interior), and transect distance in km to the nearest urban or suburban nuclei. We performed these analyses in SPSS (SPSS 1999).

To explore the structure of the bird community, both species and subunits were ordinated by means of a detrended correspondence analysis (DCA, a unimodal, indirect gradient analysis; Hill and Gauch 1980, ter Braak and Smilauer 1998). A weighting factor was assigned to species depending on their relative abundance. By canonical correspondence analysis (CCA) we analyzed the species-habitat interactions within a context of road proximity (ter Braak and Smilauer 1998, Pearman 2002). Goodness-of-fit for variables exerting significant effects on bird abundance was assessed by Monte Carlo permutation tests with 500 randomizations. Previously to the ordination, we identified redundant environmental information by exploring the relationships within our variable pool through factor analysis (Principal Components Analysis, PCA, Gauch 1982). We followed the Kaiser-Meyer-Olkin adequacy test ($KMO \geq 7$), sphericity test ($p < 0.05$), selecting eigenvalues > 1 and Varimax rotation of the analytical solution.



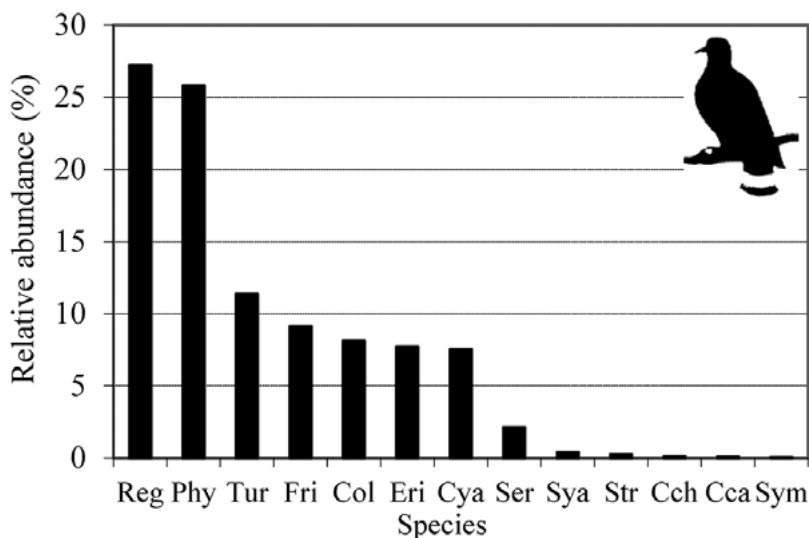


Figure 2. Composition and distribution of relative abundance of laurisilva birds in the breeding season (road and interior data combined). Species codes: Cca: *Carduelis carduelis*; Cch: *Carduelis chloris*; Col: *Columba bollii*; Eri: *Erithacus rubecula*; Fri: *Fringilla coelebs*; Cya: *Cyanistes teneriffae*; Phy: *Phylloscopus canariensis*; Reg: *Regulus regulus*; Ser: *Serinus canarius*; Str: *Streptopelia turtur*; Sya: *Sylvia atricapilla*; Sym: *Sylvia melanocephala*; Tur: *Turdus merula*.

The responses in population density to roads were analyzed for each species by locally weighted regression scatterplot smoothing (LOWESS, Cleveland *et al.* 1992). With this we aimed to explore the shape and strength of the association between bird species density and habitat structure. We thus adjusted the best available function to successive pairs of data, without assuming a linear relationship between dependent (bird density) and independent (habitat) variables. For DCA, CCA and LOWESS analysis we used CANOCO v. 4.5 (ter Braak and Smilauer 1998).

RESULTS

BIRD COMMUNITY COMPOSITION AND STRUCTURE

We recorded a total of 13 bird species, 11 passeriformes and 2 columbiformes (fig. 2). The community was dominated by two small passerines, *Regulus regulus* and *Phylloscopus canariensis*, which made ca. 53% of the bird assemblage (fig. 2, table 3). The other quantitatively important species were *Turdus merula*, *Fringilla coelebs*, *Columba bollii*, *Erithacus rubecula*, *Cyanistes teneriffae* and, in smaller numbers, *Serinus canaria*, *Sylvia atricapilla* and *Streptopelia turtur*.

TABLE 3. DENSITY (BIRDS/10 HA, MEAN \pm 1 STANDARD DEVIATION, SD), FOR THE THREE CENSUS REPLICATES COMBINED. SHOWN IS THE SPECIES FREQUENCY (N.º OF 0.5 HA SUBUNITS WITH A SPECIES PRESENCE N= 185 \times 3 = 555 SAMPLES) AND RELATIVE ABUNDANCE IN THE COMMUNITY (%)

SPECIES	DENSITY	FREQUENCY	%
<i>Regulus regulus</i>	29.9 \pm 23.79	374	27.21
<i>Phylloscopus canariensis</i>	28.4 \pm 21.89	391	25.80
<i>Turdus merula</i>	12.5 \pm 16.69	223	11.37
<i>Fringilla coelebs</i>	10 \pm 17.47	161	9.13
<i>Columba bollii</i>	8.93 \pm 19.26	132	8.12
<i>Erethacus rubecula</i>	8.49 \pm 12.46	181	7.72
<i>Cyanistes teneriffae</i>	8.29 \pm 14.39	152	7.54
<i>Serinus canarius</i>	2.34 \pm 9.01	38	2.13
<i>Sylvia atricapilla</i>	0.44 \pm 2.93	11	0.40
<i>Streptopelia turtur</i>	0.28 \pm 2.66	6	0.25
<i>Chloris chloris</i> *	0.16 \pm 2.18	3	0.14
<i>Carduelis carduelis</i> *	0.12 \pm 1.54	3	0.11
<i>Sylvia melanocephala</i>	0.08 \pm 1.259	2	0.07

Chloris chloris, *Carduelis carduelis* and *Sylvia melanocephala* represented only 0.32% of the assemblage, and were present at only few local spots of secondary growth or bushy marginal patches. *Chloris* and *Carduelis* were detected only at the road edge nearby the suburban forest limit at transect #1 (table 3).

COMMUNITY AND SPECIES LEVEL RESPONSES TO ROAD PROXIMITY AND ROAD ACTIVITY

Structure and composition of the laurisilva bird community were not significantly different between road edges and forest interior (fig. 3, table 4). There were slightly higher richness, diversity, equitativity, overall population density and single species densities near road margins. General bird abundances were slightly higher along road edges, except for both *Columba* species. Two passerines (*Fringilla* and *Phylloscopus*) were significantly more abundant along road edges than at forest interior, whereas the endemic pigeon *Columba* was significantly more abundant at forest interior (table 5).

Traffic density varied between 175 and 3199 vehicles/day between the eastern (most remote) and the western suburban ends of the gradient (fig. 4). Noise levels were neatly higher along road edges [Leq = 43.3 \pm 7.9 dB(A); maximum = 96.2 dB(A)] than at forest interior [Leq = 36.7 \pm 4.8 dB(A); maximum = 69.7 dB(A)] (U = 13.049, p<0.001) (fig. 5).



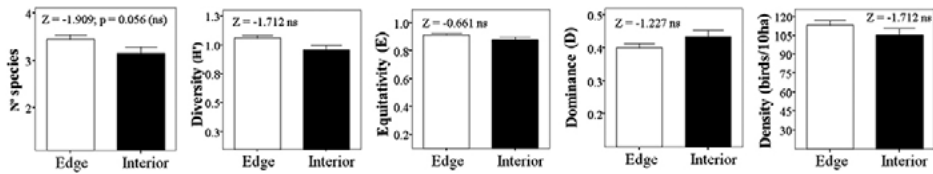


Figure 3. Comparison of parameters of bird community structure between road edge and forest interior (mean + 1 SE) and Mann-Whitney's tests; ns = not significant.

TABLE 4. DESCRIPTORS OF THE BIRD COMMUNITY OF THE TENERIFE LAUREL FOREST FOR EACH TRANSECT (SHOWN ARE MEAN \pm 1 STANDARD DEVIATION, DT), COMBINED OVER THE 3 REPLICATE TRANSECTS; TRANSECT CODES AS IN TABLE 1)

TRANSECT	HABITAT	S, SPECIES NUMBER	SHANNON'S H'	SHANNON'S E	SIMPSON'S D	DENSITY (BIRDS/10 HA)
1	Road edge	4 \pm 2	1.25 \pm 0.5	0.41 \pm 0.02	0.33 \pm 0.18	134 \pm 72
2A	Road edge	4 \pm 2	1.10 \pm 0.4	0.40 \pm 0.02	0.38 \pm 0.14	134 \pm 65
2B	Road edge	3 \pm 1	1 \pm 0.32	0.42 \pm 0.02	0.40 \pm 0.11	104 \pm 45
3	Interior	5 \pm 1	1.43 \pm 0.32	0.41 \pm 0.01	0.27 \pm 0.09	173 \pm 71
4	Road edge	3 \pm 2	0.95 \pm 0.54	0.40 \pm 0.03	0.46 \pm 0.25	112 \pm 78
5	Interior	2 \pm 2	0.63 \pm 0.54	0.41 \pm 0.03	0.55 \pm 0.27	69 \pm 60
6	Road edge	3 \pm 1	1.03 \pm 0.47	0.41 \pm 0.02	0.41 \pm 0.21	107 \pm 57
7	Interior	3 \pm 2	0.88 \pm 0.49	0.42 \pm 0.02	0.46 \pm 0.22	93 \pm 67
8A	Road edge	4 \pm 2	1.15 \pm 0.47	0.41 \pm 0.02	0.35 \pm 0.17	110 \pm 53
8B	Road edge	4 \pm 1	1.32 \pm 0.41	0.41 \pm 0.02	0.31 \pm 0.17	143 \pm 65
9	Interior	3 \pm 2	0.93 \pm 0.52	0.40 \pm 0.04	0.47 \pm 0.25	105 \pm 57
10	Road edge	2 \pm 2	0.72 \pm 0.59	0.42 \pm 0.01	0.53 \pm 0.29	70 \pm 57
11	Interior	3 \pm 1	1.02 \pm 0.52	0.43 \pm 0.01	0.38 \pm 0.21	72 \pm 45
Total		3 \pm 2	1.02 \pm 0.53	0.41 \pm 0.02	0.41 \pm 0.23	110 \pm 69

Minimum and maximum noise levels were significantly higher along roads than at forest interior (Minimum levels: $U = 5.079$, $p < 0.001$; maximum levels: $U = 13.406$, $p < 0.001$). This was largely determined by peak noise recordings along roads (fig. 5). Apart from higher “baseline” noise levels, traffic noise generated a more variable and unpredictable sound environment near road edges than at forest interior (fig. 5).

We did not detect a significant association between maximum noise level (as a proxy for maximum negative impact on birds) and bird density or richness along road edges (table 6). Only 3 species showed a significant negative association

TABLE 5. DIFFERENCES (MANN-WHITNEY'S) IN MEAN DENSITY BETWEEN ROAD EDGE AND INTERIOR FOREST FOR THE MOST FREQUENT BIRD SPECIES IN LAURISILVA. THE NUMBER (N) OF 0.5 HA CENSUS SUBUNITS (3 REPLICATES INCLUDED) IS SHOWN; NS = NOT SIGNIFICANT

SPECIES	ROAD EDGE (N = 339)	INTERIOR (N = 216)	U
<i>Regulus regulus</i>	1.54 ± 1.2	1.42 ± 1.2	1.29 ns
<i>Phylloscopus canariensis</i>	1.5 ± 1.0	1.28 ± 1.2	2.44 *
<i>Turdus merula</i>	0.65 ± 0.9	0.58 ± 0.8	0.89 ns
<i>Fringilla coelebs</i>	0.59 ± 1	0.35 ± 0.6	2.50 *
<i>Erithacus rubecula</i>	0.44 ± 0.6	0.40 ± 0.7	1.25 ns
<i>Cyanistes teneriffae</i>	0.42 ± 0.7	0.41 ± 0.7	0.49 ns
<i>Columba bollii</i>	0.3 ± 0.8	0.7 ± 1.2	4.90 **
<i>Serinus canarius</i>	0.14 ± 0.5	0.07 ± 0.3	1.45 ns
<i>Streptopelia turtur</i>	0.02 ± 0.2	-	1.88 ns

* p<0.05; ** p<0.001

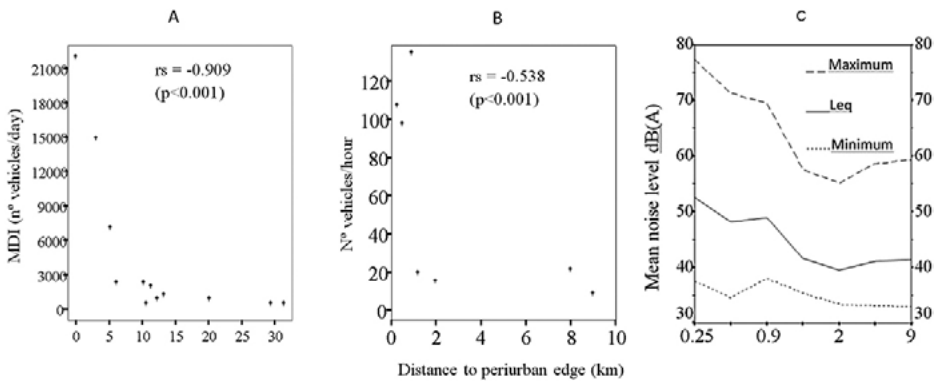


Figure 4. Effect of distance of bird road transects to the periurban zone on traffic density and noise level. A, MDI: Mean Daily Intensity (vehicles/day) (Cabildo de Tenerife 2001). Distance measured as kilometers of “driving” distance on the road, to obtain a measure of accessibility to cars and humans; B, hourly traffic intensity; C, noise level recorded during bird censuses (distance measured in straight line on a map). Shown are Spearman correlations and p values.

with maximum noise levels (table 6). Population density of *Columba* was negatively associated with noise level. On the other hand, densities of *Serinus* and *Cyanistes* showed weak positive associations with noise levels. Vehicle traffic density, measured both as n.º vehicles/h (from our transects) and official MDI data (Cabildo de Tenerife, 2001) was significantly higher near the suburban area and followed a decreasing gradient toward the eastern end of Anaga (table 1, fig. 4).

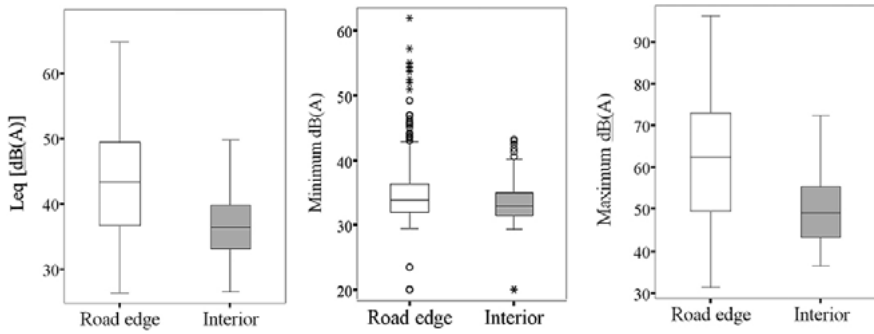


Figure 5. Variation in levels of traffic noise between road edge and laurel forest interior. Diagrams show median (horizontal line), quartiles, standard error, extreme values (o) and atypical values (*).

TABLE 6. SPEARMAN (r_s) AND PARTIAL CORRELATIONS (C_p , EDGE VS INTERIOR) BETWEEN THE MAXIMUM NOISE LEVEL [DB(A)], TRAFFIC DENSITY (N.° VEHICLES/H), DISTANCE TO THE MAIN URBAN AREA (KM) AND DENSITY OF THE MOST FREQUENT LAUREL FOREST BIRD SPECIES. NOISE-ABUNDANCE CORRELATIONS WERE ONLY CALCULATED FOR BIRDS ALONG FOREST ROAD EDGES

SPECIES	r_s (VEHICLES/H)	r_s DISTANCE TO URBAN AREA (KM)	C_p DISTANCE TO URBAN AREA (KM)	r_s dB(A)
<i>Regulus regulus</i>	-0.025 ns	0.372*	0.342 ns ²	0.037 ns
<i>Phylloscopus canariensis</i>	0.078 ns	0.018 ns	-0.222 ns	0.105 ns
<i>Turdus merula</i>	-0.034 ns	0.039 ns	-0.150 ns	0.148 ns
<i>Fringilla coelebs</i>	0.209 ns	0.023 ns	-0.075 ns	0.086 ns
<i>Erithacus rubecula</i>	-0.115 ns	0.310 ns	-0.114 ns	-0.139 ns
<i>Cyanistes teneriffae</i>	0.038 ns	-0.020 ns	-0.132 ns	0.294**
<i>Columba bollii</i>	-0.730***	0.604***	0.326 ns ¹	-0.278**
<i>Serinus canarius</i>	0.137 ns	-0.294 ns	-0.306 ns	0.272**
Overall population density (birds/10 ha)	0.156 ns	-0.280 ns	-0.382*	0.062 ns
Richness (n° of species)	0.065 ns	-0.238 ns	-0.433*	0.102 ns
Shannon's diversity (H')	0.168 ns	-0.269 ns	-0.470**	0.023 ns
Shannon's equitativity (E)	0.194 ns	-0.384*	-0.552***	-0.036 ns
Simpson's dominance (D)	-0.152 ns	0.302 ns	0.478**	-0.042 ns

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns: not significant; ¹ $p = 0.06$; ² $p = 0.05$.

The noise level showed a significant but weak negative correlation with distance to the suburban area (maximum dB(A): $r_s = -0.240$, $p < 0.001$; minimum

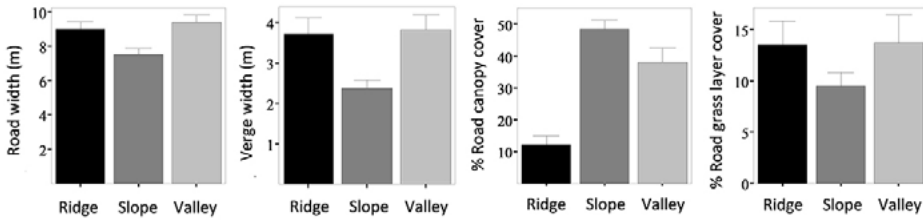


Figure 6. Variation in road width (total and road edges only) and vegetation cover along a topographic gradient in laurisilva.

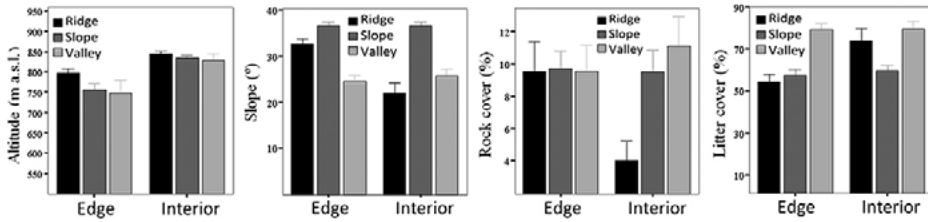


Figure 7. Comparison of variation in altitudinal location, slope and substrate features along a topographic gradient in laurisilva roads and interior areas.

dB(A): -0.170 , $p < 0.001$; Leq : -0.222 , $p < 0.001$). Between gradient extremes, the difference in maximum sound pressure was 17 dB(A), whereas basal sound pressure was only 4 dB(A) and Leq increased in 11dB(A) between the suburban road and remote forest areas (fig. 4).

Population density of the pigeon *Columba* decreased near the suburban edge and showed a strong negative response to traffic density (table 6). Density of *Regulus* also decreased near the suburban edge, although it showed no significant response to noise levels (table 6). On the other hand, densities of *Cyanistes* and *Serinus* were positively correlated with noise levels (table 6). Densities of the remaining species were not significantly related with traffic density or noise levels (table 6).

After controlling for situation (road edge vs. interior) by partial correlation, population density of all species combined increased significantly near the suburban edge. Finally, community richness, diversity and equitativity showed a significant increase toward the suburban edge (table 6).

HABITAT HETEROGENEITY, TOPOGRAPHY AND ROAD PROXIMITY

The studied sites encompassed a relatively narrow altitudinal range (~ 100 m) within the Anaga laurisilva, and we considered that the altitude effect on bird community composition was negligible at the ecosystem scale (fig. 6). Mean slope was similar for hillsides and valleys in both edge and interior (fig. 7). Roads and

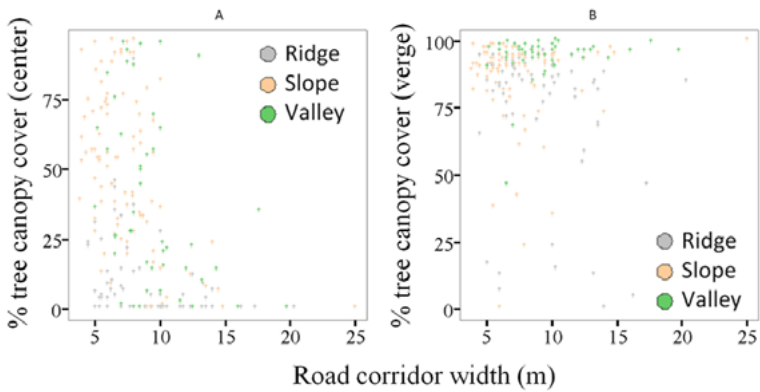


Figure 8. Effect of road width (asphalt lanes + open verges) on canopy cover [at the center of the road (A) and at 5 m from edge (B)] controlling for topography. Partial correlations: (A) $r = -0.456$, $p < 0.001$; (B) $r = -0.095$, $p = 0.183$.

road edges were wider in valleys and ridges, and narrower in hillsides (fig. 6, overall mean road width: 8.4 ± 3.3 m).

Grass cover within the road corridor was directly correlated with verge width. Ridges and valleys showed a denser grass layer than slopes (fig. 6). Rock cover increased significantly from ridges to hillsides to valleys, but only at forest interior (fig. 7). Litter cover was lower along ridge road edges than in other situations, but it did not differ between slopes and valleys nor between edge and interior (fig. 7). Tree cover over the road was denser on slopes (~45-50%) and valleys (~40%) than on ridges (~10%) (fig. 6). Tree canopy cover over the road center, and road width, were negatively correlated (fig. 8).

With only a few exceptions, the structure and floristic composition followed similar patterns of variation with topography when comparing edge and interior (fig. 9). Canopy height, cover, tree species richness, number of fleshy-fruited plant species, number of vertical vegetation strata, and number of trees with DBH > 10 cm increased from ridge to slope to valley, regardless of road proximity (fig. 9). Conversely, shrub cover and richness, stump density, and number of trees with DBH ≤ 10 cm decreased from ridge to slope to valley, and mostly regardless of road vicinity. Ridge habitats were an exception because shrub richness and cover, grass cover and density of trees with DBH < 10 cm were higher at forest interior than along road edges. Stump density (an indicator of intensity of selective wood extraction) was always larger near road edges than at forest interior.

A great heterogeneity was observed in bird abundance regarding the topographic pattern in interaction with road proximity (fig. 10). Abundance of 6 of the 8 most frequent species did not vary among topographic categories. *Columba* was more abundant in valley bottoms than on slopes or ridges, and in forest interior than at the forest edge. *Phylloscopus* was more abundant on hillsides



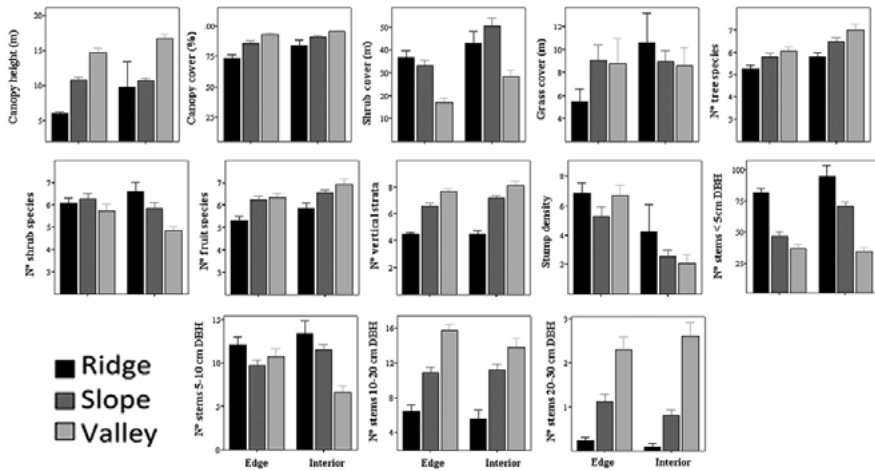


Figure 9. Variation in vegetation structure and floristic composition along the topographic gradient in laurisilva roads and interior areas.

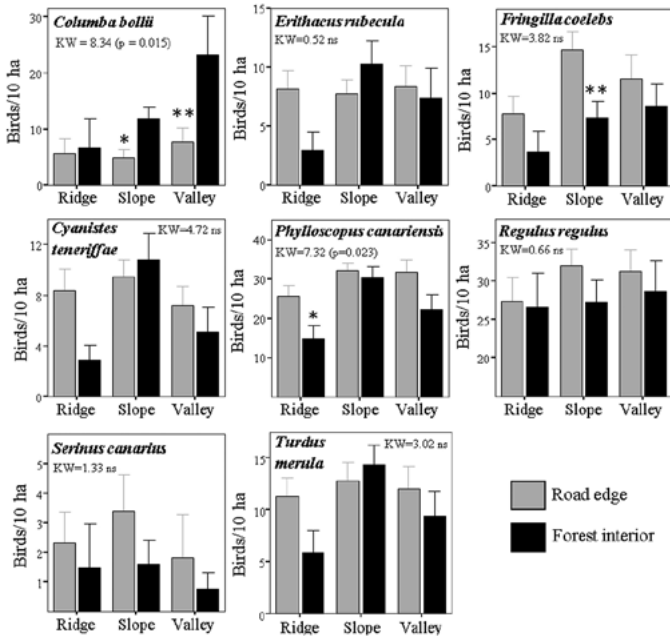


Figure 10. Variation in bird population density along the topographic gradient in laurisilva roads and interior. For each species: Kruskal-Wallis chi-square tests and p values are shown; ns = not significant ($p > 0.05$); significant differences between road edge and interior for each topographic category (Mann-Whitney's U, * $p < 0.05$; ** $p < 0.01$); the remaining edge-interior differences were not significant.

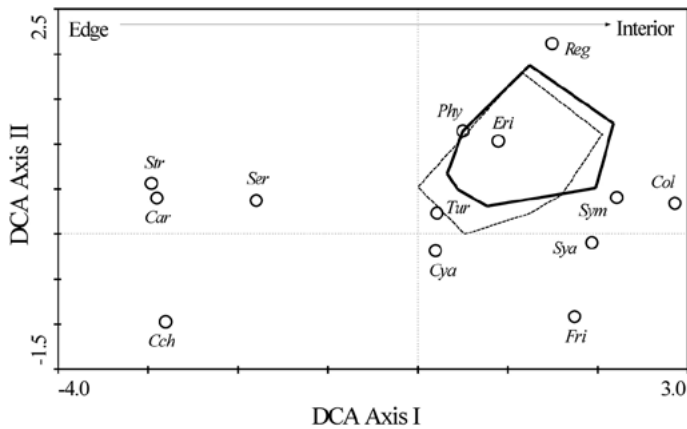


Figure 11. Detrended Correspondence Analysis (DCA) of the laurisilva bird community. Plot of species in the ordination space defined by the 2 first axes. Polygons comprise the sample space of road edges (dotted line) and interior (black line). Axis units are mean typical deviations (DT) of species turnover. Species codes as in fig. 2.

and valley bottoms than along ridges, where it was more abundant along road edges. *Fringilla* was more abundant at the edge and did not exhibit variation regarding topography. The remaining species presented higher population densities along road edges excepting *Erithacus*, *Cyanistes* and *Turdus*, which were more abundant at the interior of hillside forests.

VEGETATION GRADIENTS AND MULTIVARIATE ASSOCIATIONS

Forest edge and interior showed a high degree of overlapping in terms of bird species composition and abundance (fig. 11). The two first DCA axis described 40% of variance in the distribution of bird species, with the first axis indicating the most intense gradient (Axis I: -26%, Axis II: -14%; table 7, fig. 11). The small spatial segregation of samples between edge and interior is explained by the scarce separation of dominant species along the first axis (compare abundances in tables 3 and 5). Habitat generalists like *Phylloscopus*, *Cyanistes*, *Erithacus*, and *Turdus* had an intermediate position along the gradient. The first ordination axis sorted the edge-related species (*Chloris*, *Carduelis*, *Serinus* and *Streptopelia*). Both *Sylvia* species scored high mainly in marginal habitats. *Columba* exhibited a higher dependence of forest patches far from roads, as suggested by its high scoring on the first axis.

Direct gradient analysis (CCA) accounted for a significant contrast in habitat features between edge and interior. First and second axis explained 41.3 and 17% of the variance in the relationship birds-habitat (table 7, fig. 12). Axis I showed significant positive correlations with canopy tree species richness, canopy cover



TABLE 7. RESULTS OF DCA AND CCA ON BIRD ABUNDANCE AND 13 RELEVANT FEATURES OF HABITAT STRUCTURE. VARIABLE CODES AS IN TABLE 2. ONLY SIGNIFICANT CORRELATIONS ARE SHOWN FOR EACH AXIS, SORTED BY MAGNITUDE

DCA (SPECIES)	Axis I	Axis II
Eigenvalues	0.182	0.1
% cumulative variance	25.8	40
Gradient length	2.173	1.875
CCA (SPECIES-HABITAT RELATIONSHIPS)		
Eigenvalues	0.029	0.012
% cumulative variance	41.3	58.3
Species-habitat correlations	0.490	0.391
Habitat variables-axis correlations		
TreeSpp	-0.639	
CCover	-0.629	
CHeight	-0.465	
T20	-0.416	
GrassCov	0.405	
T10	-0.366	
ShrubCov	0.340	
Slope	0.328	
T30	-0.163	
ShrubHe		-0.593
T5		0.540
Stump		0.361
NStra		-0.344

($R^2 > 0.6$), height, density of stems ≤ 20 cm DBH and grass cover ($R^2 > 0.4$) (table 7). The density of stems ≤ 10 cm and > 30 cm DBH, average terrain slope and shrub cover had a weak significant influence (axis I) on bird abundance ($R^2 < 0.4$) (fig. 12). Axis II had higher scores in variables describing marginal forest conditions (taller shrub patches, higher density of stems < 5 cm DBH [$R^2 > 0.5$], diversity of vegetation layers and higher disturbance due to selective wood extraction of mainly stems < 5 cm DBH [$R^2 \sim 0.3-0.4$]). These factors were related to more dense vegetation next to road edges, where bird density was slightly higher, contrasting with interior mature stages largely preserved from human disturbance.



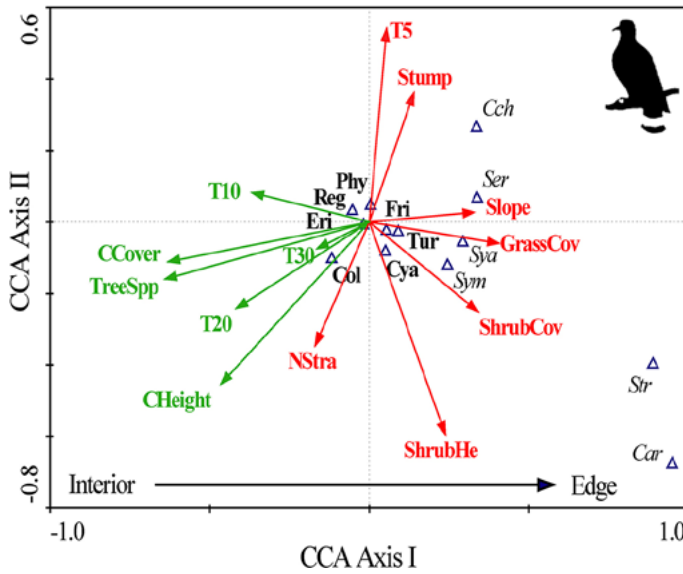


Figure 12. Canonical Correspondence Analysis (CCA) of the bird-habitat relationships.

Biplot of species/variables in the ordination space defined by the first 2 axis (table 7).

Arrows: direction of the most intense environmental change in the focal variable; its length is directly related to the importance in community structuring; its direction shows its degree of association to the respective axis; angles between arrows indicate correlation between variables (the smaller angle, the stronger correlation); the position of species regarding variables suggests habitat preferences. Species and variable codes as in fig. 2 and table 2. The following variables were excluded to avoid redundancy based on a previous PCA: RockCov, LittCov, Tm30, FruitSp, ShrubSp. The positive section of Axis I scored high in variables related to marginal habitats and secondary forest (red), which were in general more densely vegetated. The negative section of Axis I scored high in variables indicating more mature forest (green). Note the aggregation of dominant bird species (bold) near the axes coordinate origin. The variables showing a stronger correlation with Axis I were CHeight, TreeSp, CCover and T20 whereas ShrubHe, T5, Stump and NStra were related more strongly with Axis II (table 7).

MODALITY OF BIRD RESPONSES TO ROAD PROXIMITY AND HABITAT CONFIGURATION

The responses (Lowess regression curves) of species density to habitat gradients were very heterogeneous (fig. 13). *Erithacus* and *Regulus* exhibited clear unimodal responses along both axes. *Phylloscopus* displayed higher densities at intermediate conditions between edge and interior (fig. 12). *Columba*, *Fringilla*, *Cyanistes*, *Serinus*, *Streptopelia* and *Turdus* revealed lineal associations with different gradients. *Columba* responded negatively ($R^2=0.3$) to forest disturbance depicted by increases of Axis I (fig. 12). The remaining 5 species exhibited the opposite trend, positive responses to increases in the disturbance gradient (Axis I). *Fringilla* was

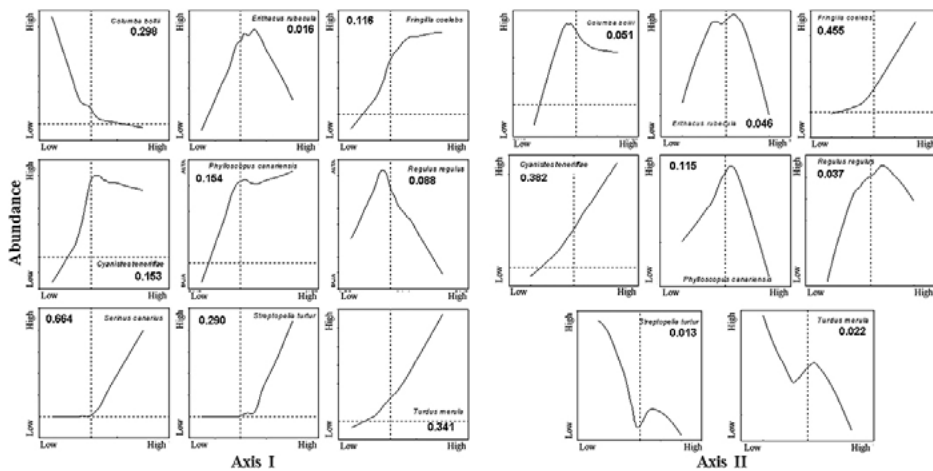


Figure 13. Species-habitat relationships. Locally-weighted regression functions (Lowess) on bird abundances along the environmental gradient defined by the CCA (table 7, fig. 11). Shown are R^2 values for each function. The R^2 for *Serinus canarius* on Axis II was 0 (no adjustment obtained).

associated to greater vegetation density and disturbance degree occurring along road margins (Axis II). *Cyanistes* showed a linear monotonic increase in abundance toward road edges. Both *Cyanistes* and *Fringilla* exhibited more intense responses to changes in forest structure with independence of road proximity (Axis II). However, *Serinus*, *Turdus*, and *Streptopelia* showed higher positive influence of road proximity (larger variance explained by Axis I).

DISCUSSION

RESPONSES OF THE LAURISILVA BIRD COMMUNITY TO ROAD PROXIMITY

Our results revealed that: 1) the general structure of the laurisilva breeding bird community changed relatively little in the vicinity of narrow forest roads; 2) regarding population density, 91% of the assemblage is formed by Passeriformes (only 2 insectivores equaled 50% of the overall density); with such a distinctively high dominance, it seems not surprising that the community profiles, species composition and abundance of different guilds were very similar between interior and road edges; any contrast could be ameliorated by generalized high densities of all principal species (especially of *Phylloscopus*); 3) although most species showed wide tolerance to road proximity, the palaeoendemic *Columba bollii* was characterized as the most interior-preferring species of the assemblage. Abundance of this pigeon decreased neatly near roads. Responses to road proximity of the two dominant passerines were



weakly positive (*Regulus*) or even moderately positive (*Phylloscopus*); this was also the situation for the rest of mostly habitat-generalist species (including passerines and *Streptopelia*); 4) moderate increase of bird population density along road edges remained consistent after controlling for the effects of traffic, noise, habitat structure and foraging behavior.

We found similar abundance and diversity indicators between road edges and interior in a previous study in Tenerife forests (Delgado *et al.* 2008). In coherence with this finding, most bird species showed only slight differences in abundance between road edges and forest interior. Only *Turdus* was more abundant along unpaved tracks than at forest interior or asphalt roads, whereas four birds (*Columba*, *Fringilla*, *Regulus* and *Serinus*) were more abundant at forest interior (Delgado *et al.* 2008).

Our results are consistent with the traditional hypothesis of increase of density and richness of bird populations at ecotonal zones (Odum 1971, De Graaf 1992). However, this occurs at the cost of reduced presence of species sensible to road edges, whilst gaining generalist elements near road margins. At a landscape scale, this would involve an overall reduction in richness, diversity, and singularity for the island laurisilva. Blair (1996) also found that the more sensitive native species were less frequent and abundant towards areas with a higher road proliferation and human use. However, richness, diversity and global bird biomass increased at the intermediate disturbance levels. The Anaga laurisilva would exemplify a similar situation, even when sensitive species (*Columba bollii*) responded negatively.

The laurisilva bird community could be divided into three classes regarding road tolerance. A first group is formed by a single, interior-preferring species (Bolle's pigeon). Apart from their status as palaeoendemics, these pigeons have several functional traits which distinguish them from the other bird species (Appendix 1). *Columba bollii* has a long incubation period, and a small clutch size (1 egg) involving higher risk of predation (Hernández *et al.* 1999, Martín and Lorenzo 2001). Rats are the chief nest predators of both *Columba* species in laurisilva (Hernández *et al.* 1999, Delgado *et al.* 2005). Road synergies with alien predators such as rats may induce losses in vulnerable birds. Rats are widespread in the laurisilva of Tenerife, occupying all vegetation layers (Contreras 1988, Hernández *et al.* 1999). In the Anaga laurel forest, rats exerted higher predation pressure along road edges than at forest interior, and along road margins on ridges and slopes than at ravine beds (Delgado *et al.* 2001). Breeding success in Bolle's pigeon has been found correlated with low density of bush understory, distance of nest to trunk and distance to inferior canopy (Hernández *et al.* 1999). Sparse understory and larger and taller trees are typical features of the interior patches of laurisilva. These findings are all consistent with our result of a higher abundance and activity of Bolle's pigeons at forest interior than near roads. At least for this forest-dependent species, large forest areas would ensure mature forest structure, high-quality nesting sites, food, and adequate distance from road disturbance.

The group of edge-preferring taxa (formed by *Sylvia melanocephala* and *S. atricapilla*, *Carduelis*, *Chloris*, *Serinus*, and *Streptopelia*) was more frequently found near road edges. Finally, a group of road-tolerant birds (*Cyanistes*, *Erithacus*, *Phylloscopus*, *Regulus*, *Fringilla*) can be defined, species with variable responses to



road vicinity. In this group, *Regulus* is the most forest-dependent and road-avoiding element, and *Phylloscopus* the most road-tolerant (coherently, it is also the most widely distributed passerine in the Canary Islands; Martín and Lorenzo 2001).

ROAD EDGE EFFECTS ON FOREST BIRDS FROM A BIOGEOGRAPHICAL PERSPECTIVE

Research on bird community responses to road edges has reported both absence and existence of edge effects in temperate forests. Large expanses of territory have been transformed into homogeneous agricultural land, where contrasting roadside vegetation is associated to high bird density and diversity (Forman *et al.* 2002a). Kroodsmá (1984) found similar densities along edges and interior of North American forests. Small and Hunter (1989) did not find changes in abundance and composition at forest-corridor ecotones. Hunter *et al.* (2001) found that birds of early successional stages or disturbance-dependent birds benefited from road edge use. Higher bird population densities have been described from abrupt edges in North America and Europe (DeGraaf 1992). Other works, however, have associated road proximity with negative effects on native and migrant birds (Ferris 1979, Rich *et al.* 1994). In agricultural land in Australia, most passeriformes responded negatively to disturbed road margins, because they offered low quality nesting and foraging sites and of refuge against predators (Lynch and Saunders 1991). Roads may favor generalist species depending on the type of traversed habitat (Meunier *et al.* 1999). Blair (1996) found that richness, diversity and global bird biomass increased at intermediate disturbance levels along a gradient of road density and human use. Persistence of bird populations of the forest-dependent species can be negatively affected by roads, as in Iberian pine fragments surrounded by agricultural matrix (Brotons and Herrando 2001).

As far as human-generated edges are concerned, a latitudinal gradient in sensitivity of the avifauna seem to occur. Tropical forests usually suffer net losses of density and diversity near edges (Bierregaard 1990, Báldi 1996, Canaday 1997, Watson *et al.* 2004), whereas temperate forests frequently experience general increases (Wilcove *et al.* 1986, Santos and Tellería 1998). Some induced forest edges, however, experience increases in open-canopy or edge species whilst interior species avoid these zones (Whitcomb *et al.* 1981, McWethy *et al.* 2009). In tropical forests overall biodiversity and climatic homogeneity over large spatial scales are comparatively higher than in temperate zones, and this would be related to differential sensitivity of birds to proliferation of artificial edges (Dale *et al.* 1994). On the contrary, in temperate ecosystems human influence is secular, both natural and artificial fragmentation is intense and the landscape heterogeneous (Harris 1984, Báldi 1996), features that would increase presence of species of wider ecological amplitude. The laurisilva bird community shows mostly features typical of a temperate-zone assemblage. Many bird species shared by the Canaries and the Palearctic have similarly weak density responses or even edge-proneness (Carrascal *et al.* 1992, Moskát and Waliczky 1992, Meunier *et al.* 1999, Brotons and Herrando 2001, Carrascal and Palomino 2005, Morelli *et al.* 2014).



Several factors may be postulated to explain the moderate to low road edge effect appreciated in this bird community. Firstly, insularity is related with fewer species, increases in average density per species (which compensates for absence of competing taxa), interannual stability in species composition, species richness and niche expansion (Báez 1992, Oliveira *et al.* 1998, Whittaker & Fernández-Palacios 2007); species impoverishment and niche expansion have also been suggested in other studies (Carrascal *et al.* 1992). These processes could provide adaptive advantages to many bird species in the fragmented laurisilva. Secondly, higher availability of marginal habitats coinciding with high prevalence of species related to such environments (Brotons and Herrando 2001).

From the review by Báldi (1996: p. 165) on anthropogenic edges in mainland temperate areas, 30-75% (mean: ~60%) of species was indifferent to edges, 34% was formed by edge species and only 10% were strictly interior species. The overall response of the avifauna of subtropical laurisilva is consistent with this geographical pattern. In our study, out of 13 species, 12 (~92%) showed indifference or appetence for road edges. We neither found a strong contrast between vegetation structures used by birds along roads or interior (fig. 12). In sum, this result is consistent with a majority of species showing some affinity or/and ample limits of tolerance for narrow road edges (Delgado *et al.* 2008).

INTERACTION OF TRAFFIC AND OROGRAPHY: IMPLICATIONS FOR LAUREL FOREST BIRDS

Many factors are involved in appetence for or avoidance of roads by birds. Negative effects of roads on bird populations have been most frequently attributed to traffic noise and mortality (Forman *et al.* 2002a). This depends on the type of habitat, species vulnerability, requirements and tolerance to road disturbance, and on the magnitude, extension and chronicity of impacts derived from road use (Jaeger *et al.* 2005). Noise produced by busy roads has been correlated to large reductions in abundance of breeding bird populations (Reijnen and Thissen 1987, Reijnen *et al.* 1997, Forman *et al.* 2002b, Parris and Schneider 2008). Along with induced topographical complexity, road corridors on grassland introduce prominent and diverse vegetation elements attracting a variety of bird species, leading to local increment in species richness and abundance, especially along the quieter and narrower roads (Forman *et al.* 2002). It has been also suggested that birds tend to avoid infrastructures more consistently in open habitat than in forests (Benítez-López *et al.* 2010).

Orographic complexity in the laurisilva is a shaping factor in vegetation pattern and the associated bird assemblages (Martín *et al.* 2000). Levels of traffic noise would be strongly modulated by relief and remoteness in highly convoluted mountain roads such as in our study area. Noise avoidance and aversion to the road right-of-way and passing cars by birds, may be ameliorated by screening of dense vegetation, steep slopes and convoluted road design adapting to relief (Wolf *et al.* 2013).

Among causes adduced to explain why birds avoid roadsides include sing distortion and stress (Reijnen and Foppen 1994, Reijnen *et al.* 1995, Parris and



Schneider 2008). These pressures reduce habitat quality of breeding insectivorous passerines (eg, *Phylloscopus trochilus*, Reijnen and Foppen 1994). Reijnen *et al.* (1997) found that 33 of 45 forest species (73.3%) decreased their population densities near highways. These authors found that *Regulus* and *Fringilla* were negatively affected by noise. In another study, however, *Turdus* and other birds did not experience reductions due to traffic noise (Reijnen and Thissen 1987). Brotons and Herrando (2001), in *Pinus halepensis* fragments found lower occurrence of forest species (both specialist and generalist birds) near highways, although the effects were weaker for secondary roads. In our case, most bird species (or their close relatives) shared with mainland areas, did not show significant negative responses to traffic noise.

Some roads have been suggested to offer suitable nesting sites in their vicinity that could be scarce in the adjacent habitats, and this factor could compensate reductions in habitat quality due to traffic (Morelli *et al.* 2014). Increases in species richness along highway edges with forest and cultured land have also been found even with traffic intensities of 25,000-52,000 cars/day (Meunier *et al.* 1999). Environmental factors such as roadside vegetation structure, quality of adjoining habitats, or topography would affect noise levels and other road-related disturbances acting on birds (Reijnen *et al.* 1997). For lower noise pressures, some authors have not observed negative effects on bird abundance. Under a 36-58 dB(A) threshold in forests, bird abundance was not affected, though it was reduced 35-100% when noise levels exceeded 58 dB(A) depending on species (Reijnen *et al.* 1997). In our work, traffic intensity was lower (averaging ~1229 vehicles/day) than those recorded in most studies (table 1). Sound levels were nevertheless relatively high on all the segments, and peak values were recorded even at the most remote forest stands along the road transect. Notably, noise levels were negatively correlated with abundance of the two most neatly forest-dependent species in these laurel forests (*Regulus* and *Columba*) although the negative response of the endemic pigeon was the most intense. These results add evidence of negative impact of traffic noise amplitude on passerines and other birds (Weiserbs and Jacob 2002, Peris and Pescador 2004).

The Bolle's pigeon may be considered a key frugivorous bird species in the laurel forest (Martín *et al.* 2000, Marrero *et al.* 2010). Its presence and abundance indicates the degree of conservation of the forest and of other taxa, largely due to its fruit consumer role. Roads in this study reach forest stands far from urban areas, facilitating human accessibility to critical areas for such sensible birds. At the same time, forest roads extend edge effects at local and regional scales, inducing additional disturbances of forest areas (road and trail construction, edifications, trampling, dumping, tourism, noise, illegal hunt, among other factors; Martín *et al.* 2000), as shown from other places (Heilman *et al.* 2002, Weiserbs and Jacob 2002, Riitters and Wickham 2003). This cumulative process is clearly harmful for vulnerable birds like *Columba*, which demand large (or at least quiet, undisturbed smaller forest patches) and exhibit forest dependence for mating, breeding and foraging (Canaday 1997; Martín *et al.* 2000). In contrast with most small to medium-sized forest birds, our results suggest, from several angles, detrimental impacts on the frugivorous pigeons next to the suburban edge in Anaga. Traffic intensity, noise level, suboptimal altered vegetation structure and composition (lower height, cover,



tree diversity, and higher understory density from logging) are the main suggested factors of disturbance. Other potential road impacts which could create negative synergies with the above mentioned are the alteration of roadside microclimate, alteration of vegetation structure and composition, nest predation, and collision with vehicles. Relatively high traffic noise levels and road-related disturbances to populations of some forest-dependent species may be produced even by narrow roads in these island forests.

Some of the limitations of our study refer to palaeoendemic pigeons (focused on the more abundant *Columba bollii* in our study area). We have not included here the detailed use of foraging space or daily and seasonal activity patterns (mating and foraging activities), which include extensive movements of Bolle's pigeons (Martín *et al.* 2000, Martín and Lorenzo 2001). These columbiforms are regular users of the roadsides in their search for food and water, especially in the early or late afternoon when there is little or no traffic, and not unfrequently, they use road and trail edges for nesting. The use of habitat by pigeons can be significantly influenced by variation in human presence and motorized traffic, which increases on weekends in these forest areas due to tourism. Studies are needed on the use of the habitat and its spatio-temporal variation depending on the incidence of traffic and the human presence and accessibility to the protected pigeon habitats.

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