



Road encroachment mediates species occupancy, trait filtering and dissimilarity of passerine communities

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ARTICLE INFO

Keywords:

Transportation infrastructures
Species loss
Community composition
Habitat degradation
Land sharing/land sparing
Road density

ABSTRACT

Assessing the road effects on biodiversity is challenging because impacts may depend on both wildlife responses to roads and on the spatial arrangement of roads. We questioned whether an increase in road encroachment leads to significant changes in species occurrence and community composition. Using a large citizen-science dataset of point-counts performed throughout Iberian Peninsula, we modelled the effect of road density on the occurrence of common birds ($n = 78$ species), while accounting for potential confounding effects of environment and survey effort. We then tested if species' occurrence patterns would be linked to specific traits related to the ability to cope with human presence. Finally, we assessed how road density affects the community compositional dissimilarity. We estimated 36 (46%) and 18 (23%) species to be negatively and positively affected by roads, respectively. Increased road encroachment was positively related with urban dwelling and fecundity, and negatively related with nesting on the ground. Furthermore, increasing road density translated into an increasing community compositional dissimilarity, mostly due to species turnover. Overall, we found that different species-specific responses to roads translate into changes at the community level. Landscape and road-network management should be conceived acknowledging that roads are contributing to biodiversity changes. As so, building upon the concepts of land sharing/land sparing, conservation actions should be tailored according to the different species responses e.g., road verge management targeting species having a positive relation with road density; and compensation actions targeting species showing a negative response toward roads.

1. Introduction

Roads have become the most conspicuous infrastructure in the landscapes of developed countries (Ibsch et al., 2016; Laurance and Balmford, 2013). These infrastructures are known to promote direct negative impacts on biodiversity, including roadkill, barrier and edge effects, pollution and perturbation (Trombulak and Frissell, 2000; Van der Ree et al., 2015). Such impacts may foster local population depletion and a reduction of habitat quality (D'Amico et al., 2016; Santos et al., 2013). Yet, roads may also benefit some species, for example by providing foraging habitat for small mammals and perching structures for hunting and nesting for birds (Ascensão et al., 2012; Morelli et al., 2014). As such, it is likely that an increase in road encroachment affect the composition of communities and, consequently, the different ecological processes and ecosystem functioning. We refer to road encroachment to describe the advancement of roads into non-urban

areas, involving habitat change and increased human presence (e.g., urban sprawl and agriculture activities).

Improving our understanding on the effects associated to road encroachment on species and communities is therefore important for both road and landscape management, as well for biodiversity conservation. Yet, while we know that roads affect the occurrence of several species (Cooke et al., 2020b; D'Amico et al., 2016; Santos et al., 2016), there is still a gap of knowledge regarding how they affect the composition of ecological communities, which is especially relevant given the rarity of studies on road effects focusing on large extents, from landscape to global scales, despite their value to support decisions for planning road mitigation measures (Barrientos et al., 2021). Here, we questioned whether road encroachment leads to significant changes in species occurrence, and whether those changes are linked to specific traits related to perturbation sensitiveness and therefore acting as filters and increasing the community compositional dissimilarity.

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We focused our study on birds, and particularly on passerines (i.e., the order *Passeriformes*), as these species are key components of ecosystems by providing a multitude of services, being pest predators, pollinators or seed dispersers, among others roles (Whelan et al., 2008), as well important indicators of environmental health and ecosystem integrity (Fraixedas et al., 2020). Also, passerines are a widely distributed and well-studied group, especially by systematic point-count surveys, thus providing suitable data for large-scale analyses and inferences. On the other hand, human activities have greatly impacted bird populations, with estimates of 20–25% of global reduction in the number of bird individuals from pre-agricultural times (Gaston et al., 2003), and a 27–30% decline from 1970s abundance in North America (Rosenberg et al., 2019). In Europe, there is also mounting evidence of ongoing farmland bird decline and compositional change (Bowler et al., 2019; Burns et al., 2021; Donald et al., 2001; Inger et al., 2015). There is growing evidence that roads may be contributing to this general decline (Cooke et al., 2020b; Santos et al., 2016). Consequently, passerines are not only suitable study species due to methodological issues, but they are also an ecologically relevant group globally threatened by roads.

We tested the following three hypotheses: H_1) species are differentially affected by roads, and therefore their probability of occurrence can be negatively, neutrally, or positively associated to local road density; H_2) the effect of roads on species is not random, being instead linked to a prevalence of traits, overall indicating a process of filtering; and H_3) such specific responses lead to changes in community composition dissimilarity. We expected to observe a higher number of species avoiding areas with higher road encroachment, given the associated threat of roadkill and increased perturbations (e.g., pollution or direct disturbance by human presence). Still, we expected species able to cope with human presence (e.g., synanthropic species) to be more prevalent in areas with a higher road density. As such, some traits related to resource exploitation and ability to cope with human activities may allow some species to take advantage of road presence, and therefore be more prevalent in areas with higher road encroachment. Furthermore, such responses were expected to increase the compositional dissimilarity when comparing areas with high and low road density, respectively. Yet, it was not easily foreseen if such increased community dissimilarity would be dominated by species turnover (i.e., species replacement) or by the loss or gain of species between roadside and roadless communities (i.e., species nestedness).

We focused on a large and coherent biogeographically unit, the Iberian Peninsula, covering nearly 600,000 km² and including regions of considerable physiographic and climatic heterogeneity. It is a discrete, relatively isolated biogeographical unit, as its connection to the European mainland is crossed by the Pyrenean Mountain chain. These characteristics make this region particularly suitable for large-scale ecological studies. Yet, our framework can easily be replicated in any other region and taxa, producing key information for planning mitigation measures.

2. Methods

We analysed the data from the eBird (Sullivan et al., 2014; Wood et al., 2011), one of the most comprehensive and successful citizen-science platforms, which permitted to compile a geographically wide knowledge over a relevant ecological group. We modelled the species occurrence (presence/absence), bird traits and community compositional dissimilarity in relation to road density, while accounting for other predictors that may influence bird occurrence, namely land use and climate. We used QGIS 3.12 (QGIS.org, 2020) and R 3.6.3 (R Development Core Team, 2020) for all data preparation and analyses.

2.1. Bird data

The citizen-science platform eBird is a web-enabled community of bird watchers that aims users to collect, manage, and store their

observations in a globally accessible unified database (available in URL: ebird.org), therefore providing a large and comprehensive open dataset on bird species occurrence (Sullivan et al., 2014; Wood et al., 2011). Importantly, contributors upload the information regarding the sampling effort, including time and number of observers, survey method (e.g., point-count or walking transect), location (coordinates) and date, together with the species information, allowing data to be used in ecological research (Johnston et al., 2020). We downloaded eBird datasets for Iberian Peninsula (Portuguese and Spanish continental territories, hereafter referred as Iberia, Fig. 1), for ten years, between 2011 and 2021.

2.2. Road data

We compiled information of road spatial distribution from OpenStreetMap (OSM) using the R package ‘osmdata’ (Padgham et al., 2017). Nearly all roads have been digitized for European countries (Barrington-Leigh and Millard-Ball, 2017). We retained only the paved roads (i.e., those classified in OSM as ‘motorway’, ‘trunk’, ‘primary’, ‘secondary’, and ‘tertiary’), and respective ‘links’ (Fig. 1), as these have medium/high traffic volume and thus are more likely to have stronger positive (i.e., attraction) or negative (e.g., population depletion or avoidance) effects on birds (Cooke et al., 2020b).

2.3. Environmental data

We compiled information for a set of environmental variables that may influence the distribution pattern of bird species, namely land cover and altitude (Table 1). Environmental variables were chosen based on bibliography reporting the importance of land cover and climate as determinants of bird occurrence (Howard et al., 2020; Morelli et al., 2013). Altitude is known to correlate important climatic patterns, notably temperature and precipitation, while also affecting species distribution (Irl et al., 2015). We used the Digital Elevation Model from Copernicus (DEM; Table 1) to obtain the altitude layer, which was aggregated to 1 × 1 km resolution (averaging values).

Land cover was obtained from Copernicus' CORINE land cover, from which we considered the nine dominant classes, covering >70% of Iberian Peninsula (Table 1). We aggregated all CORINE classes related to urban areas (classes 111 to 142 of CORINE), which were combined into a single Urban layer. This Urban layer was used to remove point-counts performed in dense urban areas (see ‘Point-count data pre-processing’ below). For each land cover class (including Urban), we created an individual layer of presence/absence. As the CORINE has a 100 m resolution and bird species are likely to be influenced by land cover at larger extents, we also aggregated each individual CORINE class layer to 1 × 1 km resolution, in which each raster cell represents the proportion of cover (0–100%).

We further included the information on tree cover density from Copernicus (Table 1), as a measure of vegetation structure (ranging from 0 to 100% of tree cover), and the information on water proximity, as it may affect species occurrence (D'Amico et al., 2015). For this water distance layer, we used the information on water presence from the high-resolution layer ‘Water and Wetness’ from Copernicus (Table 1). We converted this layer to presence/absence of water and calculated the distance for any cell that contained water. Both tree cover density and water distance were resampled to match the same extent and resolution (1 × 1 km) as the previous layers.

We then ran a Principal Component Analysis on these environmental predictors (CORINE except Urban, DEM, water distance and tree cover density) to reduce the multi-dimensionality and the correlations among environmental variables. We preserved the first six principal components (raster layers), which altogether retained 76% of variation, and were used in following analyses (Supplementary material S1).

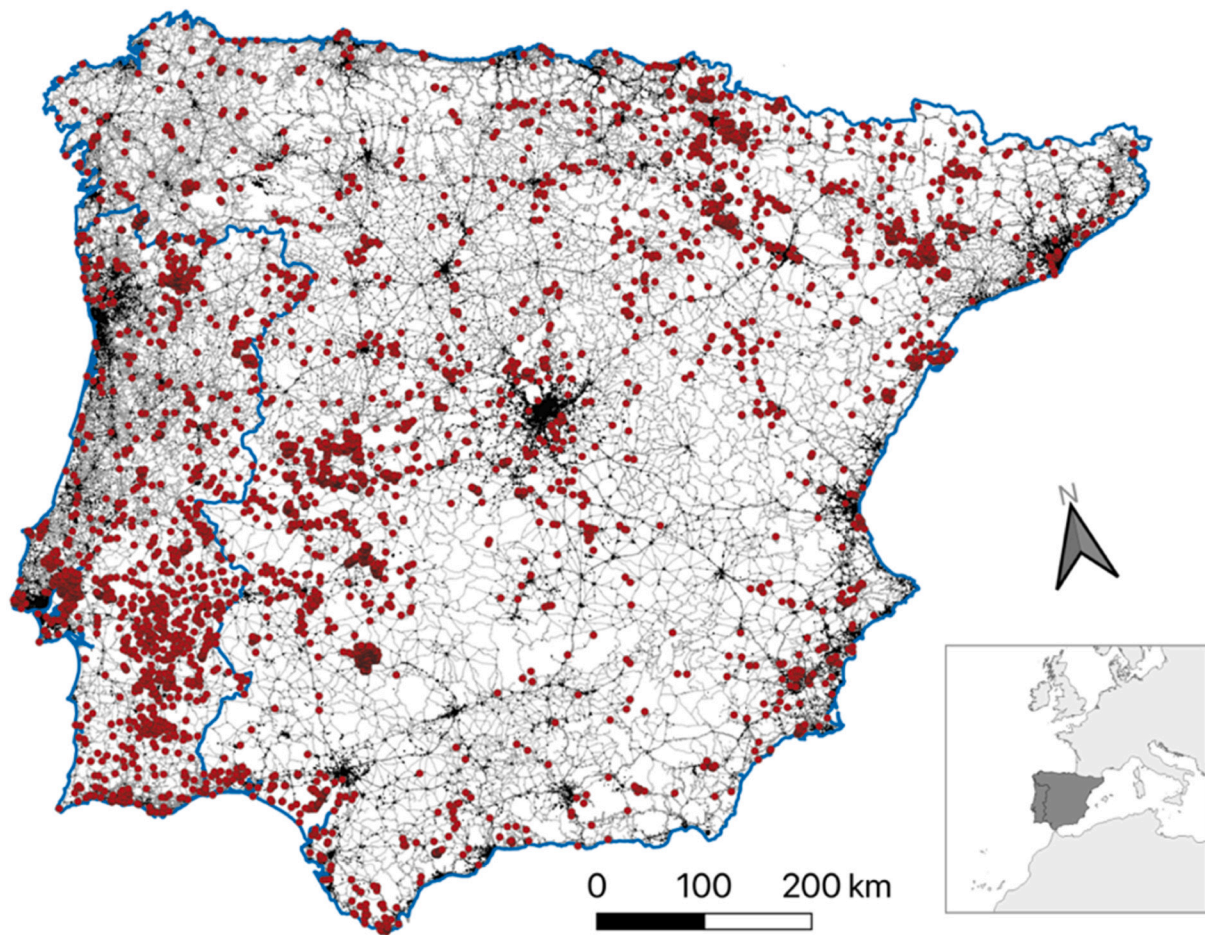


Fig. 1. Point-count location (dots) in Iberian Peninsula (dark area in inset) used in analyses. Black areas and lines stand for major urban areas and paved roads, respectively. Roads were extracted from OpenStreetMap (OSM).

2.4. Data analysis

2.4.1. Point-count data pre-processing

We filtered the eBird data keeping only the complete checklists (a complete checklist is any eBird list where birding is the primary purpose, and every species is identified to the best of surveyor ability), performed using the protocol “stationary count” (point-counts), with the duration of 5 to 15 min, and by up to four observers. Most point-counts in our dataset (87% of total) were performed by a single observer for 5 min (43%), 5–10 min (27%) and 10–15 min (17%).

We restricted our analysis to passerines as these species are more likely to be recorded and targeted for while performing point-count surveys (Bibby et al., 1992). As the bird community changes significantly between breeding and non-breeding seasons, and roads probably affect resident species differently during these periods (e.g., when choosing nesting sites), we opted to filter the data to consider only point-counts performed during the breeding season (from March to June). We further filtered the dataset to include surveys performed during the morning period (between 5:00 and 11:59 am), as in this period all songbirds are more active and therefore more likely to be detected. This pre-processing allowed us to keep surveys with known survey effort and performed with a relatively similar sampling protocol across the entire study area. It also provided high confidence that the records reported were obtained on the location reported (point-count), reducing the probability of being recorded during a travelling census (i.e., crossing different habitats and distance to putative roads).

Each retained point-count site was then characterized according to the six principal components of environmental information by

extracting the corresponding value of each layer at the survey site. We discarded those point-counts performed in areas with >20% of urban area, as bird communities inhabiting more dense urban areas are exposed to several human-related pressures (Callaghan et al., 2019; Maklakov et al., 2011; McKinney, 2006) which, together with the existing higher density of roads, could potentially confound the effects of road encroachment. Also, as the detectability of birds can be affected by the proximity of roads with high traffic volumes (Cooke et al., 2020a), we further discarded those point-counts carried out close (<50 m) to a main road (highway, trunk and primary, and respective links). There is a low effect of low frequency background noise (traffic) on the surveyors' ability to detect birds at >50 m (Pacifiçi et al., 2008).

For each remaining point-count site, we calculated the road density by summing all paved road segments intercepting a 1 km buffer radius from the point-count site. We choose this distance assuming that most significant road-effect zones span within 1 km from paved road (Forman and Deblinger, 2000). For each point-count event, we calculated the survey effort as number of observers \times survey time.

In order to assess whether the point-counts covered the environmental variability in the Iberian Peninsula, we compared the density plots on environmental information obtained at the location of the point-counts with that obtained in 5000 random locations using density plots (Supplementary material S1).

2.4.2. Road effects on species occurrence

To test if species are differentially affected by roads (H_1), we assessed the relationship between the species' presence/absence and the road density and environmental predictors, using Generalized Linear Models

Table 1

Road and environmental information considered to examine how roads affect the bird occurrence.

| Name and source | Observations |
|---|---|
| Environmental information | |
| Digital Elevation Model https://land.copernicus.eu/image-ry-in-situ/eu-dem/eu-dem-v1.1 | Year 2016. Resolution of 25 m. |
| CORINE land cover https://land.copernicus.eu/pan-europe-an/corine-land-cover/clc2018 | Inventory of land cover with 44 classes. Year 2018. Resolution of 100 m. Main classes here considered (% of cover): Non-irrigated arable land (18), Broad-leaved forest (10), Coniferous forest (9), Sclerophyllous vegetation (8), Transitional woodland-shrub (7), Natural grasslands (6), Agro-forestry areas (5), Permanently irrigated land (5), Olive groves (5), overall covering >70% of Iberia. All urban related classes were aggregated into a single Urban class. |
| Forest Cover Density https://land.copernicus.eu/pan-europe-an/high-resolution-layers/forests/tree-cover-density/status-maps/2015 | Level of tree cover density in a range from 0 to 100%. Status map for 2015. Resolution of 100 m. |
| Water distance https://land.copernicus.eu/pan-europe-an/high-resolution-layers/water-wetness/status-maps/2015 | Distance to water bodies (water and wet surfaces). Status map for 2015. Resolution of 100 m. |
| Road information | |
| Paved road density OpenStreetMap via R environment (Padgham et al., 2017) | Density of paved roads. We used a custom R code with the package 'osmdata.' |

(GLM) with binomial error and logit link function. Road density was scaled to allow comparisons between models estimates for this variable. As one third of the point-count sites were surveyed on more than one occasion, we aggregated the information from the different surveys retaining all registered species (presences) and summing all survey effort. Total survey effort was included in GLMs as an offset (log-transformed). Importantly, for each species, we only considered those point-counts performed where the species is resident year-round or breeds, which was assured by overlaying the point-count locations (with presences and absences) with the corresponding range distribution as compiled by the BirdLife International (data retrieved in May 2021). We only considered those distribution polygons in Iberia where species are known to occur or breed during the considered period (March to June). Before analyses, we searched for collinearity between road, environmental information (the six principal components), and survey effort using Pearson correlations. All pairs of variables had Pearson's $|r| < 0.5$ and therefore no variable was discarded.

We only considered those native species recorded in at least 30 distinct point-count sites to guarantee sufficient model discrimination power (see Table S1.1). Model discrimination power was assessed by the area under the receiver operational curve (AUC). For each species, the coefficient of the Road variable and its 95% confidence interval (CI) of the respective GLM were used to classify the species with respect to its response to roads as follows: as 'negatively' or 'positively' associated with road density if the CI was below/above zero, respectively, and as 'neutral' if zero was within the CI. We further calculated the Nagelkerke's pseudo- R^2 (Nagelkerke, 1991) of the full model, as well for the models without the environmental variables and for the model without the road information. We used these three values to estimate the relative importance of the road information alone in explaining species occurrence patterns, using a variance partitioning procedure (Borcard et al., 1992), as implemented in 'modEvA' R package (Márcia Barbosa et al., 2013).

2.4.3. Road effects on trait diversity

To test if the species' occurrence patterns would be linked to specific traits related to the ability to cope with human presence and activities (H_2), we considered six ecological traits corresponding to major differences in bird life strategy, grouped into three main trait categories: *Morphological attributes*, *Environmental tolerance*, and *Resource use*.

For *Morphological attributes*, we analysed the body mass as this trait is related to many others physical attributes, namely height or wingspan. We expected that larger species would be less frequent in areas with higher road encroachment, as many of them are more sensitive to roadkill and consequent population depletion (Santos et al., 2016). We complemented this with analysis using the hand-wing index, widely adopted as a proxy for flight efficiency and dispersal in birds, obtained from Tobias et al. (2022), expecting that those species having higher index values (higher flight manoeuvrability), such as swallows, to be more common in areas with higher road encroachment. We also analysed the brain mass, using the residuals of the linear model relating brain volume and body mass, given the high correlation between both traits (Pearson's $r > 0.8$). It has been shown that brain mass correlate with several measures of behavioural flexibility and ability to survive in novel ecological conditions (Callaghan et al., 2019; Fristoe et al., 2017; Maklakov et al., 2011). We therefore expected a positive association between road encroachment and brain mass.

For traits related to *Environmental tolerance*, we analysed the ability to thrive in cities (city dwelling or urban tolerance). We expected road encroachment to be related to an increase of city dwellers in rural areas (McKinney, 2006). We also tested if road encroachment could filter species nesting on the ground, expecting that higher road encroachment refrain such species to occur in the breeding season, given their vulnerability to nest predation, particularly of domestic cats associated to humans (Pita et al., 2009; Polak et al., 2013). Related with nesting behaviour, we further tested if the bird fecundity was associated with the road encroachment, expecting that species with higher fecundity, to be more common in areas with higher road encroachment, given the higher mortality risk therein due to roadkill. Fecundity was measured as the average number of eggs produced per clutch (Lislevand et al., 2016, 2007).

Finally, for *Resource use*, we analysed the diet and the foraging behaviour. Birds feeding on invertebrates are likely to have higher visual acuity (Tyrrell and Fernández-Juricic, 2017) and therefore be able to better perceive incoming vehicles. Also, road verges may have vegetated areas with low management intensity, particularly when compared to intensive agricultural areas (Ascensão et al., 2012), thus benefiting invertivorous birds due to higher invertebrate abundance (Muñoz et al., 2015; Villedemey et al., 2018). Hence, we expect invertivorous species to be more common with increasing road encroachment. Likewise, the foraging behaviour was expected to affect species' responses to road encroachment, with those species spending more time foraging at the ground level avoiding higher road encroachment due to higher human activity therein.

For each individual trait considered, we built different phylogenetic regression models, relating the coefficient of the road variable obtained in the GLM as the response variable and the trait value per species as single predictor. Phylogenetic regression models allow controlling for phylogenetic relatedness, as related species tend to share many traits due to shared evolutionary history, and therefore cannot be used in statistical analysis as truly independent observations (Paradis et al., 2004). For body mass, brain mass (log transformation), diet (arcsin transformation), and foraging (arcsin transformation), hand-wing index and fecundity, we used phylogenetic linear models; for ground nesting and urban tolerance we used phylogenetic logistic regression models. We only considered those species previously classified as being 'negatively' or 'positively' associated to roads to reduce the nuisance from 'neutral' responsive species, and therefore increase the chance of detecting significant differences.

We replicated the phylogenetic regression models, for each trait,

across 100 random and equally plausible phylogenetic trees (replicates) to evaluate the consistency of the relation between road response and each trait, as a sensitivity analysis. The distributions of the 95% confidence intervals of the regression coefficients of each trait, per replicate, were used to classify the association of the road responsive value and each trait (positive, negative, or neutral), per replicate. Phylogenetic trees were based on the Ericson backbone (Ericson et al., 2006) and obtained from the BirdTree (Jetz et al., 2012). Phylogenetic regressions were performed using the R package 'phylolm' (Tung Ho and Ané, 2014) (see Supplementary material S3 on phylogenetic regression models and compiled trait data).

As an outcome of the phylogenetic models, we searched for 'super-tolerant' and 'super-avoider' species toward roads. Super-tolerant species were those bringing together the traits most associated with road surroundings. On the other hand, super-avoiders were all the species bringing together all the traits related to road avoidance.

2.4.4. Road effects on community dissimilarity

To test the effect of roads on community dissimilarity (H_3), we selected paired point-counts, in which each pair had one point-count performed in a roadless area (i.e., no paved roads in a radius of 1 km), and one point-count nearby having paved roads within that buffer radius. The selection of pairs of points obeyed to the following sequential rules: first, for each roadless point-count (randomly selected), we searched for a roaded point-count nearby (i.e., within 1100 m radius). If more than one neighbour existed, we randomly selected one site. If there was no neighbouring site, we increased the search radius by 100 m. This procedure was repeated until at least one neighbouring roaded point-count was selected or the search radius reached a maximum of 2000 m, so that the roadless point-count location would be beyond the road-effect zone distance while ensuring similar environmental conditions. Each point-count location was used in only one pair of points, to reduce pseudo-replication issues.

There are two potential ways in which road and roadless species assemblages can be 'different': by species replacement (i.e., turnover), with the substitution of species in one site by different species in the other site, and by species loss or gain, which implies the elimination or addition of species in only one of the sites, and leads to the poorest assemblage being a strict subset of the richest one (i.e., nestedness) (see Baselga, 2010). We applied this approach for partitioning the total Sørensen dissimilarity into the two components, obtaining the dissimilarity derived solely from turnover and the dissimilarity derived from nestedness, allowing us to assess which process dominates eventual changes in communities. Following Baselga (2010), the Sørensen dissimilarity index (β_{sor}), Simpson dissimilarity index (turnover, β_{sim}) and nestedness (β_{nes}) are formulated as:

$$\beta_{sor} = \frac{b+c}{2a+b+c}; \beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)}; \beta_{nes} = \frac{\max(b,c) - \min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)},$$

where a is the number of species common to both sites, b is the number of species that occur in the first site but not in the second and c is the number of species that occur in the second site but not in the first. Therefore, the dissimilarity measure accounting for all aspects of beta diversity can be partitioned into two additive components accounting for pure spatial turnover and nestedness: $\beta_{sor} = \beta_{sim} + \beta_{nes}$. Dissimilarity metrics were calculated using the R package 'betapart' (Baselga and Orme, 2012).

We further used the total Sørensen dissimilarity and their components (turnover and nestedness) as response variables in three beta regression models. The difference in road density across each pair of point-counts was used as a predictor. To further control for environmental and survey effort differences across the pairwise points, the models also integrated information on: i) the Euclidean distance

between sites, ii) the distance between the six PCA components, and iii) the difference in survey effort. The distance between the five PCA components were computed as $\sqrt{\sum_{pc=1}^6 (x_i - y_i)^2}$, where pc are the principal components. Beta regression models were built using the R package 'glmmTMB' (Brooks et al., 2017).

3. Results

Our dataset comprised 131 bird species, recorded during 9602 survey events in 4568 unique point-count sites (see Table S2.1 in Supplementary material S2 for species names and totals). The comparisons suggested that the point-count sites generally encompassed the variability of the predictors considered across the study area, although point-counts were overall closer to roads and had higher road density, when compared to random points. Likewise, point-counts seemed to have been carried out in general closer to water points (Supplementary material S1).

3.1. Road effects on species occurrence

We built occurrence models for 78 focal species (species recorded in at least 30 sites within their known range area according to the BirdLife International). These models achieved a mean \pm SD AUC of 0.74 ± 0.06 (range: 0.61–0.88), representing a reasonable discrimination power across the models (Metz, 1978). Nearly half of these species ($n = 36$, 46%) were classified as being negatively affected by roads (such as the Iberian grey shrike *Lanius meridionalis* and Dartford warbler *Currucundata*), while one quarter (18, 23%) were classified as being positively affected by roads (such as the Eurasian blackbird *Turdus merula*), and 24 (31%) as neutral (Fig. 2). The estimate on variance explained were low across species (mean \pm SD: 0.15 ± 0.10). Yet, the road information was responsible for a considerable amount of the explained variation, being $11.3 \pm 9.2\%$ for those species showing a negative effect and $16.9 \pm 20.1\%$ for those showing a positive effect. For neutral species, the variance explained by road information was nearly zero.

3.2. Road effects on trait diversity

The individual phylogenetic models suggested that increased road encroachment is positively related with a higher prevalence of urban dwellers and negatively related with the occurrence of species nesting on ground (the proportion of replicates having CI overlapping zero was zero; Fig. 3D, E). Results further suggested that road encroachment may be somehow positively associated with higher fecundity, as all the estimates across replicates were positive and away from zero and the CI of 53% of replicates did not cross zero (Fig. 3F). There was no evidence for an association of body mass, brain mass, hand-wing index, ground foraging or invertivory with road density (Fig. 3A, B, C, G, H).

Based on these results, we ordered the species according to the traits most associated with road surroundings use (i.e., city dwellers, not nesting on the ground, and high fecundity). Two species previously classified as being positively associated with roads showed all these traits, namely the great tit *Parus major* and blue tit *Cyanistes caeruleus*, but several other species (among them several warblers) showed at least two traits, which may be referred to species super-tolerant to roads. On the other hand, super-avoiders were all the species bringing together all the traits related to road avoidance (i.e., species avoiding urban areas, nesting on the ground, and having a lower fecundity), such as the Eurasian skylark *Alauda arvensis* and crested lark *Galerida cristata* (Fig. 4).

3.3. Road effects on community dissimilarity

We combined 313 pairs of point-counts to access the road effects on the pairwise dissimilarity (pairwise Euclidean distance averaged 1210

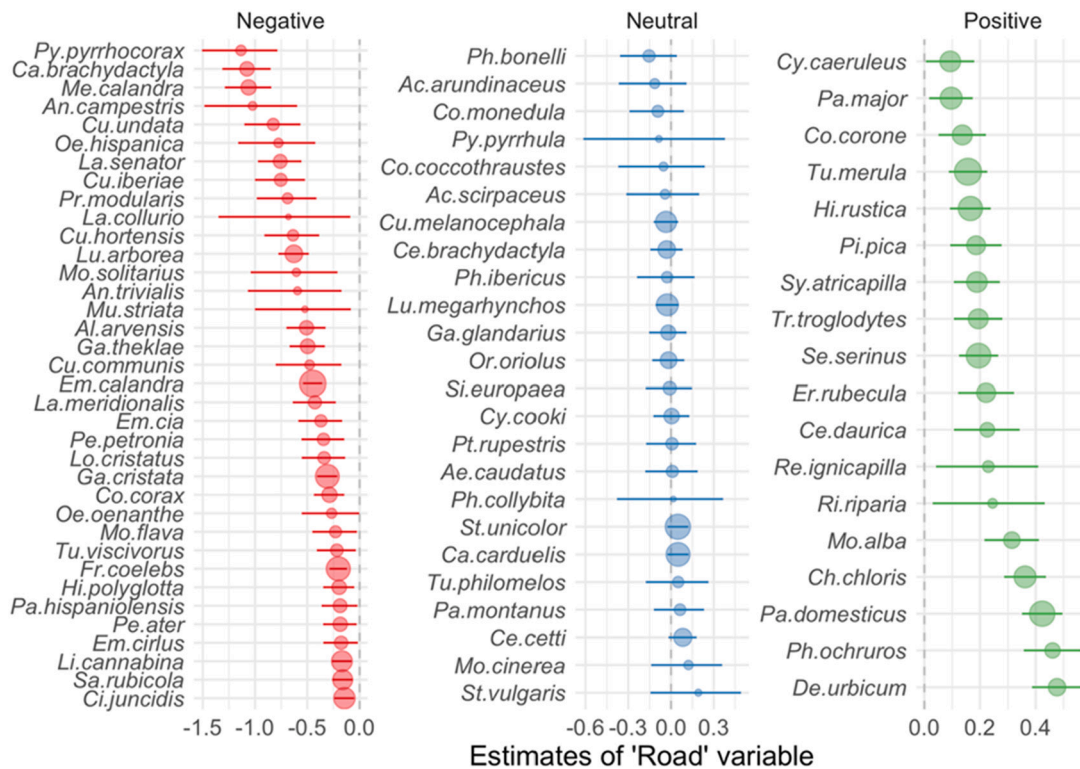


Fig. 2. Association type (negative, neutral, or positive) between road density and species occurrence. The association was determined by the estimate and confidence intervals of the Road variable from the GLMs relating species occurrence in point-counts with road and environmental variables. Size of the dot is proportional to the number of point-count sites in which the species was recorded. Vertical dashed line represents zero value. Complete scientific names of species are shown in Table S1.1.

± 464 m). The mean ± SD of the total Sørensen dissimilarity was 0.57 ± 0.25. When decomposing the total dissimilarity into the turnover and nestedness components, results suggest that most of observed dissimilarity is due to turnover of species between roaded and nearby roadless sites (Fig. 5).

As expected, the Sørensen dissimilarity increased with the distance between point-count sites, but also with the increasing road density (Table 2). The turnover of species followed the same pattern, while the component nestedness of Sørensen dissimilarity was not significantly related to any predictor (Table 2).

4. Discussion

We studied the responses of passerines to the presence of roads by formulating hypotheses about the effect of road density on their occurrence, trait prevalence, and community dissimilarity, allowing to understand how changes at the species level translate into changes at community level. Our study support previous research showing that roads can have negative, neutral and positive effects on the occurrence of different species (Cooke et al., 2020b), but we showed that at least three species' traits have a relation with such road responses, and that such trait filtering is probably causing a high species turnover between bird communities occurring in roaded and nearby roadless areas.

Our results suggest that species more sensitive to perturbation, like those nesting on the ground such as the Eurasian skylark, avoid areas with higher road density, probably due to the higher human presence and activity (Polak et al., 2013; Summers et al., 2011), which reduce the habitat quality for those birds and consequently their occurrence. With a massive long-term decline of ground-nesting bird species across Europe (McMahon et al., 2020), it is possible that road encroachment and related impacts are contributing to this trend by further reducing or degrading existing habitats (Maxwell et al., 2016). On the other hand,

species with higher fecundity seem to be more likely present in areas with higher road encroachment, probably as a consequence of higher predation rates near roads, particularly those with a medium and low volume of traffic (Pescador and Peris, 2007; Pita et al., 2009). Conversely, the city dwellers, such as the house sparrow *Passer domesticus*, showed a strong association with road density. These species are often generalists, known to be the most urban-tolerant and adaptable of birds (Callaghan et al., 2019; Evans et al., 2011; McKinney, 2006). These results suggest that increasing road encroachment may promote the prevalence of urban-tolerant species that are less likely to be present in roadless areas, while impacting more sensitive species. The prevalence of city dwellers had been previously shown for urban environments, including the consequent homogenization of communities (Clergeau et al., 2006; McKinney, 2006; Proppe et al., 2013), and we suggest that this effect may spread to rural and even more natural environments as road encroachment increases. The phylogenetic models also suggested that species with larger brain mass may be more capable to cope with increased road encroachment. This is probably due to their behavioural flexibility and ability to survive in novel ecological conditions (Callaghan et al., 2019; Fristoe et al., 2017; Maklakov et al., 2011).

Our study further showed that the different species-specific responses to roads translate into changes at the community level, mostly due to species turnover, as previously suggested by a meta-analysis on this topic (Kroeger et al., 2021). Such species and community-level changes may come with negative consequences for the ecosystem functioning and the provision of ecosystem services, including a high toll for global economy. If so, increasing road densities may be affecting the ecosystem functioning and their integrity (Glennon and Porter, 2005), as well their ecological networks, particularly on species interactions (Tylianakis et al., 2008). In fact, functions performed by certain species may become over or underrepresented, and ecosystem services may be impoverished or lost, with further costs to human

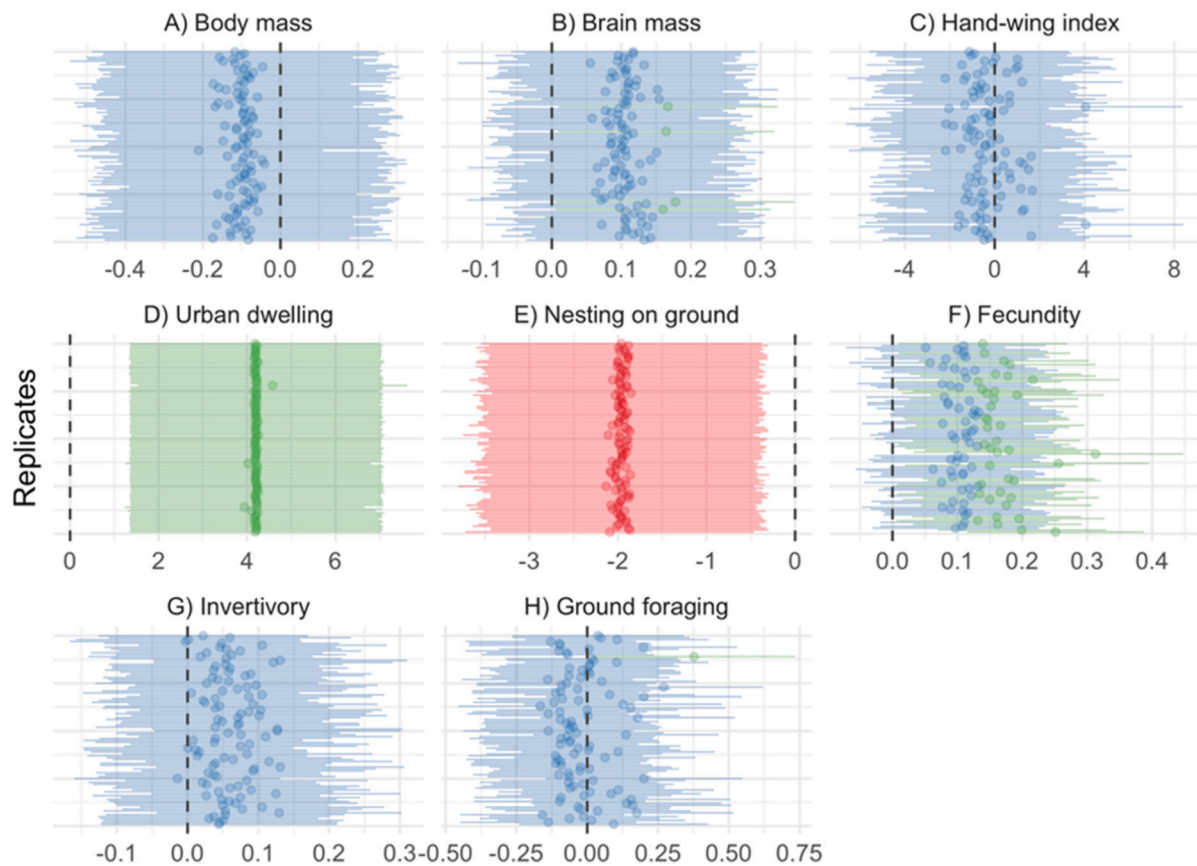


Fig. 3. Relation between road density and eight traits associated to physical attributes (A, B, C), environmental tolerance (D, E, F), and resource use (G, H). Each line stands for one replicate of phylogenetic regression models using different equally plausible phylogenetic trees. The dots and bars indicate the estimate and CI of the mean road density variable, coloured according to the type of relation with the trait (negative, not significant, and positive). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activities (McWilliams et al., 2019). For example, tree-dwelling insectivorous birds and bats are well known predators of insect pests, thus providing a valuable ecosystem service (Ceia and Ramos, 2016; Herrera et al., 2021; Karp et al., 2013). Yet, high roadkill rates could reduce local population abundance and richness of these predators, and consequently affect the biocontrol services.

Note that we did not analyse data collected in urban environments, where the processes of changes are likely to be more pronounced due to the higher road densities and higher human activities therein. Moreover, we focused on paved roads, although there is some evidence that dirt roads may also promote habitat degradation with consequent impacts for some species (Cooke et al., 2020b; Mammides et al., 2016). Also, our study disclosed how road encroachment appears to be related to spatial patterns of occurrence of species and their traits but did not address the mechanism that promotes this change in communities. It is possible that many of the species move away purposefully as others actively seek their proximity. Furthermore, it must be considered that, for some species, roads may work as ecological traps, as shown for birds (Ben-Aharon et al., 2020; Norris et al., 2013), and other species (Egri et al., 2017; Noonan et al., 2021). For example, high roadkill mortality can free up territories of apparently optimal habitat, attracting individuals who successively occupy these areas, and eventually causing population depletion (Norris et al., 2013). In fact, it has been shown that species with higher prevalence in road vicinity areas are more impacted by roadkill than expected, including for Eurasian blackcap *Sylvia atricapilla* and European goldfinch *Carduelis carduelis* (Santos et al., 2016). Likewise, one can expect that some species are adapted to anthropized areas (i.e., synanthropic species) but may not select areas near roads. This may be the case of those species that showed a negative occurrence relation

with road density in our study, despite being highly common in urban areas, such as chaffinch *Fringilla coelebs* and dunnock *Prunella modularis*.

We also note that the volume of data available from citizen-science sources is rapidly growing, and not surprisingly, is being increasingly used for addressing a wide range of ecological-research questions (e.g., Callaghan et al., 2022). Still, data from large-scale citizen science typically present a number of challenges that may inhibit robust ecological inferences, including both species and spatial biases, variation in effort, and also variation in observer skills (Johnston et al., 2021). To circumvent these biases when using eBird data, it is advised the use of complete checklists (rather than presence-only data), and the use of covariates describing variation in effort and detectability for each checklist. Our modeling approach agreed with these best practices, although it is vulnerable to variation in observer skills. Still, given the large dataset used here, we believe the patterns are robust enough to support our conclusions (Callaghan et al., 2022).

4.1. Management recommendations

Landscape and road-network management should be conceived acknowledging that roads are contributing to biodiversity changes. As so, building upon the concepts of land sharing (i.e., the integration of nature conservation into more anthropized areas) and land sparing (i.e., the separation between areas planned for human development and nature conservation) (Fischer et al., 2014), we suggest that management actions should be tailored according to the different species responses.

Concerning land sharing, the management of road verges and surrounding areas should target the conservation of species having a positive relation with road density, especially super-tolerant species such as

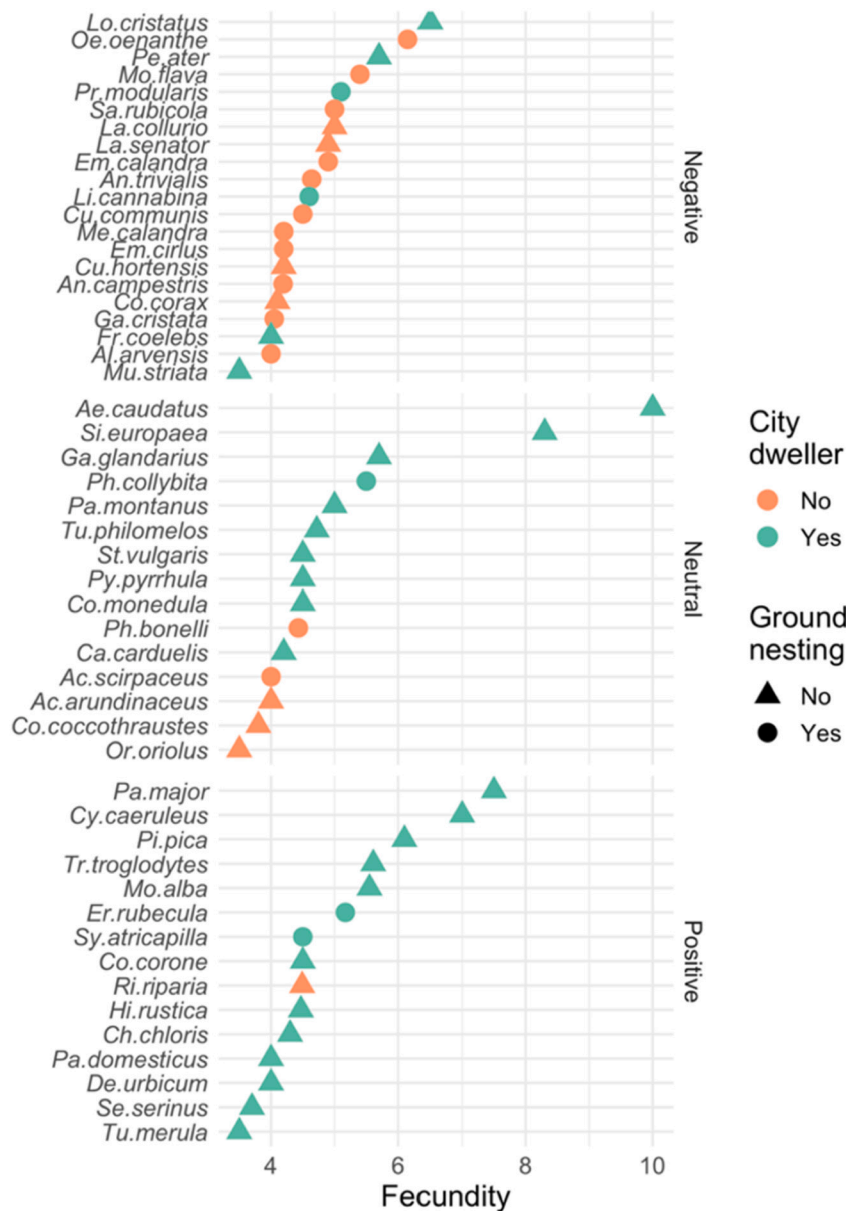


Fig. 4. Characterization of species according to three traits that varied significantly with road density: city dwelling (symbol colours), ground nesting (symbol shape) and fecundity (symbol position along the XX-axis, measured as the average number of eggs produced per clutch). Species are grouped according to the association between road density and species occurrence (negative on top, neutral in the middle, and positive in the bottom). See Supplementary material S2 for species information. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the great tit and more generalist warblers. Road verges have been already acknowledged as important areas for biodiversity conservation (Meunier et al., 1999; Phillips et al., 2020). We suggest that roadsides can play a role as refuges, also for passerines, and recommend verges to be managed favouring the creation of habitat for super-tolerant species, especially those species providing ecosystem services, such as for example insectivorous birds. This goal can be achieved especially on wide roadsides, where there is room for creating different vegetation density and structure (Leach and Recher, 1993; Meunier et al., 1999), especially outside the mowed vegetation strip adjacent to the roadway, potentially sustaining higher plant species richness and pollinator abundance (Monasterolo et al., 2020). For example, a possible roadside design can include some patches with taller shrubs and other patches without shrubs but with a higher grass layer. These actions can be primarily implemented along minor roads (i.e., having lower roadkill risk) or along major highways (i.e., generally with wide verges that allow vegetation improvements far from traffic lanes). It must be considered that roadkill is not the only risk related to roads, so other possible threats should be considered before promoting the presence of passerines along roadsides; for example, by avoiding attracting birds to road verges

having high noise levels, which may disrupt communication (e.g., Templeton et al., 2016).

Concerning land sparing, compensation actions (namely preserving areas devoid of roads) should target species showing a negative response toward roads, especially threatened super-avoiders. In fact, roadless areas have been targeted as key areas for conservation (Ibisch et al., 2016), and therefore should be kept free from road encroachment. However, roadless-areas' preservation should not only focus on larger protected areas (Kati et al., 2022). We showed that several small roadless areas are (heterogeneously) distributed across two developed countries (i.e., Spain and Portugal), and that they host relatively well-conserved passerine communities. Any landscape planning should therefore consider the preservation of these biodiversity refuges (Riva and Fahrig, 2022). One of possible strategies to reach this goal is the optimization of road-networks, which should aim to reduce road redundancy by avoiding the existence of several alternative paths between the same urban areas, combining human connectivity into fewer transport corridors, more effective and probably multimodal. While this approach may have huge benefits for conservation and society in developing countries (Hopcraft et al., 2015), in more developed regions

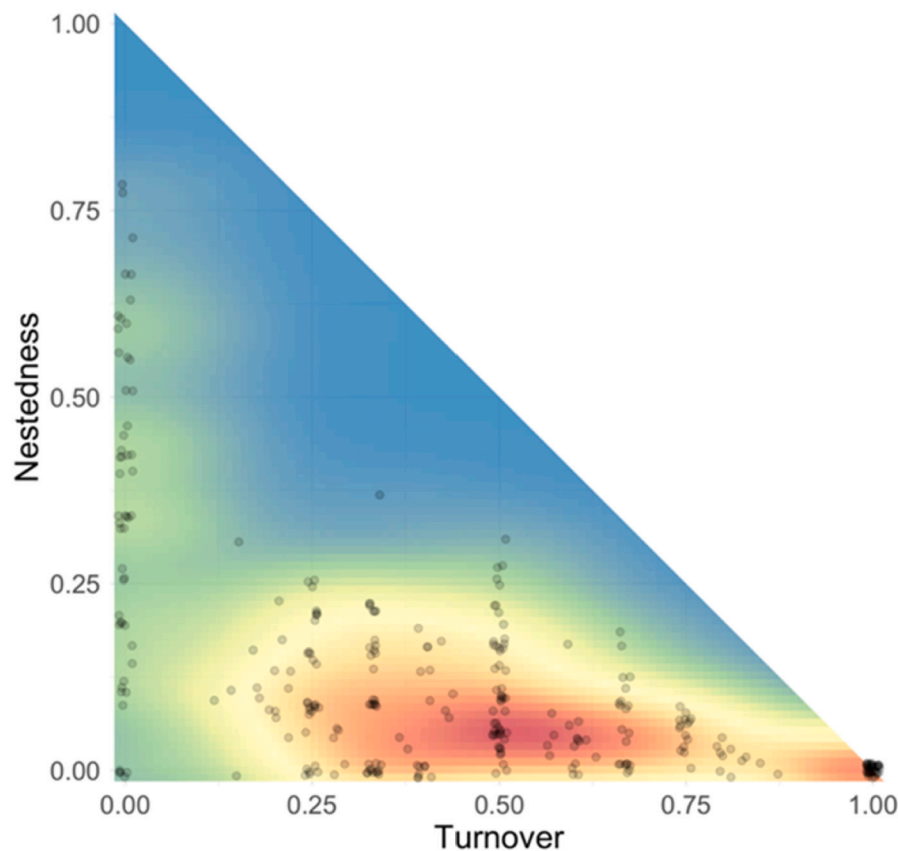


Fig. 5. Sørensen dissimilarity decomposed into the two components turnover and nestedness. Each point stands for one pair of point count sites used to access the community dissimilarity. Colour gradient is the two-dimensional kernel density estimation, with redder colours indicating higher concentration of points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Summary results for the beta regression models relating the community dissimilarity β_{sor} (total Sørensen dissimilarity), and its components β_{sim} (turnover) and β_{nes} (nestedness), with pairwise difference of environment (Env. dist.), survey effort, Euclidean distance, and road density. Est. – estimate, CI – confidence interval.

| Predictors | β_{sor} Sørensen | | β_{sim} (turnover) | | β_{nes} (nestedness) | |
|-----------------|-------------------------------|-----------|---------------------------------|-----------|-----------------------------------|-----------|
| | Est. | CI | Est. | CI | Est. | CI |
| Intercept | 1.36** | 1.20–1.55 | 0.60** | 0.51–0.70 | 0.12** | 0.10–0.14 |
| Env. dist. | 1.08 | 0.95–1.23 | 0.96 | 0.83–1.12 | 1.00 | 0.89–1.14 |
| Survey effort | 1.12 | 0.98–1.29 | 0.93 | 0.81–1.06 | 1.00 | 0.88–1.14 |
| Euclidean dist. | 1.18* | 1.04–1.35 | 1.23** | 1.06–1.42 | 1.04 | 0.91–1.17 |
| Road density | 1.27** | 1.12–1.45 | 1.31** | 1.12–1.52 | 0.89 | 0.79–1.00 |

* $p < 0.05$.

** $p < 0.01$.

such optimization can be achieved through the decommissioning of redundant roads (D'Amico et al., 2016).

In all cases, the connectivity between habitat patches should be guaranteed, namely by improving the gap permeability, both along roads for tolerant species and across roads for avoiders. This can be achieved by improving the habitat quality for tolerant species along major roads and field margins (Hall et al., 2018), but also implementing vegetated wildlife road-crossing structures (the so-called ecoducts or overpasses) for connecting habitat patches for both tolerant species and, importantly, super-avoiders (Pell and Jones, 2015). Finally, we tested our hypotheses on a very large scale (i.e., the Iberian Peninsula), suggesting that such patterns (and related management implications) can be general in regions with similar road-network development, as in many developed countries. However, our results can also be considered preventively for road-network planning in developing countries, where a large number of new infrastructures are being planned and even built (Ascensão et al., 2018) with potential alarming implications for

biodiversity conservation.

CRediT authorship contribution statement

FA collected the data, developed the methods, performed the data analysis, and prepared the first draft of the paper. FA, MD, ER and HMP contributed to the design of the research, discussed data, and contributed to writing the final manuscript.

Declaration of competing interest

The authors declare not to have any conflict of interest.

Acknowledgements

We thank all eBird contributors, without whom research such as this would not be possible, and the eBird program for providing this platform

and facilitating data analyses. FA was funded by Fundação para a Ciência e Tecnologia (contract CEECIND/03265/2017). MD was funded by a JdC-Inc postdoctoral grant (IJC2019-039662-I) from the Spanish Ministry of Science and Innovation (MICINN). The authors declare that there is no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109590>.

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