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Impacts of roads on bird species richness: A meta-analysis considering road types, habitats and feeding guilds

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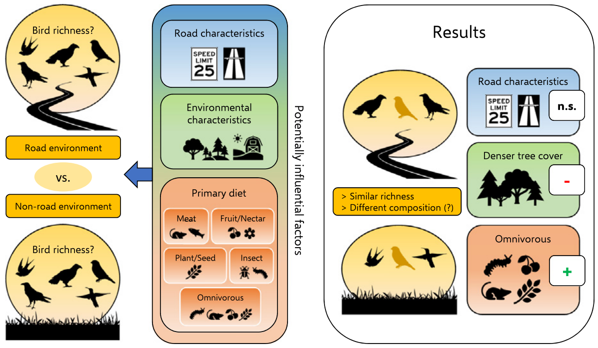
HIGHLIGHTS

- We used meta-analyses to quantify road effects on bird richness.
- Bird richness was similar in roadside and non-roadside habitats.
- Roads affected bird richness more negatively in habitats with denser tree cover.
- Richness differences between habitats depended on the primary diet of species.
- Species turnover likely explains some of the results.

GRAPHICAL ABSTRACT



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ABSTRACT

Roadsides can harbour remarkable biodiversity; thus, they are increasingly considered as habitats with potential for conservation value. To improve construction and management of roadside habitats with positive effects on biodiversity, we require a quantitative understanding of important influential factors that drive both positive and negative effects of roads. We conducted meta-analyses to assess road effects on bird communities. We specifically tested how the relationship between roads and bird richness varies when considering road type, habitat characteristics and feeding guild association. Overall, bird richness was similar in road habitats compared to non-road habitats, however, the two apparently differ in species composition. Bird richness was lowered by road presence in areas with denser tree cover but did not differ according to road type. Richness differences between habitats with and without roads further depended on primary diet of species, and richness of omnivores was positively affected by road presence. We conclude that impacts of roads on bird richness are highly context-dependent, and planners should carefully evaluate road habitats on a case by case basis. This emphasizes the need for further studies that explicitly test for differences in species composition and abundance, to disentangle contexts where a road will negatively affect bird communities, and where it will not.

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1. Introduction

The worldwide development of road networks and related road impacts are a major driver of current biodiversity loss (Forman et al., 2003; van der Ree et al., 2015). Road development is also a direct contributor to biotic homogenization, i.e. increase in genetic, taxonomic and functional similarity of different locations over a specified time interval (McKinney and Lockwood, 2001; Olden et al., 2004; Olden and Rooney, 2006). At the species level, this homogenization process generally implies a decrease in abundance of more susceptible species, leading to an increase of extinction risk, while a few tolerant species increase in abundance (Olden and Rooney, 2006). The mechanisms through which infrastructure development, particularly roads, can contribute to this process and negatively impact biodiversity include habitat loss, traffic collisions, edge and barrier effects, as well as increased human access (Trombulak and Frissell, 2000; Forman et al., 2003; Coffin, 2007).

However, it is becoming increasingly evident that roads can also have positive effects on biodiversity (Meunier et al., 1999; Rotholz and Mandelik, 2013; Morelli et al., 2014; Vasconcelos et al., 2014; Reck and van der Ree, 2015), and even save threatened species in intensely-anthropized landscapes (Noordijk et al., 2009). Positive effects of roads have been attributed to various factors and may be due to roadsides providing suitable habitat with foraging opportunities (including scavenging for roadkill; Lambertucci et al., 2009; Morgan et al., 2010; but see Barrientos and Bolonio, 2009), availability of overwintering and nesting sites (Schaffers et al., 2012), a heat source to help with conserving metabolic energy (Whitford, 1985), and reduced predation pressure (Rytwinski and Fahrig, 2007, 2013). Also, while roads are barriers for some species, they may constitute stepping-stones and dispersal corridors for other species (Deckers et al., 2005; Coffin, 2007) and can increase habitat heterogeneity at a local scale (Meunier et al., 1999). In order to construct and manage road habitats in a way that mitigates negative effects on biodiversity and takes advantage of the potential benefits, understanding of how different factors influence different species and ecological processes is required.

One factor that can be important in determining species-specific success in roadside habitats is the size of the road. Larger roads may have more negative effects on some species because they cause increased disturbance, thereby counteracting potential positive effects. Large roads typically also have higher traffic volumes than small roads. Intensification of traffic may lead to an increase in wildlife-vehicle collisions, with the caveat that some animals are discouraged from attempting road crossings when traffic is above a certain threshold (e.g. Clarke et al., 1998). Another factor that may play an important role in how the road environment affects species is the type of habitat through which the road is built. In more homogenous landscapes, for example, landscapes with intense agriculture or with forest managed for timber (i.e. landscapes that have been highly human-modified), roads may have a positive effect on species by increasing habitat heterogeneity (Meunier et al., 1999; Helldin and Seiler, 2003). In more pristine habitats (i.e. with little anthropogenic impact), however, the disturbance introduced by roads likely outweighs potential positive effects. In addition, effects are dependent on species-specific requirements and behaviours. For example, raptors and other scavenging birds often have higher densities close to roads due to feeding opportunities, including roadkill and other sources related to human activities (Knight and Kawashima, 1993; Dean and Milton, 2003; Lambertucci et al., 2009). Mammalian predators, however, tend to avoid roads (Fahrig and Rytwinski, 2009; Grilo et al., 2015).

Birds constitute an important component of most ecosystems of all biomes; they contribute to many ecosystem services (Millennium Ecosystem Assessment, 2003; Whelan et al., 2008), and can be useful indicators of habitat quality and biodiversity (Blair, 1999; Kati et al., 2004; Orme et al., 2005; Frederick et al., 2009; Fraixedas et al., 2020). It is well documented that birds can be both negatively and positively affected by linear infrastructure (Benítez-López et al., 2010; Rytwinski and Fahrig, 2012; Morelli et al., 2014; Ouédraogo et al., 2020), and they have been widely studied in most contexts, including road ecology. The large amount of available data means that birds represent an attractive taxonomic group for investigating different factors that may influence biodiversity in road habitats. Since it can be challenging to summarise and evaluate results across a large body of literature, we conducted meta-analyses to quantify whether, on average, roads are negatively or positively associated with bird richness. Further, we aimed at identifying what the important underlying factors are that influence bird richness in road habitats. We focused on species richness as a diversity metric because meta-analyses require a high number of comparable studies, and richness is by far the most common measure, despite its limitations (Fleishman et al., 2006; Hillebrand et al., 2018).

We expected an overall negative effect of roads across contexts, not least because negative factors have been more commonly studied in the past. We further hypothesised that characteristics of the road and the surrounding habitat are important in determining road effects on bird richness. Specifically, we predicted that larger roads have more negative effects than smaller roads, that road effects are more detrimental in pristine habitats, and that road presence positively affects bird richness in highly modified landscapes. Finally, we predicted road effects to differ among avian feeding guilds, with different negative effects on richness in all dietary groups except predators, scavengers and omnivores, which we expected to exhibit a positive relationship with roads.

2. Methods

2.1. Search strategy and selection of articles

The source for our data was a large literature search implemented in the context of the EPICROADS project: a scientific collaboration between different European institutions from 2017 to 2021, funded through the Conference of European Directors of Roads (CEDR). EPICROADS was built on a systematic review from a Swedish MISTRA EviEM project (Bernes et al., 2017), which covered the years before 2017, to which it added updated searches for the period 2017–2020. Searches for the EPICROADS database targeted articles on biodiversity in different relationships with roads i.e. species, communities, species diversity, functional groups and ecosystem function; articles where impacts of roads and road-related factors on species and ecological processes were unknown were excluded. EPICROADS used the same broad search string and terms as the MISTRA systematic review (n.b. an asterisk * serves as a wildcard, representing any group of characters, including no characters):

Population	roadside*, ‘road side*’, (road* AND (verge* OR edge*)), roundabout*, ‘traffic island*’, ‘median strip*’, ‘central reservation*’, boulevard*, parkway*, (avenue* AND tree*)
Outcomes	*diversity, dispers*, species, abundance, vegetation

The terms within the categories ‘Population’ and ‘Outcomes’ were combined using the Boolean operator ‘OR’, and the two categories were combined using the operator ‘AND'. EPICROADS also used the same search engines and publication databases than the MISTRA project, with the caveat that the most recent search (2019–2020) only used Google Scholar and Web of Science as search engine and publication database, respectively.

For the meta-analyses on bird richness in relation to roads, we carefully screened titles and abstracts for all articles found through the EPICROADS and MISTRA literature searches (see flow diagram in Fig. S1, Supporting information), published in all years up until May 2020. We adopted a conservative approach, where articles were retained if relevance was unclear at first. We only included papers in

English and excluded grey literature, because it often contains insufficient detail to perform meta-analyses. Articles identified as potentially relevant during the title and abstract screening, i.e. the topic indicated a potential association between roads and bird communities, were then examined on full text. During this stage we retained articles based on a pre-defined set of inclusion criteria:

- *Relevant study objects*: Any bird communities, irrespective of geographical location, as most basic responses to roads are likely to be similar across the globe.
- *Relevant types of exposure*: Road presence or proximity to roads (i.e. road habitats compared to non-road habitats, a dichotomous classification; or close to the road compared to distant from the road, a continuous measure).
- *Relevant types of comparator*: Non-road habitats or furthest recorded distance from a road (in the case of studies that recorded bird richness at different distances from roads).
- *Relevant types of outcome*: Bird richness in road habitats compared to non-road habitats.

Articles that did not match these criteria and/or that did not provide the necessary statistical detail (see following section) to conduct meta-analyses were excluded at this point (Fig. S1; Supporting information).

2.2. Data extraction

For each article, we extracted sample means for bird richness in road and non-road habitats (n.b. in the case of studies measuring bird richness at different distances from the road, we focused on means for the closest and furthest recorded distances, respectively), sample sizes, and a measure of variance (usually standard errors or standard deviations, depending on the study) to calculate an effect size. If a study reported separate summary statistics for different years, we combined means and standard errors for those years. If an article had collected data in different habitats or road types, and reported bird richness separately for these data sets, we extracted multiple data points from that article and treated each as a separate study. For example, the same article may have compared bird richness in road versus non-road habitats for highways and carried out the same comparison in a separate data set focusing on smaller roads. In such an example, our approach extracted two pairwise comparisons.

If summary statistics were not provided by a study, we either calculated them from raw data (if they were available as supplementary material or provided by the authors when requested), or, if possible, extracted them from graphical images (using Engauge Digitizer). We considered each surveyed site as one sampling unit, thus, if there were multiple surveys for the same site (e.g. different seasons or times of day), we took the sum of the total number of species found in that site across surveys, and calculated sample means across all road and non-road sites, respectively.

We recorded information related to road type and habitat characteristics, and classified roads into three categories: 'large paved roads' (typically highways/roads with 3 < lanes), 'small paved roads' (typically 1–2 lanes) and 'unpaved roads'. Studies were further assigned to one of three habitat categories, namely 'woodland', 'arable land' or 'open habitat' (e.g. grass- or shrubland), based on site descriptions given in the studies. In addition to the habitat category, we created an alternate dichotomous variable, which classified habitats as being either highly or less human-modified/managed ('high' vs. 'low'), in order to differentiate between for example plantations used for wood production (i.e. high modification) and relatively pristine forests (i.e. low modification; Tables S1–2; Supporting information).

We recorded coordinates for each study to extract variables related to climate and other environmental conditions from various online databases and explore them as sources of heterogeneity. Variables extracted this way included cumulative human pressure (2009 Human Footprint Release; Venter et al., 2016), mean annual temperature (°C) and annual precipitation (mm; WorldClim database; Fick and Hijmans, 2017), tree cover (30 m pixel percent tree cover; Landsat data; Hansen et al., 2003), MODIS net primary productivity (NPP; g/m^2/year; Running et al., 2004) and biome category (Olson et al., 2001). We further stored data on the country and the years during which the study was carried out, type of predictor for road (categorical 'road presence vs. absence' or the continuous predictor 'distance'), sampling methods (split into five categories: point counts, transects, territory mapping, area search methods or capture mark-recapture studies, i.e. mist-netting), and study design (i.e. control-impact, before-after or before-after-control-impact).

To explore differences of road impacts on species richness among subgroups of birds belonging to different feeding guilds, we attempted to source raw data for each study. Due to variation in classification systems among studies, we grouped birds according to the EltonTraits database (Wilman et al., 2014), which assigns species to one of five diet categories, namely 'plant or seed eaters', 'omnivores', 'nectar or fruit feeders', 'insectivores' and 'meat eaters' (carnivores, piscivores or scavengers), depending on their primary food source. For each study, we then calculated means and standard deviations for species richness within each diet category. To ensure that a given feeding guild was adequately represented, we only used data for a category if there were at least ten observations of individuals belonging to that respective category across all road and non-road habitat surveys. Thus, two individuals belonging to the same species were counted as two, and two individuals belonging to two different species were also counted as two.

We ended up with two separate related data sets in our analyses, a 'full data set' and a 'diet data set'. In both data sets, standardized mean difference (SMD) effect sizes were derived for all responses using Hedges' *g* statistic. They were calculated as the difference between the mean bird richness in road habitats and the mean bird richness in non-road habitats, divided by the pooled standard deviation. Thus, positive effect sizes indicate that bird richness is higher in road habitats than non-road habitats and vice versa. Effect size estimates were weighted by the inverse of their variances, which gives more weight to studies with higher sample sizes if distributions are similar (Borenstein et al., 2009).

Values for effect sizes and variances, details about variables, information regarding means and standard deviations for each data point, sample sizes, habitat descriptions and coordinates used for each study site, can be found in Tables S1 and S2 (Supporting information). Collinearity among continuous explanatory variables was examined in Fig. S2 (Supporting information). We also examined spatial turnover of species for studies that had available raw data (Fig. S3).

2.3. Statistical analyses

To determine whether, overall, roads have a positive or negative impact on bird richness, and to test for differences of road impacts on bird richness depending on dietary requirements, we carried out random-effects meta-analyses on the full data set and the diet data set, respectively. We used restricted maximum likelihood (REML) as an estimator to derive pooled effect sizes. The random-effects model is deemed more appropriate if there is no strong reason to assume that all studies share a common effect size, and thus allows for variation among studies (Hedges and Olkin, 1985). We used the metafor package (Viechtbauer, 2010) in R version 3.6.3 (R Core Team, 2020) to build all models.

Heterogeneity was assessed by examining forest plots and tests of heterogeneity (Q). Publication bias was assessed through funnel plots of asymmetry (graphical detection using a scatterplot of effect size against the sampling error). Subgroup analyses (i.e. mixed-effects meta-regressions, including study ID as random effect and selected moderators as fixed effects) were used to test for associations between effect sizes and candidate predictor variables. Specifically, to address our research questions regarding the influence of road size and habitat attributes on bird richness, we conducted meta-regressions on the full data set, while including categorical moderators of either road or habitat type. We removed the intercept in these models to view estimates for each predictor level, as opposed to setting one as a reference level. We also fitted a two-level interaction between road and habitat type to test whether road impacts on bird richness differ depending on specific combinations of those two factors. To further explore factors introducing heterogeneity, we built a series of meta-regression models, each including one of the previously defined explanatory variables related to environmental conditions (i.e. human pressure, mean annual temperature, annual precipitation, tree cover, NPP and biome) or related to study design (sampling method, type of predictor for road and distance to nearest road for non-road sites, if applicable).

During the review process we identified two articles which had reported that changes in bird richness were mainly driven by the presence of an aggressive competitor species (noisy miner, *Manorina melanocephala*; Hall et al., 2018; Maron and Kennedy, 2007). Since removal of these two articles did not change the overall results of the models and moderator analyses, they were retained in the full data set. In the diet data set however, the differences among feeding guilds became more apparent after these two studies were excluded, even though the overall significance of the moderator did not change. Thus, the final diet data set excluded these studies, as they may be confounding road impacts on bird richness of specific diet categories. We further examined Cook's distances to identify studies with a high influence on the overall outcome and carried out sensitivity analyses for both the full and diet data sets.

3. Results

A total of 7071 articles were screened on title and abstract, and of those 177 were screened on full text. We retained 18 articles (ten of which we were able to obtain raw data for), published 1991–2019, which met the inclusion criteria and had the necessary statistical information to conduct meta-analyses (Fig. S1; Supporting information). Studies were spread across Europe (6), Australia (4), North America (3), Asia (3) and South America (2); study locations are shown in Fig. S4 (Supporting information). We extracted more than one data point from five articles that had collected data for different road and/or habitat types, treating each as a separate study, which resulted in a total of 26 effect-size values (‘studies’) in the final data set. For the diet data set, we extracted 46 effect-size values from the raw data sets, split across the five diet categories (some articles with data for different road and/or habitat types yielded multiple data points for the same diet category). All studies had a control-impact design (CI); see Supporting information Tables S1 and S2 for a full list of all included articles and associated information.

3.1. Bird species richness in road and non-road habitats

The pooled weighted mean effect size derived from all 26 effect size values showed that overall bird richness did not differ between road and non-road habitats, although this finding was marginal ($ES_g = -0.32$; 95% CI: -0.71, 0.06; $N = 26$; Fig. 1a). The heterogeneity of effect sizes was large ($Q = 307.64$; $p < 0.01$; $N = 26$), indicating that there was substantial variation in how road habitats impact bird richness. A funnel plot of asymmetry indicated little publication bias (Fig. S5; Supporting information), and removal of the study that had the data point with the highest influence (Fig. S6; Supporting information) did not significantly affect the overall outcome ($ES_g = -0.22$; 95% CI: -0.58, 0.14; $N = 25$; model heterogeneity: $Q = 202.14$; $p < 0.01$). Since excluding influential data points had no qualitative impacts on the study's findings, all data points were retained in the final model.

3.2. Effects of road type and habitat attributes

Road effects on bird richness did not vary according to road type ($Q_M = 4.39$, $p = 0.223$, $N = 10, 7, 9$; Fig. 1b), habitat type ($Q_M = 5.15$, $p = 0.161$, $N = 16, 4, 6$; Fig. 1c) or differences in human-modification/management ($Q_M = 3.65$, $p = 0.162$, $N = 12, 14$; Fig. 1d). Effect size estimates for individual studies are included in more detailed figures in supporting information (Figs. S7–S9).

However, meta-regression analysis showed that effects of roads were more negative in environments with higher tree cover (i.e. dense forest; $ES_g = -0.02$; 95% CI: -0.02, -0.01; $N = 21$; Fig. 2; Table 1). There was no association between effects of roads on bird richness and the other environmental predictor variables in our study (i.e. human pressure, mean annual temperature, annual precipitation, NPP and biome), nor the interaction between road type and habitat category (Table 1). Also, sampling method, predictor type, and actual distance to road did not significantly affect the association between roads and bird richness (Table S3; Supporting information).

3.3. Differences between bird feeding guilds

The pooled weighted mean effect size derived from all 46 effect sizes in the diet data set also showed no association between bird richness in road habitats compared to non-road habitats ($ES_g = 0.13$; 95% CI: -0.15, 0.41; $N = 46$). Again, heterogeneity of effect sizes was large ($Q = 304.71$, $p < 0.001$, $N = 46$), indicating substantial variation in how roads impact bird richness. Moderator analyses showed that effects of roads on bird richness varied significantly according to diet category ($Q_M = 160.65$, $p < 0.01$, $N = 13, 12, 4, 13, 4$), and indicated a positive impact of road habitats on the species richness of omnivorous birds (Fig. 3). Removal of the study that had the data point with the highest influence (Fig. S10; Supporting information) did not significantly affect the overall outcome ($ES_g = 0.07$; 95% CI: -0.20, 0.33; $N = 45$; model heterogeneity: $Q = 302.48$; $p < 0.001$); thus, all 46 data points were retained.

4. Discussion

Across 26 studies included in this meta-analysis, roads had no consistent effect on bird richness, and there was considerable variation among studies. The lack of an overall significant effect of roads on bird richness in the meta-analysis is not surprising, given that roads are known to have both positive and negative effects on birds, and our sample covers many different contexts. However, when we examined potential influential factors that may drive bird richness in road habitats by grouping studies according to road, habitat or diet type, we found some evidence that differences in richness between habitats with and without roads depend on specific contexts covered by those subgroups.

4.1. Road type

Contrary to our prediction, the results did not support the hypothesis that road impacts on bird richness depend on the type of road (i.e. unpaved, small or large paved). Other studies have shown that positive effects of roads tend to be more frequently associated with less-highly frequented or unpaved roads, and larger roads may present increased disturbance, which could reduce or negate any potential positive effects (Morelli et al., 2014; Reijnen and Foppen, 2006; Ouédraogo et al., 2020).

Indeed, another recent meta-analysis found negative impacts of highways, but not of other paved roads on bird richness (Ouédraogo et al., 2020). On the other hand, some species may prefer larger roads, which could also contribute to our result. For example, a study in butterflies showed that butterfly diversity was higher along highways compared to urban or rural roads, likely because the wider verges of highways provide a better variety of breeding habitats (Saarinen et al., 2005). It has also been shown that some species do better in habitats

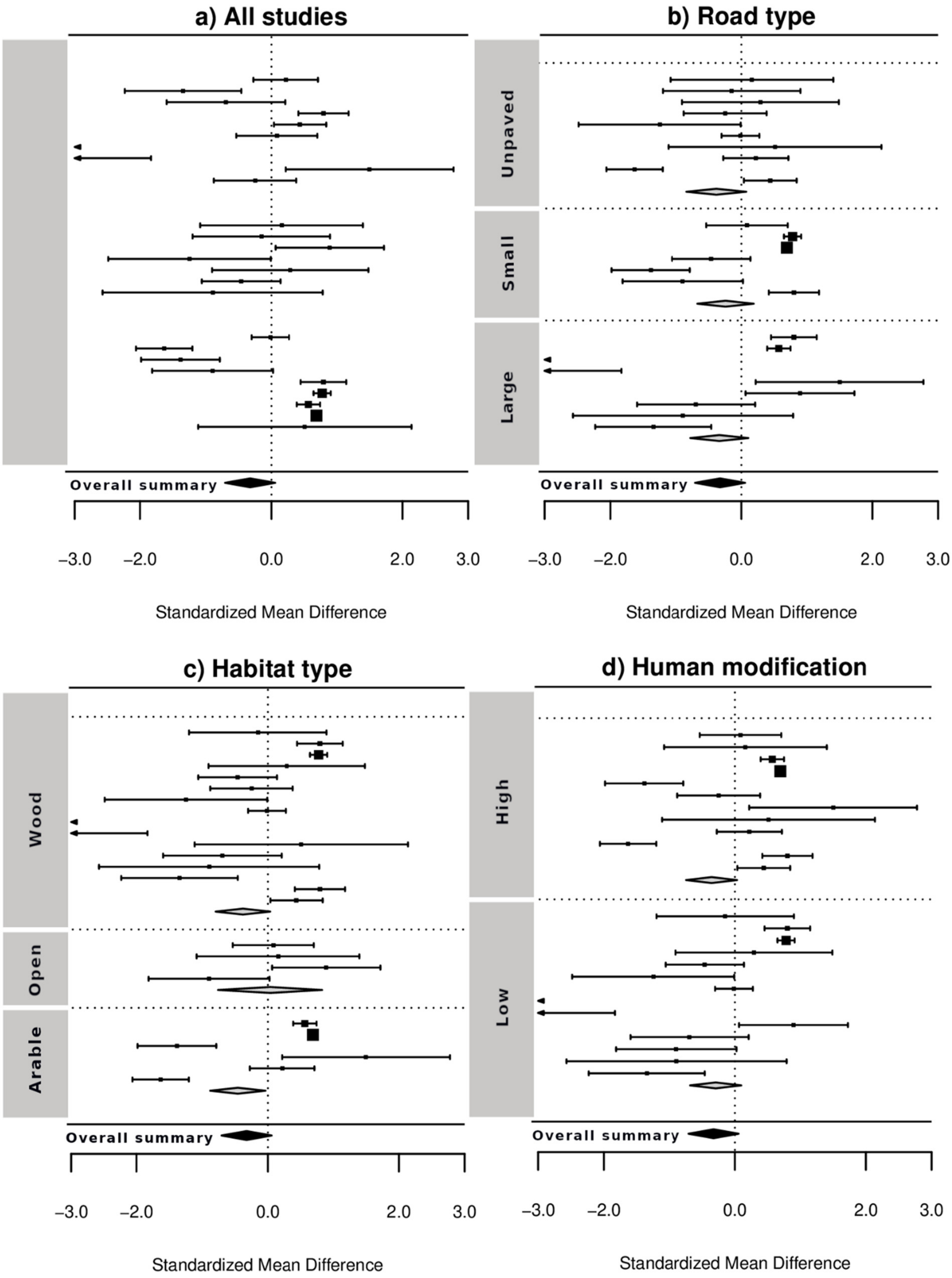


Fig. 1. Forest plot showing weighted mean effect size estimates (Standardized mean differences) for (a) all studies and for all studies grouped by (b) different road types, (c) habitat types adjacent to the road and (d) the amount of human modification/management in the habitat adjacent to the road. Each row represents one case (study). Summary estimates for road categories (unpaved, small paved, large paved), habitat categories (woodland, open habitat, arable land) and categories of human modification of the environment (high, low) were derived from mixed-effects meta-regressions. Error bars indicate 95% confidence intervals and arrows represent cases where the estimate and/or confidence interval extend beyond the axis limit, which was restricted for illustration purposes. Point size indicates sample sizes (i.e. weight) and the "overall summary" represents the overall pooled effect size across all 26 effect size values (i.e. studies/cases) from 18 articles.

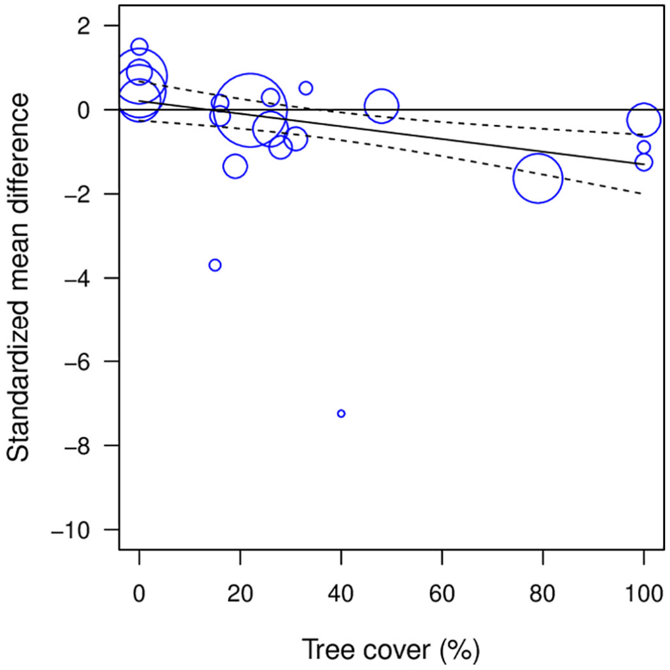


Fig. 2. Bubble plot showing the results of meta-regression analyses testing the moderation of the association between roads and bird richness by tree cover percentage. The size of the bubble is proportional to the precision of the study (i.e. larger studies are represented by larger bubbles; inversely proportional to the variance of the Standardized mean difference).

with greater road densities due to reduced predation (Rytwinski and Fahrig, 2007; Fahrig and Rytwinski, 2009; Munro et al., 2012); possibly similar effects occur in verges of larger compared to smaller roads. In addition, birds are a rather mobile taxon, and it has been suggested that some species may be less affected by roads if they are able to avoid deadly collisions (Jaeger et al., 2005); if so, road size per se may not be that important. These hypotheses remain to be explicitly tested.

4.2. Habitat type and other environmental effects

We also did not find any consistent differences in bird richness in road habitats compared to non-road habitats when we grouped studies according to habitat type (i.e. woodland, arable land, open habitat). Positive effects of roads are often expected in more homogenous landscapes (Helldin and Seiler, 2003; Morelli et al., 2014), where roads may add heterogeneity. Conversely, negative effects are expected to be strongest in landscapes that have been less impacted by human activity, for example in natural forests.

We note that the 'woodland' category in our study comprised any type of woodland, including managed production forests that are also under high human impact (and likely more homogenous than other types of woodland — hence, we additionally tested for effects of human impact). For example, Šálek et al. (2010), showed a strong positive effect of roads on bird richness, contrary to many other studies in the woodland category. The latter study was carried out on a spruce plantation used for timber production, and the authors concluded that (unpaved) logging roads may add heterogeneity and attract bird species to production forests. However, we did not find any effects of meta-regressions of human pressure (i.e. human footprint; Venter et al., 2016) on the overall data set, nor of the variable that classified studies in two arbitrary categories based on the level of human modification/ impact (i.e. 'low' = relatively unmanaged habitats or habitats managed

Table 1

Mean effect sizes (ES_g) with statistical significance of moderators for separate meta-analytical regression models, testing the effects of human pressure, annual mean temperature, annual precipitation, net primary productivity (NPP), tree cover percentage, biome category, and the interaction between road type and habitat category, respectively, on bird richness. The reference level for road type (R) is 'large', and the reference level for habitat category (Hab) is 'arable land'. Significant effects are shown in bold.

Moderator variable	ES_g	CI (lb)	CI (ub)	$p(ES_g)$	Q_E[1]	Q_M[2]	$p(Q_M)$	n
Intercept	−0.26	−0.99	0.48	0.50				–
Human pressure	−0.00	−0.04	0.03	0.81	139.56	0.06	0.81	21
Intercept	0.08	−0.56	0.72	0.80				–
Annual mean temperature	−0.03	−0.08	0.01	0.12	128.53	2.35	0.12	21
Intercept	−0.09	−0.77	0.59	0.79				–
Annual precipitation	−0.00	−0.00	0.00	0.40	144.13	0.72	0.40	21
Intercept	1.48	−0.56	3.51	0.16				–
NPP	−0.00	−0.01	0.00	0.05	136.37	3.76	0.05	21
Intercept	0.21	−0.26	0.67	0.39				–
Tree cover	**−0.02**	**−0.02**	**−0.01**	**<0.01**	**84.89**	**9.47**	**<0.01**	**21**
Biome category[3]					136.14	5.59	0.47	21
Trop & Subtrop Moist Broadl Forests	−0.47	−1.76	0.82	0.48				2
Trop & Subtrop Dry Broadl Forests	−0.89	−3.19	1.41	0.45				1
Temp Broadl & Mixed Forests	−0.24	−0.83	0.36	0.43				11
Trop & Subtrop Grassl, Sav & Shrubl	−0.55	−1.79	0.69	0.39				2
Montane Grasslands & Shrublands	0.89	−0.88	2.67	0.33				1
Mediterranean Forests, Woodl & Scrub	−0.99	−2.27	0.29	0.13				4
Road type ∗ habitat category[4]					174.18	6.55	0.59	26
Intercept	−0.41	−0.94	0.12	0.13				
R[Small]	0.08	−0.11	0.26	0.41				
R[Unpaved]	−0.31	−1.49	0.87	0.61				
Hab[Open]	1.30	−0.42	3.02	0.14				
Hab[Wood]	−0.05	−0.43	0.32	0.77				
R[Small] ∗ Hab[Open]	−1.33	−3.33	0.67	0.19				
R[Unpaved] ∗ Hab[Open]	−0.54	−3.12	2.04	0.68				
R[Small] ∗ Hab[Wood]	0.15	−0.24	0.55	0.45				
R[Unpaved] ∗ Hab[Wood]	0.44	−0.81	1.69	0.49				

[1] Residual heterogeneity.

[2] Between groups/model heterogeneity.

[3] Biome categories: Tropical & Subtropical Moist Broadleaf Forests, Tropical & Subtropical Dry Broadleaf Forests, Temperate Broadleaf & Mixed Forests, Tropical & Subtropical Grasslands, Savannahs & Shrublands, Montane Grasslands & Shrublands, Mediterranean Forests, Woodlands & Scrub.

[4] Road and habitat categories = Large roads (reference level), small paved roads (Small) and unpaved roads (Unpaved), arable land (reference level) woodland (Wood) and open habitat (Open).

in the interest of wildlife or nature reserves, vs. 'high' = arable land or production forests).

When examining results of individual studies, it is noticeable that there are more studies which reported positive effects of roads on bird richness in more modified landscapes, and more studies with negative effects in more pristine landscapes. This illustrates the significance of weighting effect size estimates prior to conducting meta-analyses. Also, if some species preferably use anthropized habitats, this may contribute to our results. For example, raccoons (*Procyon lotor*) often choose anthropized areas to utilise related food resources (Prange et al., 2003, 2004), and Eurasian collared doves (*Streptopelia decaocto*) have been found prefer urbanized areas with road infrastructures compared to agricultural or forested areas (Battisti and Zullo, 2019).

The only candidate environmental predictor that explained variation in bird richness response to roads was tree cover. It showed that effects of roads on bird richness were more negative in landscapes with higher tree cover. This is in line with previous studies in road habitats (e.g. Meunier et al., 1999; Radford et al., 2005), as well as meta-analyses on intra-urban biodiversity across a range of taxa, showing that bird richness in particular was strongly positively associated with tree cover (Beninde et al., 2015). Denser tree cover in woodland may imply that the environment in question has seen less human modification, and it would make sense that more pristine habitats suffer stronger negative impacts of roads. Roads could be considered a 'clearing' in the landscape, so it is not surprising that road effects are less noticeable in habitats that are more open to begin with. It has previously been shown that bird species that primarily frequent more closed habitats (e.g. forests) tend to be more negatively affected by roads than species that prefer more open environments (Morelli et al., 2015). This can be explained through tolerance differences to sensory pollution (i.e. light and noise) and to disturbance in general between the two types of species. For example, birds in forest habitats are more sensitive to noise and have decreased reproductive success compared to birds living in more open environments, probably because their vocalisations are at frequencies which are more susceptible to masking through anthropogenic noise (Senzaki et al., 2020).

4.3. Feeding guild association

Feeding guild association is likely an important factor in determining bird species success in road habitats. We specifically found positive impacts of roads on omnivorous birds, which matches our expectation that species with less specialised primary dietary requirements do better in road habitats than birds with more specialised requirements (i.e. frugivores, insectivores and granivores). Indeed, some omnivorous species are known to have great capacity to adapt their diets, which allows them to use resources made available through anthropogenic activity. For example, ravens (*Corvus corax*) were more abundant along highways compared to control areas at a distance from highways, likely because they were exploiting road-killed carrion (Knight and Kawashima, 1993).

Contrary to expectation, there was no significant positive effect on species with a primary dietary requirement of meat (i.e. predators or scavengers). However, the sample size was very small, and the four available data points all had positive estimates for road impacts, suggesting that carnivorous birds may benefit from road environments. Our results imply that negative effects of roads can be particularly expected in habitats with many bird species that have very specialised diets. Further, the differences among feeding guilds became more apparent after we removed two studies which had been carried out in environments with an aggressive competitor species, whose occurrence has strong negative impacts on other bird species, regardless of road presence or absence (Hall et al., 2018; Maron and Kennedy, 2007). Thus, road habitats are less likely to offer opportunities to promote species richness if strongly competitive species thrive in roadsides, as well as other habitats.

4.4. Species turnover

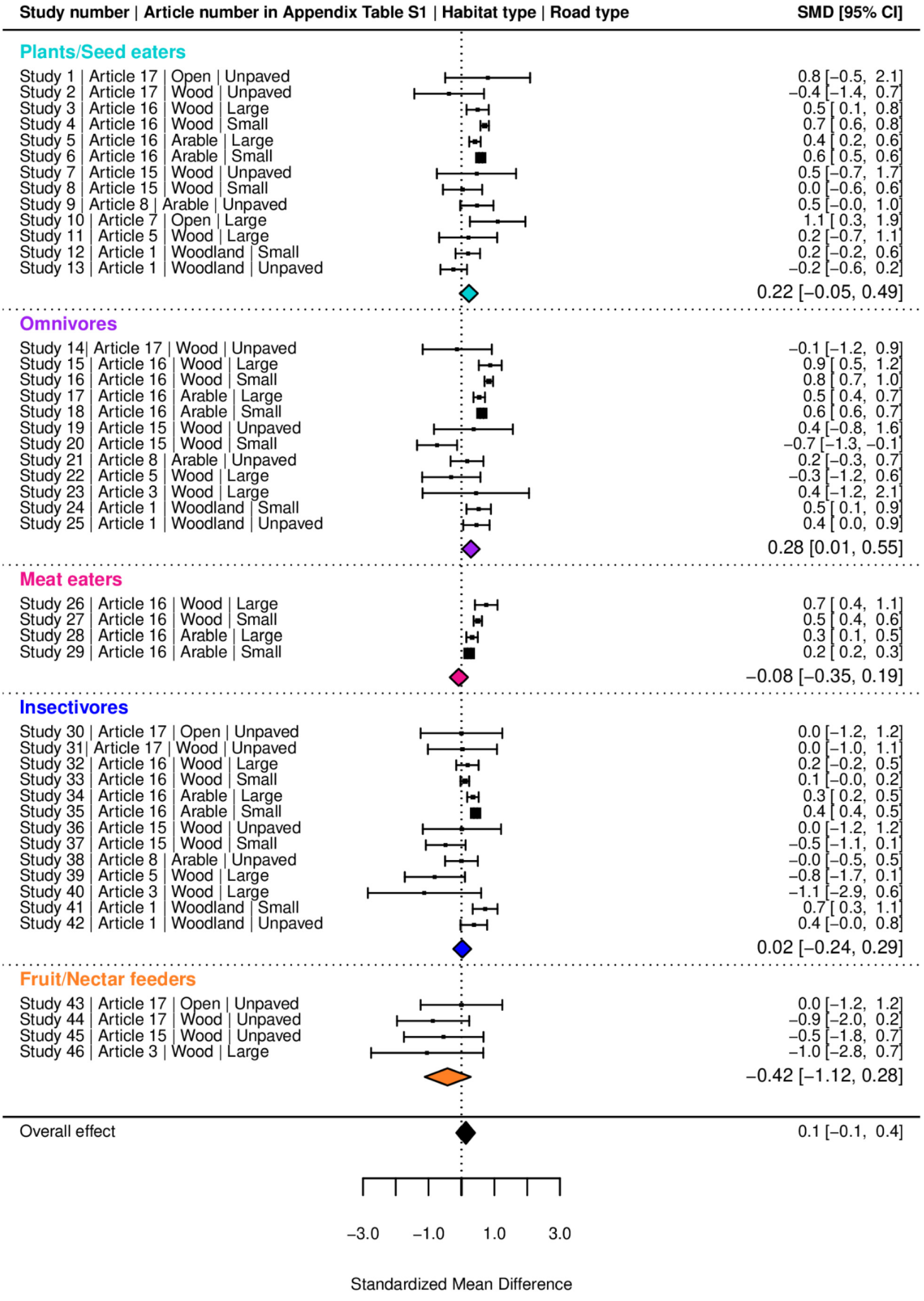
One likely reason for the lack of significant differences in bird richness between road habitats and non-road habitats for some of the subgroups in our analyses is that there may be species turnover. Indeed, when looking at the number of species that were shared with, new to, or absent from road habitats compared to respective non-road habitats for studies with available raw data, it became apparent that in various cases there were considerable differences in community composition between habitats with and without roads (Fig. S3; Supporting information). For example, in woodland sites, Lynch and Saunders (1997) found 35 species in road habitat compared to 32 species in non-road habitat. However, only 22 of those species were shared between non-road and road habitats. The pattern was similar for grassland sites, with 21 total species in road habitat compared to 19 species in non-road habitat, and of those, 11 species were present in both road and non-road habitats.

Notably, positive effects in the form of increases in species richness do not necessarily equate to positive effects on conservation status or other conservation policy targets. Indeed, richness alone may not always be informative, because there may be changes in abundance and in community composition, which can impact ecosystem functioning. What is desirable, is an increase in biodiversity, which in addition to richness, also comprises aspects of identity, rarity and dominance, among other things (Hillebrand et al., 2018). Thus, understanding biodiversity change is not always straightforward, and this has sparked much debate (e.g. Thomas, 2013; Vellend, 2017). Despite its shortcomings though, species richness remains the most common and straightforward biodiversity metric. In addition, it is probably the only one that offers the possibility to carry out robust comparisons across habitats, taxa and different spatio-temporal scales, given that it has been reported in a sufficiently standardized way (Vellend, 2017).

4.5. Other considerations

A previous meta-analysis of road impacts on bird richness reported a bigger sample size for roads in the 'large' category (i.e. highways; Ouédraogo et al., 2020), but also a noticeably smaller sample size for 'small' roads. This demonstrates that the observed outcome strongly depends on composition of the final data set. The difference likely arose due to different inclusion and exclusion criteria, and further, the source for the literature reviewed in our study was a database which was built on systematic review approaches with a relatively broad search string. Similarly, generating the data set for the feeding guild subgroup analyses (i.e. diet data set) depended on what studies we were able to obtain raw data for. It is possible that adding further studies may significantly affect the outcome in some of the subgroups. The same could be said for road and habitat subgroup analyses, however, concerning the main data set, it is unlikely that a larger sample size would considerably change the overall result, given that road effects on bird richness are highly context-dependent.

All included studies had a control-impact (CI) design, which is useful in that it made them more comparable. Before-after and before-after-control-impact designs are very rare for the types of studies used in our meta-analyses, but should be highly encouraged in future studies, because there tends to be quite a bit of variation in control sites, and it is not always clear how different they are from road habitats aside from the absence of a road (also see Christie et al., 2020). We did test for effects of the type of predictor that studies were using to measure road impacts, and found no significant difference depending on whether they used 'absence' of roads (as opposed to 'presence', i.e. a categorical predictor) or 'far distance from roads' (as opposed to 'close distance', i.e. a continuous predictor) as a comparator. Impacts of roads on bird richness did also not differ depending on sampling methods used, or actual distance between road- and control sites.


Study number | Article number in Appendix Table S1 | Habitat type | Road type
SMD [95% CI]
Plants/Seed eaters
Study 1 | Article 17 | Open | Unpaved 0.8 [−0.5, 2.1]
Study 2 | Article 17 | Wood | Unpaved −0.4 [−1.4, 0.7]
Study 3 | Article 16 | Wood | Large 0.5 [0.1, 0.8]
Study 4 | Article 16 | Wood | Small 0.7 [0.6, 0.8]
Study 5 | Article 16 | Arable | Large 0.4 [0.2, 0.6]
Study 6 | Article 16 | Arable | Small 0.6 [0.5, 0.6]
Study 7 | Article 15 | Wood | Unpaved 0.5 [−0.7, 1.7]
Study 8 | Article 15 | Wood | Small 0.0 [−0.6, 0.6]
Study 9 | Article 8 | Arable | Unpaved 0.5 [−0.0, 1.0]
Study 10 | Article 7 | Open | Large 1.1 [0.3, 1.9]
Study 11 | Article 5 | Wood | Large 0.2 [−0.7, 1.1]
Study 12 | Article 1 | Woodland | Small 0.2 [−0.2, 0.6]
Study 13 | Article 1 | Woodland | Unpaved −0.2 [−0.6, 0.2]
0.22 [−0.05, 0.49]
Omnivores
Study 14| Article 17 | Wood | Unpaved −0.1 [−1.2, 0.9]
Study 15 | Article 16 | Wood | Large 0.9 [0.5, 1.2]
Study 16 | Article 16 | Wood | Small 0.8 [0.7, 1.0]
Study 17 | Article 16 | Arable | Large 0.5 [0.4, 0.7]
Study 18 | Article 16 | Arable | Small 0.6 [0.6, 0.7]
Study 19 | Article 15 | Wood | Unpaved 0.4 [−0.8, 1.6]
Study 20 | Article 15 | Wood | Small −0.7 [−1.3, −0.1]
Study 21 | Article 8 | Arable | Unpaved 0.2 [−0.3, 0.7]
Study 22 | Article 5 | Wood | Large −0.3 [−1.2, 0.6]
Study 23 | Article 3 | Wood | Large 0.4 [−1.2, 2.1]
Study 24 | Article 1 | Woodland | Small 0.5 [0.1, 0.9]
Study 25 | Article 1 | Woodland | Unpaved 0.4 [0.0, 0.9]
0.28 [0.01, 0.55]
Meat eaters
Study 26 | Article 16 | Wood | Large 0.7 [0.4, 1.1]
Study 27 | Article 16 | Wood | Small 0.5 [0.4, 0.6]
Study 28 | Article 16 | Arable | Large 0.3 [0.1, 0.5]
Study 29 | Article 16 | Arable | Small 0.2 [0.2, 0.3]
−0.08 [−0.35, 0.19]
Insectivores
Study 30 | Article 17 | Open | Unpaved 0.0 [−1.2, 1.2]
Study 31| Article 17 | Wood | Unpaved 0.0 [−1.0, 1.1]
Study 32 | Article 16 | Wood | Large 0.2 [−0.2, 0.5]
Study 33 | Article 16 | Wood | Small 0.1 [−0.0, 0.2]
Study 34 | Article 16 | Arable | Large 0.3 [0.2, 0.5]
Study 35 | Article 16 | Arable | Small 0.4 [0.4, 0.5]
Study 36 | Article 15 | Wood | Unpaved 0.0 [−1.2, 1.2]
Study 37 | Article 15 | Wood | Small −0.5 [−1.1, 0.1]
Study 38 | Article 8 | Arable | Unpaved −0.0 [−0.5, 0.5]
Study 39 | Article 5 | Wood | Large −0.8 [−1.7, 0.1]
Study 40 | Article 3 | Wood | Large −1.1 [−2.9, 0.6]
Study 41 | Article 1 | Woodland | Small 0.7 [0.3, 1.1]
Study 42 | Article 1 | Woodland | Unpaved 0.4 [−0.0, 0.8]
0.02 [−0.24, 0.29]
Fruit/Nectar feeders
Study 43 | Article 17 | Open | Unpaved 0.0 [−1.2, 1.2]
Study 44 | Article 17 | Wood | Unpaved −0.9 [−2.0, 0.2]
Study 45 | Article 15 | Wood | Unpaved −0.5 [−1.8, 0.7]
Study 46 | Article 3 | Wood | Large −1.0 [−2.8, 0.7]
−0.42 [−1.12, 0.28]
Overall effect 0.1 [−0.1, 0.4]
−3.0
−1.0
1.0
3.0
Standardized Mean Difference

4.6. Implications

The negative effect of increased tree cover on bird richness in road habitats suggests that introducing a clearing in forests is more detrimental than building a road in a landscape that is more open to begin with. Most woodland in our analyses was (near)natural forest, so forests that had seen low levels of human modification. It has previously been suggested that relatively undisturbed areas should be kept as intact as possible, and road-planners should focus on areas that are more homogenous as a result of higher human activity (Benítez-López et al., 2010; Ibisch et al., 2016; D'Amico et al., 2019; Ascensão et al., 2021). However, benefits of added heterogeneity may depend on specific local factors that need to be taken into consideration on a case by case basis. Roads may have positive effects in terms of making the landscape more heterogeneous, and/or increase overall species richness, yet if there are highly competitive species (either aggressive local competitors or invasive species), potential positive effects of roads may be counteracted, suggesting that there is a need to consider communities as a whole. Also, in one study that found strong effects of noisy miners, control sites (riparian habitat) in fact had lower abundance of this competing species (Hall et al., 2018), implying that planners should adopt a landscape perspective and not just look at roadsides in isolation (van der Ree et al., 2011). Indeed, benefits of road habitats may depend on how they contrast with the surrounding landscape (Meunier et al., 1999). In addition, if the target of a given road management or construction project is to promote establishment of specific species, dietary requirements of those species should be considered in the context of the given landscape.

4.7. Conclusions

We identified no overarching negative or positive effect of roads on bird richness. However, this does not imply that the presence of roads unproblematic, or that roadsides do not offer opportunities to serve as habitats with conservation value. The absence of an overall significant impact of roads indicates that effects differ a lot across studies, and that they are highly dependent on the context. Nonetheless, our meta-analyses did allow us to identify a couple of factors that significantly influence the relationship between roads and bird richness, i.e. tree cover and feeding guild association. When examining individual studies, it becomes clear that effects of roads also differ according to road and habitat type, and likely an interplay of other factors. The absence of significant effects of road or habitat type in the meta-analyses is likely due to species turnover and highlights that species richness alone may not be a suitable indicator for biodiversity or habitat quality, depending on the research agenda and goals of potential conservation efforts.

There are individual cases where roads have clear negative effects on species richness and the surrounding bird fauna (Fig. S3; Supporting information), or where no clear effects are apparent. Thus, in practise, it may be best to adopt a conservative approach: since there are risks, all roads should be considered potentially problematic, and not be considered beneficial until this has been proven. This should motivate future research which explicitly tests for differences in species composition and abundance, to try and disentangle contexts where a road will have negative effects, and where it will not. Indeed, it would be interesting to repeat the same kind of study for different biodiversity metrics and taxa. In birds, it would be possible to assimilate a data set for species abundance, although it is unlikely there would be enough data to carry out guild-specific analyses on the same data set.

CRediT authorship contribution statement

Svenja B. Kroeger: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Visualization, Writing – review & editing. **Hans M. Hanslin:** Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **Tommy Lennartsson:** Funding acquisition, Conceptualization, Writing – review & editing. **Marcello D'Amico:** Funding acquisition, Conceptualization, Writing – review & editing. **Johannes Kollmann:** Funding acquisition, Conceptualization, Writing – review & editing. **Christina Fischer:** Writing – review & editing. **Elena Albertsen:** Investigation. **James D.M. Speed:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Fig. 3. Forest plot showing mean effect size estimates (standardized mean differences) for studies grouped by feeding guilds. Estimates for the "plant/seed eater" (turquoise), "omnivore" (purple), "meat eater" (pink), "insectivore" (blue) and "fruit/nectar feeder" (orange) categories were derived from mixed-effects meta-regressions. Error bars indicate 95% confidence intervals. Point size indicates sample sizes (i.e. weight) and the overall summary represents the overall pooled effect size across all 46 effect size values extracted from 8 different articles. Article numbers correspond to the same article numbers in Appendix Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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