Effects of linear openings in forest canopy on temperate bird communities

Mariela Yapu-Alcazar[1], Raphaël Benerradi[2], Michael Wohlwend[1], Ilse Storch[1], Grzegorz Mikusinski[3], and Manisha Bhardwaj[1]

[1]University of Freiburg Faculty of Environment and Natural Resources
[2]University of Montpellier
[3]Swedish University of Agricultural Sciences

May 02, 2025

Abstract

Narrow, unpaved roads and paths are a ubiquitous feature of managed forest landscapes worldwide, with the potential to influence bird communities. However, compared to large roads with confirmed negative impacts like fragmentation and noise on birds, the effects of linear canopy openings and other structural changes caused by unpaved small forest roads and paths are less understood. In this study, we investigate the influence of narrow linear openings in the forest canopy caused by forest roads and paths on bird communities in the southern Black Forest, Germany. We aim to understand how these linear canopy openings affect species richness, community composition, and functional traits in forest birds. We surveyed bird communities in four distinct plot types, representing a gradient of 'canopy openness': forest interior, forest paths, forest roads, and forest edges. Forest roads and paths represent intermediate conditions between undisturbed interior forests (closed canopy) and a forest edge (open canopy). Our results show that while bird species richness remains relatively similar among those four plot types, the community composition at forest edges differs from the other plot types. In addition, functional traits like body mass and wing shape showed a weak response to the linear canopy openings. These results suggest that although unpaved forest roads and paths potentially introduce resources and structural modifications in the canopy, the effect on the birds seems limited compared to more pronounced habitat transitions, like those on forest edges. Our findings contribute to a better understanding of birds' responses to linear and small-scale fragmentation introduced by unpaved forest roads and paths. However, there is a need for more research to distinguish the ecological impact on bird communities in temperate managed forests along a gradient of canopy openness.

Mariela Yapu-Alcazar[1+], Raphaël Benerradi[1,2+], Michael Wohlwend[1], Grzegorz Mikusińsk[3], Ilse Storch[1], Manisha Bhardwaj[1]*

[1] *Chair of Wildlife Ecology and Management, University of Freiburg, Stefan-Meier Str 76, 79106 Freiburg, Germany*

++slugcomment: *To be submitted to the Astrophysical Journal Letter*

[2]*University of Montpellier, INRIA, Batiment 5 - 860 rue de St Priest, Montpellier, Occitanie 34095*

[3]*School for Forest Management, Swedish University of Agricultural Sciences, Box 43, 739 21 Skinnskatteberg, Sweden*

+ Authors should be considered shared first authors

**Corresponding author: mari14121991@gmail.com*

Abstract

Narrow, unpaved roads and paths are a ubiquitous feature of managed forest landscapes worldwide, with the potential to influence bird communities. However, compared to large roads with confirmed negative impacts like fragmentation and noise on birds, the effects of linear canopy openings and other structural changes caused by unpaved small forest roads and paths are less understood. In this study, we investigate the influence of narrow linear openings in the forest canopy caused by forest roads and paths on bird communities in the southern Black Forest, Germany. We aim to understand how these linear canopy openings affect species richness, community composition, and functional traits in forest birds. We surveyed bird communities in four distinct plot types, representing a gradient of 'canopy openness': forest interior, forest paths, forest roads, and forest edges. Forest roads and paths represent intermediate conditions between undisturbed interior forests (closed canopy) and a forest edge (open canopy). Our results show that while bird species richness remains relatively similar among those four plot types, the community composition at forest edges differs from the other plot types. In addition, functional traits like body mass and wing shape showed a weak response to the linear canopy openings. These results suggest that although unpaved forest roads and paths potentially introduce resources and structural modifications in the canopy, the effect on the birds seems limited compared to more pronounced habitat transitions, like those on forest edges. Our findings contribute to a better understanding of birds' responses to linear and small-scale fragmentation introduced by unpaved forest roads and paths. However, there is a need for more research to distinguish the ecological impact on bird communities in temperate managed forests along a gradient of canopy openness.*Keywords:* Canopy openings, forest roads, functional traits, habitat fragmentation.

Introduction

The expansion of road networks has widely impacted forested landscapes and species living in them (Vepakomma et al., 2018). For instance, in temperate and boreal forest environments, road networks of different scales crisscross these areas, creating corridors across the landscape and linearly breaking the continuity of the forest canopy (Riitters and Wickham, 2003). The ecological impacts of the disruption of the habitat continuity by roads, particularly on wildlife, have been widely studied and can be perceived as either beneficial or detrimental (Morelli et al., 2014). Among the negative effects, they can create habitat fragmentation (van der Ree et al., 2007), habitat loss(Kociolek et al., 2011), increased animal mortality(Reijnen and Foppen, 2006) , and pollution e.g., air, light, noise (Morelli et al., 2014). However, roads can also increase habitat heterogeneity by providing more resources originating from diversified vegetation (Helldin and Seiler, 2003; Palomino and Carrascal, 2007) and, in the case of birds, create perching and nesting opportunities (Morelli et al., 2014). Different types of linear infrastructures, including highways, rural roads, and forest roads, each have specific effects on biodiversity (Coffin et al., 2021). While much research has focused on large paved structures with high traffic volumes, unpaved minor forest roads require special attention because of their unique ecological consequences (Coffin et al., 2021; Šálek et al., 2010). On the one hand, the attractiveness of large road research is attributed to the scale of impact on biodiversity (Mammides et al., 2016). Large linear infrastructures, in addition to greatly modifying and fragmenting the landscape, also increase animal mortality and bring a greater flow of humans and pollution (Mammides et al., 2016; Robson and Blouin-Demers, 2013). In contrast, on a smaller scale, unpaved forest roads linearly fragment contiguous habitats, create openings in the canopy, and form edges that can modify the forest structure. Therefore, they are usually considered to have a weaker effect on biodiversity (Laurance, 2004; Ortega and Capen, 2002). However, the greater exposure to light due to the canopy opening modifies the microclimate and vegetation of the adjacent forest, influencing habitat availability for forest-dwelling species and even facilitating the presence of invasive plant species (Hanowski and Niemi, 1995; Mortensen et al., 2009; Tinker et al., 1998). Two kinds of roads can be identified in managed forests based on their size: big forest roads and small roads like skid trails and foot paths. The so-called forest roads provide access to heavier vehicles, while slid trails and paths are used for moving logs or by hikers(LWF, 2017; Mercier et al., 2019). These infrastructures cause linear openings, altering the ground due to compaction or trampling and altering light availability and microclimate to a greater and lesser extent, respectively. The disturbance results in a modified vegetation structure and composition, creating intermediate habitat types distinct from forest interior and forest edge conditions (Marchais et al., 2024; Zhou et al., 2020). These characteristics differ from those of more pronounced disturbances, such as intensive clear-cutting, but still play a significant role in forest ecosystems (Boston, 2016). The openness gradient may reflect an interface of structural complexity and openness, which can shape resource availability and influence biodiversity, particularly in bird communities (Šálek et al., 2010). Birds, particularly forest specialists, could be negatively affected by their dependence on undisturbed interior environments for nesting or foraging (Huhta et al., 1999). Nevertheless, generalist species might benefit from new foraging possibilities associated with openings in the canopy resulting from forest roads(da Silva et al., 2017; Kroeger et al., 2022). In some Central European forests, unpaved forest roads with reduced traffic volume can be considered environments of higher structural complexity. In areas of intensively managed forests, it has been found that these linear infrastructures could lead to an increase in the number and abundance of species of trees and shrubs compared to the forest interior (Klimo and Kulhavy, 2006). These narrow openings create corridors within the forest matrix, and although they are not the true forest edge by definition, they can still produce edge-like effects by modifying the vegetation structure and microclimate along the road (Šálek et al., 2010). Birds, for instance, may utilize the edges of forest roads for foraging (Ries et al., 2004; Yahner, 1988), highlighting the significance of these areas as environments with specific resources. The landscape supplementation hypothesis suggests that such modified areas, like the ones introduced by the roads, can support biodiversity by providing different foraging opportunities within the larger forest matrix (Dunning et al., 1992; Šálek et al., 2010). However, increasing openness in the canopy has risks as well, like a rise in bird brood parasitism and nest predation (Fletcher and Hutto, 2008; Johnson and Temple, 1990). In fact, it has been demonstrated that the closer to the forest edge, the higher the predation risks, which would ultimately lead to a greater abundance of specifics guilds (Chasko and Edward, 1982; Cox et al., 2012). The creation of linear openings in the canopy impacts bird diversity and influences interspecific competition via traits related to size and mobility (Newbold et al., 2013; Robertson et al., 2013). More open habitat types often represent areas with altered resource availability, where species with greater body mass, usually associated with competitive dominance, may be better equipped to exploit resources. Conversely, smaller species may struggle in these environments because of strong competition from larger species (Brown, 2007; Pfeifer et al., 2017). The traits related to mobility would considerably affect how species navigate through fragmented habitats, affecting their capacity to reach and utilize available environments in line with the habitat complexity-maneuverability constraints hypothesis (Polo and Carrascal, 1999). Birds with a higher hand-wing index (HWI) and body mass, which implies greater flight capacity and efficiency, would be better able to move along the linear openings, between habitat margins and adjacent forest patches, allowing them to use resources from several environments. On the other hand, less mobile species (with lower HWI) and small size would have fewer resource availability and dispersal options, thereby restricting their ability to benefit from alternative, more open habitats (Claramunt et al., 2012a; Sheard et al., 2020). Forest roads create canopy disruptions, partially resembling forest edges from a bird's perspective, and exhibit ecological characteristics that can both have positive and negative impacts (Helldin and Seiler, 2003; Palomino and Carrascal, 2007; Wu et al., 2023). However, limited research has been done on this phenomenon in areas with dense networks of such roads, such as managed temperate forests. Šálek et al. (2010) reported that low-traffic forest roads in Czech secondary production forests managed mostly by rotation forestry can increase bird species richness and diversity by creating edge habitats. To see if such influence applies to unevenly aged continuous-cover production forests, we focus on the southern Black Forest, Germany, where forest management practices aim to preserve biodiversity and promote natural regeneration along with production goals (Bauhus et al., 2013; Storch et al., 2020). Our study assesses two key response dimensions from birds to the linear openings in the canopy created by linear forest infrastructure: community response and trait response. For the community response, we evaluate whether species richness, diversity, and community composition of bird communities differ among sites with different levels of canopy openings - namely, forest interiors, paths, forest roads, and edges (see Figure 1). We predict that forest roads, followed by paths would allow for a more diverse and differently composed community than in forest interiors (P1). In addition, we evaluated functional traits connected to mobility, body mass, and HWI and how these influence the response of birds to linear openings in the canopy. We predict these traits will be more pronounced in species with a favorable response to habitat openings (P2). Therefore, our study evaluates whether linear openings in the canopy introduced by forest roads and paths act as complementary habitats for forest birds. Our questions align with the landscape supplementation hypothesis (Dunning et al., 1992)and the habitat complexity-maneuverability constraints hypothesis (Polo and Carrascal, 1999) to reveal the role of these areas in shaping bird community dynamics in temperate forest ecosystems. By answering these questions, we aim to provide insight into the bird communities' responses to smaller disturbances. This information can be valuable in the context of biodiversity in managed forests.

2. Methods

2.1 Study area and site selection

We conducted this study in the southern Black Forest region in Germany (47.66-48.17°N, 7.72-8.64°E) within temperate mixed mountain forests located in a low mountain region in Central Europe (altitude 516-1120 m). For biodiversity conservation, these production forests are managed under close-to-nature forestry guidelines, resulting in a mixed, uneven-aged, and structurally diverse forest with continuous canopy cover (Bauhus et al., 2013; Kändler and Cullmann, 2015). Since we were interested in exploring how different linear openings in the canopy affect bird communities, we surveyed birds on four plot types: closed forest, forest paths, forest roads, and forest edges in close proximity to one another (Figure 1, Table 1). Plots were spatially clustered into 11 distinct 'Sites' (based on the broader research framework established by the Research Training Group "Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe"; Figure 1; Storch et al., 2020). Sites were at least 5 km from each other, and plots within sites were at least 300 m apart to ensure independent sampling (Bibby et al., 2000; Sutherland, 2006), except at one site, where geographical constraints meant the plots were 200 m apart instead. The sites were far from other canopy openings caused by natural (e.g., windthrow and bark beetle) or anthropogenic factors (e.g., logged areas).

2.2 Bird survey and functional traits

We used fixed-radius point counts to assess the composition of bird communities at each plot. From the center of the plot, an observer recorded a count of each species seen or heard in a 50 m radius over four consecutive five-minute intervals (Balestrieri et al., 2017; Bibby et al., 2000; Sutherland, 2006). After each survey, we assigned the abundance of each species on the plot according to the maximum abundance recorded in any of the four five-minute point count intervals. Each plot was visited twice, with at least seven days between the two visits. For the first visit round, we started with the five sites at the lowest elevations to avoid traces of snow. With the remaining sites, we randomly chose the order of the visits to the sites and the order of the plots within the site (*random.shuffle* module of the site IDs and the plots) in Python (van Rossum and Drake, 2009). We always surveyed all four plots within a site on the same day. We conducted bird surveys between sunrise and midday and during the breeding season (April and May) in 2023 (according to Balestrieri et al. 2017). Overall, we conducted 88 bird surveys – two visits to four plots in 11 sites. To assess the impact on the functional traits, for each species observed during the bird surveys, we extracted the average HWI and body mass from the AVONET database (Tobias et al., 2022). For each plot visit, we define the average body mass and the average HWI observed as the mean of the HWI of the species, weighted by the relative abundance of each species observed during the visit.

2.3 Statistical analysis

We utilized species richness and the Shannon-Wiener Index (Pielou, 1966; Shannon, 1948) as indicators to examine the variations in bird communities across different plot types. Species richness provides an easy count of species present, reflecting an area's overall biodiversity. Conversely, the Shannon-Wiener Index considers both species richness and evenness, providing a deeper understanding of how individuals are distributed among the species found (Magurran, 2003; Whittaker, 1972). To compare these indicators across various plot types, we employed generalized linear mixed models (GLMMs), using a Poisson distribution for species richness and a Gamma distribution for the Shannon Index, including a random effect for site ID. We conducted Tukey's HSD post hoc tests to assess the mean differences of each metric across the plot types based on these statistical models (Zar, 2010). To further investigate the differences in species composition among the plot categories, we applied the Jaccard Index of Dissimilarity calculated from abundances, defined as 2B/(1+B) (Oksanen et al., 2013), where B represents Bray-Curtis dissimilarity (Jaccard, 1912). We explored dissimilarities in community compositions at each plot using Non-Metric Multi-Dimensional Scaling (NMDS) analyses (Clarke, 1993), based on the relative distance between plots according to the Jaccard index. We then conducted an Analysis of Similarity (ANOSIM) based on the NMDS representation to test for differences between the four plot types, considering the differences between bird communities per survey (Clarke, 1993). Finally, we compared the body mass and HWI, both abundance-weighted, between the types of plots by using GLMMs with Gamma distributions and applying Tukey's HSD post hoc tests on these models, similar to those for the Shannon Index. We conducted all analyses in R version 4.2.1 (R Core Team, 2023), using the packages vegan (version 2.6.2) for biodiversity indices and ANOSIM (Oksanen et al., 2013), multcomp (version 1.4-25) for Tukey's tests (Hothorn et al., 2016), and lme4 (version 1.1.35.5) for GLMMs (Bates et al., 2014).

Results

3.1 Community level responses

Average species richness tended to be higher in forest plots than in path and road plots and lower than in edge plots; however, these differences were not statistically significant ($p > 0.05$ for all combinations; Figure 2a). In contrast, the Shannon-Wiener Index was significantly lower in path and road plots compared to edge plots ($p_{\text{edge-path}} = 0.033$, $p_{\text{edge-road}} = 0.048$), but not significantly different between paths and roads (Figure 2b). Also, the index at forest plots tended to be higher than at paths and roads but lower than at edge plots, though these differences were not statistically significant (Supporting Information S2 and S3). Overall, the community compositions in forest, path, and road plots are relatively similar to one another (Figure 3). Community composition in edge plots differed the most from the other plot types (Table 2, Figure 3, Supporting Information S4). The lack of clear separation between the 95% confidence ellipses for the centroids suggests that while species compositions significantly differ between plot types, the overall dissimilarity is not strong enough to form visually distinct clusters.

3.2 Functional traits response

The weighted mean body mass tended to be lower in path plots compared to the other plot types (Figure 4), but the relationship was only significant when compared to edge plots ($p_{\text{edge-path}} = 0.03$). The average HWI was significantly higher in edges than in other types of plots ($p_{\text{edge-path}} < 0.001$); however, it did not differ among forests, paths, and roads ($p_{\text{forest-path}} = 0.27$, $p_{\text{forest-road}} = 0.99$, $p_{\text{path-road}} = 0.34$) (Supporting Information S7).

Discussion

In this study, we investigated the understudied ecological effects of linear canopy openings created by forest roads and paths on bird communities. Our results show that species richness was similar across forest interiors, roads, paths, and edges. However, we found differences in community diversity (Shannon-Wiener Index) and specific traits like body size and Hand-Wing Index (HWI). Overall, bird species and trait diversity on paths and roads were more similar to forest interiors than forest edges, contradicting our predictions that bird communities along small roads and paths would resemble those of forest edges. These results suggest that in spite of the structural differences due to the linear opening in the canopy, forest roads and paths do not act as distinct habitats like the edge itself. Rather, birds respond to these areas as embedded within the forest. Our findings reveal to what extent linear canopy openings influence bird communities, offering valuable insight into how narrow forest roads affect biodiversity in temperate managed forests.

4.1. Limited impact of linear canopy openings

We predicted (P1) that bird communities would be affected by linear canopy openings, with an increase in richness and diversity in these sites similar to the edges. However, our results show that bird communities are slightly less diverse along forest roads and paths, they do not significantly differ from the forest interior. The homogenous species richness across the four plot types supports the landscape supplementation hypothesis (Dunning et al., 1992), and suggests that birds in the Black Forest utilize the resources of the different plot types rather than being restricted to a specific one. Furthermore, the Shannon-Wiener diversity index and ANOSIM analysis revealed that only forest edge communities differed significantly from the other plot types. Thus, in our study, the expected impact of canopy openness was only observed at plots with the extreme, most open canopies, and not in the intermediate plot types. The pattern of limited sensitivity to structural differences and human-induced disturbance in forests has been previously reported in the context of European forest bird communities (Basile et al., 2021; Lelli et al., 2019; Matuoka et al., 2020). This resilience to environmental changes is a notable characteristic among generalist species, which are particularly dominant in temperate European forests such as the Black Forest. Several bird species in our study area may prefer forests as a habitat but also feed in nearby open areas (e.g., thrushes) (Chiatante, 2022; Najmanová and Adamík, 2009), demonstrating flexible habitat use. European temperate forest birds appear more adaptable to environmental changes than other bird guilds worldwide, likely reflecting a legacy effect of centuries of habitat alteration by human activity (Salisbury et al., 2012). Biodiversity in the Black Forest region has been shaped by generations of land-use practices, including intense forestry (Brandl, 2006), and bird species composition is expected to be fairly homogeneous in this production-oriented forest system (Basile et al., 2021; Freemark and Kirk, 2001). Moreover, birds in central European forests are mostly residents or short-distance migrants, with fewer tropical migrants (van Turnhout et al., 2010; Villard and Foppen, 2018). The weak response to canopy opening in our study may be due to the fact that our study area is dominated by resident species that are highly resistant to human activity (Reif et al., 2022), whereas, reported that the most the effects of habitat perturbation tend to be more pronounced in long-distance migrants (Gregory et al., 2007). The weak reduction in the Shannon-Wiener Index that we observed in paths and forest roads, compared to forest interiors, may be because narrow corridors frequently can act as ecological traps for birds, increasing predation and brood parasitism (Gates and Gysel, 1978; Henle et al., 2004; Rich et al., 1994). We suggest that the legacy of management and human alteration in the Black Forest may have curated a homogenous community composition, dominated by generalists with flexible habitat use, which likely buffers against structural changes such as linear canopy openings in our study. Therefore, the real impact of forest structural changes on birds must be assessed together with regional and historical context.

Scale of the linear canopy openings and bird mobility

The lack of response to canopy openings is also reflected in our functional trait results. We did not observe the gradual increase in body mass along the gradient of canopy openness (from forest interior through paths and forest roads to edges), that we expected. We expected body mass to be considerably higher on forest roads and paths compared to interiors, where the canopy openness allows more mobility than in forest interiors. Contrastingly, we found that interior of the forest has larger birds. Similarly, HWI does not show significant changes in the openness gradient, contradicting the habitat complexity-maneuverability constraints hypothesis (Polo and Carrascal, 1999). The increase in HWI is only found at the edges, where birds should certainly be adapted to longer flights (Claramunt et al., 2012b; Sheard et al., 2020). These findings suggest that only large openings affect these traits, and therefore, forest roads and paths in our study area do not reach the threshold width of openness necessary to influence bird mobility traits. The effects of the level of openness width have been documented in previous studies as a considerable factor (e.g.,Šálek et al., 2010; Wu et al., 2023). In both studies, where canopy openings caused by forest roads are also evaluated, the stronger effect on bird communities is reported the wider the road is. While openings like unpaved roads can increase the number of potential niches (Kociolek et al., 2011; Sander and Tietze, 2022), similar types of openings on a larger scale bring fragmentation and habitat loss, reducing the ecological value for birds(Rich et al., 1994). In our case, the canopy openings were narrow, with a 3-5 m width, contrasting the opening scale towards the forest edge. mentioned the importance of the size of fragments within a matrix like the forest. Despite the heterogeneity created by the introduction of openings, highly mobile species like birds might still perceive a continuous habitat where they cross the small breaks (Lord and Norton, 1990). This reinforces the findings of the traits and leads us to conclude that the linear canopy openings in our study area would function primarily as movement corridors within the forest rather than novel environments with unique structural features like those on the edge for birds.

Limitations and new directions

Our findings attempted to clarify the ecological impacts of linear openings in the canopy created by low-traffic roads and offer a glimpse of the bird communities' responses along an openness gradient in temperate managed forests. However, we noted that three methodological limitations should be considered when interpreting or extrapolating these results. First, the results we provide are restricted to the breeding season, and we did not include site-specific variables that would provide a bigger picture of bird response to these plot types. On the one hand, even though most of the bird research is done during the breeding season, bird dynamics in temperate forests vary with seasonality throughout the year. During early spring or winter, the linear openings in forest roads may play different ecological roles as they frequently act as early warm sunny spots during snowmelt, exposing resources important for birds replenishing gastroliths (Keyser et al., 2023; Resano-Mayor et al., 2019). Also, small trees like Rowan are more common along roads and are potential food resources before winter (Askeyev et al., 2024). Secondly, site-specific aspects, encompassing slope, orientation, and site-to-site structural changes, could significantly influence microclimatic conditions, vegetation structure, and resource availability, potentially shaping bird community responses along linear openings in the canopy (Ogée et al., 2024; Wang et al., 2014). Finally, as previously mentioned, a factor to consider that could strengthen our findings is incorporating wider linear canopy openings as Šálek et al. (2010) and Wu et al. (2023). Observations over a broader gradient may give better inferences of the impacts of resource availability and scale dependency on the response observed in bird communities. To address these challenges, we encourage future research regarding linear openings in the canopy due to forest roads to address the aforementioned variables, particularly over a greater gradient of canopy openness. Where possible, before-after control-impact (BACI) experimental designs, may provide a powerful experimental way of measuring the environmental impact of these infrastructures in the forest (Klein et al., 2022; Roedenbeck et al., 2007). Such design could be applied to both planned new forest roads and forest roads that are removed as forest restoration measure (Switalski and Nelson, 2011; van der Ree et al., 2015).

Conclusion

Our findings indicate that although forest roads and paths may induce structural heterogeneity, their role is established more as supplementary areas to the main bird habitat within or at the edge of the forest and not a distinct one. The weak response of the bird communities to these linear structures indicates that birds show a clear response to a more abrupt habitat transition such as edges. Although some species and groups respond to linear canopy openings, no evidence indicates that these features enhance diversity or mimic edge effects. The absence of significant trait-based differences further suggests that narrow forest roads and paths do not impose distinct selective pressures on species. While we cannot confirm that these roads are detrimental to bird communities, we cannot confirm a positive effect. The scope of our work allows us to clarify a small part of the bird responses involving unpaved forest roads. Future research could examine the interplay between habitat connectivity, vegetation structure, and road and canopy width openings to further disentangle their effects on bird communities in similarly managed landscapes.

Data Accessibility Statement

The data that support the findings of this study are openly available in Figshare repository at https://figshare.com/s/2a4de30d3f02750df921.

Author Contributions

Mariela Yapu-Alcazar: conceptualization (equal), investigation (equal), methodology (equal), supervision (equal), writing original - draft (lead). **Raphaël Benerradi** *:* conceptualization (equal), investigation (lead), methodology (equal), data curation (lead), formal analysis (lead), writing – original draft (equal).**Michael Wohlwend:** conceptualization (equal), supervision (equal), writing – review and editing (equal). **Grzegorz Mikusiński***:* writing – review and editing (equal). **Ilse Storch:** funding acquisition (lead), writing – review and editing (equal)*,* **Manisha Bhardwaj:** conceptualization (equal), methodology (equal), supervision (lead), writing – review and editing (lead).

Acknowledgments

We are grateful to F. Saitel for the support during fieldwork for data collection, S. Lemler for the advice on the statistical analysis, and ForstBW for allowing us to work in the area. Funding for this research was provided by the German Research Foundation (DFG) under the ConFoBi Research Training Group "Conservation of Forest Biodiversity in Multiple-Use Landscapes of Central Europe" (GRK 2123) conducted at the University of Freiburg.

Conflicts of Interest

The authors declare no conflicts of interest.

++slugcomment: *To be submitted to the Astrophysical Journal Letter*

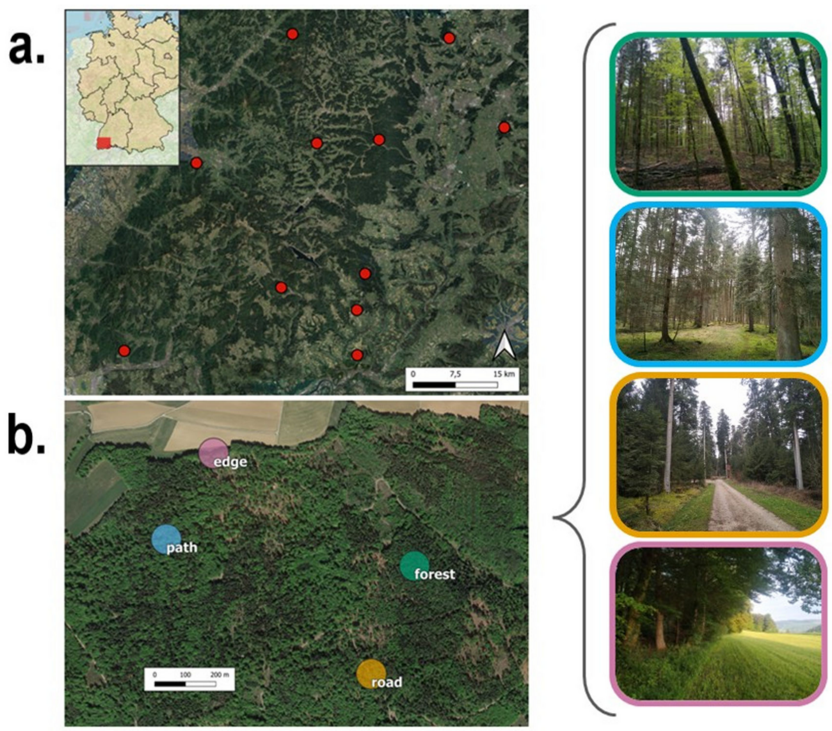
References

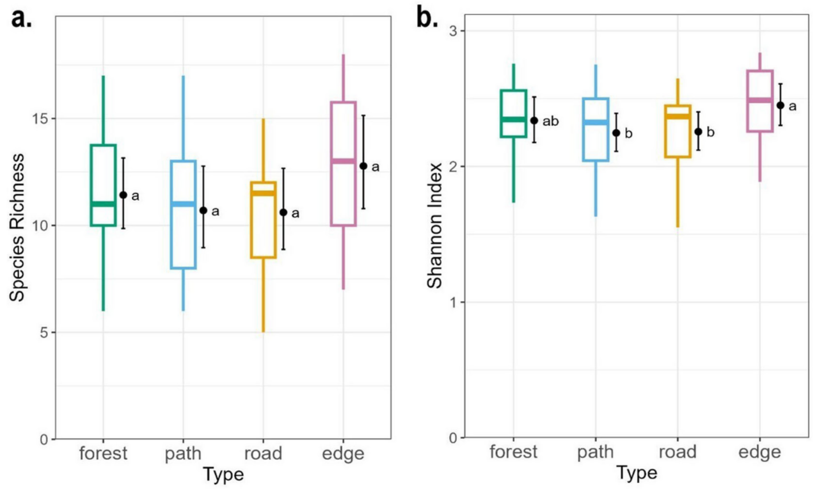
Askeyev, A., Askeyev, O., Askeyev, I., Sparks, T., 2024. Factors Affecting the Winter Distribution of Birds in Forests at the Eastern Edge of Europe. Birds 5, 308–327. https://doi.org/10.3390/birds5020020 Balestrieri, R., Basile, M., Posillico, M., Altea, T., Matteucci, G., 2017. Survey effort requirements for bird community assessment in forest habitats. Acta Ornithol 52, 1–9. https://doi.org/10.3161/00016454AO2017.52.1.001 Basile, M., Storch, I., Mikusiński, G., 2021. Abundance, species richness and diversity of forest bird assemblages – The relative importance of habitat structures and landscape context. Ecol Indic 133, 108402. https://doi.org/10.1016/j.ecolind.2021.108402 Bates, D., Maechler, M., Bolker, B., Walker, S., Haubo Bojesen, R., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., Krivitsky, P.N., Tahaka, E., Jagan, M., 2014. Linear Mixed-Effects Models using "Eigen" and S4. https://doi.org/10.48550/arXiv.1406.5823Focustolearnmore Bauhus, J., Puettmann, K.J., Kühne, C., 2013.

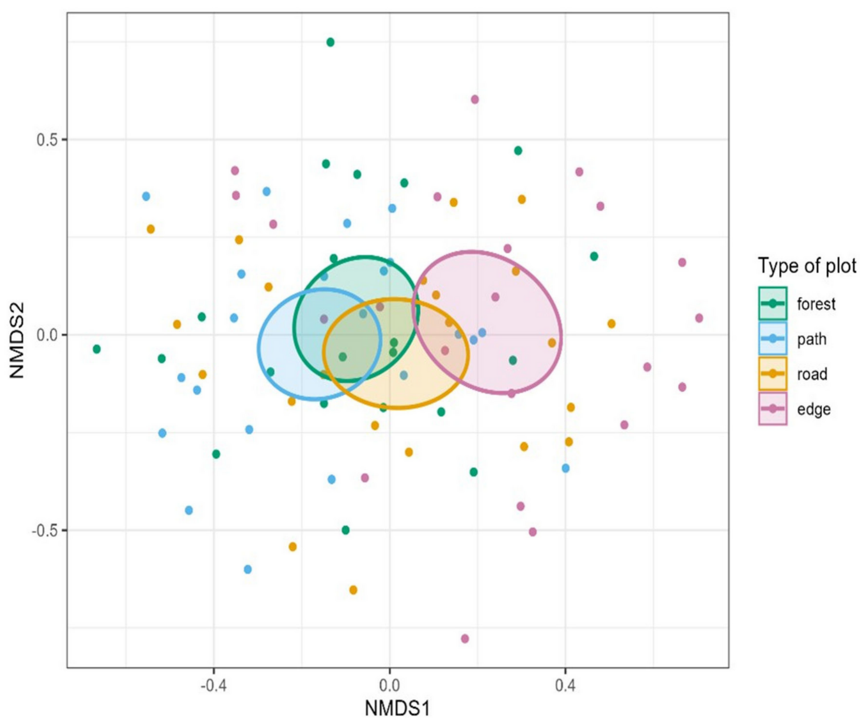
Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems?, in: Messier, C., Puettmann, K. (Eds.), Managing Forests as Complex Adaptive Systems. Routledge, New York, pp. 187–213. https://doi.org/10.4324/9780203122808 Bibby, C.J., Burgess, N., Hill, D.A., Moustoe, S., 2000. Bird census techniques, 2nd Edition. ed. Elsevier. Boston, K., 2016. The Potential Effects of Forest Roads on the Environment and Mitigating their Impacts. Current Forestry Reports. https://doi.org/10.1007/s40725-016-0044-x Brown, W.P., 2007. Body mass, habitat generality, and avian community composition in forest remnants. J Biogeogr 34, 2168–2181. https://doi.org/10.1111/j.1365-2699.2007.01766.x Chasko, G.G., Edward, J., 1982. Avian Habitat Suitability along a Transmission-Line Corridor in an Oak-Hickory Forest Region. Wildlife Monographs 82, 3–41. Chiatante, G., 2022. Habitat use of the mistle thrush (Turdus viscivorus): the importance of urban areas and permanent crops. J Vertebr Biol 71, 22041. https://doi.org/10.25225/jvb.22041 Claramunt, S., Derryberry, E.P., Remsen, J. V., Brumfield, R.T., 2012a. High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proceedings of the Royal Society B: Biological Sciences 279, 1567–1574. https://doi.org/10.1098/rspb.2011.1922 Claramunt, S., Derryberry, E.P., Remsen, J. V., Brumfield, R.T., 2012b. High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proceedings of the Royal Society B: Biological Sciences 279, 1567–1574. https://doi.org/10.1098/rspb.2011.1922 Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x Coffin, A.W., Ouren, D.S., Bettez, N.D., Daniels, A.E., Grilo, C., Jochen, J., Navarro, L., Preisler, H., Rauschert, E., 2021. The Ecology of Rural Roads: Effects, Management, and Research, Issues in Ecology. Cox, W.A., Thompson, F.R., Faaborg, J., 2012. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. Landsc Ecol 27, 659–669. https://doi.org/10.1007/s10980-012-9711-x da Silva, V., Deffaci, A.C., Hartmann, M.T., Hartmann, P.A., 2017. Birds around the road: Effect of a road on a Savannah bird community in Southern Brazil. Ornitologia Tropical 28. https://doi.org/10.58843/ornneo.v28i0.189 Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological Processes That Affect Populations in Complex Landscapes. Oikos 65, 169–175. https://doi.org/10.2307/3544901 Fletcher, R.J., Hutto, R.L., 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. Landsc Ecol 23, 727–739. https://doi.org/10.1007/s10980-008-9233-8 Freemark, K.E., Kirk, D.A., 2001. Birds on organic and conventional farms in Ontario: partitioning effects of habitat and practices on species composition and abundance. Biol Conserv 101, 337–350. https://doi.org/10.1016/S0006-3207(01)00079-9 Gates, J.E., Gysel, L.W., 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59, 871–883. https://doi.org/10.2307/1938540 Hanowski, J.M., Niemi, G.J., 1995. Experimental Design Considerations for Establishing an Off-Road, Habitat-Specific Bird Monitoring Program Using Point-Counts. Helldin, J., Seiler, A., 2003. Effects of roads on the abundance of birds in Swedish forest and farmland. Wildlife Biol 6, 111–120. https://doi.org/10.2981/wlb.2000.006 Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodivers Conserv 13, 207–251. https://doi.org/10.1023/B:BIOC.0000004319.91643.9e Hothorn, T., Bretz, F., Westfall, P.H., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S., 2016. Package 'multcomp'. Simultaneous inference in general parametric models. Project for Statistical Computing. Vienna, Austria. Huhta, E., Jokimaki, J., Rahko, P., 1999. Breeding success of pied flycatchers in artificial forest edges: the effect of suboptimally shaped foraging area. Auk 116, 528–535. https://doi.org/10.2307/4089385 Jaccard, P., 1912. The distribution of the flora in the alpine zone. New phytologist 11, 37–50. Johnson, R.G., Temple, S.A., 1990. Nest Predation and Brood Parasitism of Tallgrass Prairie Birds. J Wildl Manage 54, 106–111. https://doi.org/10.2307/3808909 Kandler, G., Cullmann, D., 2015. Regionale auswertung der bundeswaldinventur 3, wuchsgebiet Schwarzwald, Freiburg, Freiburg, Germany: Forstliche Versuchs-und Forschungsanstalt Baden-Wurttemberg (FVA).[Google Scholar]. Keyser, S.R., Fink, D., Gudex-Cross, D., Radeloff, V.C., Pauli, J.N., Zuckerberg, B., 2023. Snow cover dynamics: an overlooked yet important feature of winter bird occurrence and abundance across the United States. Ecography 2023, e06378. https://doi.org/10.1111/ecog.06378 Klein, J., Low, M., Sjogren, J., Eggers, S., 2022. Short-term experimental support for bird diversity retention measures during thinning in European boreal forests. For Ecol Manage 509, 120084. https://doi.org/10.1016/j.foreco.2022.120084 Klimo, E., Kulhavy, J., 2006. Norway spruce monocultures and their transformation to close-to-nature forests from the point of view of soil changes in the Czech Republic. Ekologia(Bratislava)/Ecology(Bratislava) 25, 27–43. Kociolek, A. V., Clevenger, A.P., St. Clair, C.C., Proppe, D.S., 2011. Effects of Road Networks on Bird Populations. Conservation Biology. https://doi.org/10.1111/j.1523-1739.2010.01635.x Kroeger, S.B., Hanslin, H.M., Lennartsson, T., D'Amico, M., Kollmann, J., Fischer, C., Albertsen, E., Speed, J.D.M., 2022. Impacts of roads on bird species richness: A meta-analysis considering road types, habitats and feeding guilds. Science of the Total Environment 812. https://doi.org/10.1016/j.scitotenv.2021.151478 Laurance, W.F., 2004. Forest-climate interactions in fragmented tropical landscapes. Philos Trans R Soc Lond B Biol Sci 359, 345–352. https://doi.org/10.1098/rstb.2003.1430 Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, O., Goldberg, I., Nascimbene, J., Tottrup, A.P., Rahbek, C., 2019. Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. For Ecol Manage 432, 707–717. https://doi.org/10.1016/j.foreco.2018.09.057 Lord, J.M., Norton, D.A., 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4, 197–202. https://doi.org/10.1111/j.1523-1739.1990.tb00109.x LWF, 2017. Feinerschliessung – Ruckegassen und Ruckewege. LWF. Magurran, A., 2003. Measuring biological diversity. John Wiley & Sons. Mammides, C., Kounnamas, C., Goodale, E., Kadis, C., 2016. Do unpaved, low-traffic roads affect bird communities? Acta Oecologica 71, 14–21. https://doi.org/10.1016/j.actao.2016.01.004 Marchais, M., Arseneault, D., Bergeron, Y., 2024. Forest roads act as habitat corridors for Populus tremuloides in the boreal forest of eastern Canada. Front Ecol Evol 11, 1336409. https://doi.org/10.3389/fevo.2023.1336409 Matuoka, M.A., Benchimol, M., de Almeida-Rocha, J.M., Morante-Filho, J.C., 2020. Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. Ecol Indic 116, 106471. https://doi.org/10.1016/j.ecolind.2020.106471 Mercier, P., Aas, G., Dengler, J., 2019. Effects of skid trails on understory vegetation in forests: a case study from Northern Bavaria (Germany). For Ecol Manage 453, 117579. Morelli, F., Beim, M., Jerzak, L., Jones, D., Tryjanowski, P., 2014. Can roads, railways and related structures have positive effects on birds? - A review. Transp Res D Transp Environ 30, 21–31. https://doi.org/10.1016/j.trd.2014.05.006 Mortensen, D.A., Rauschert, E.S.J., Nord, A.N., Jones, B.P., 2009. Forest roads facilitate the spread of invasive plants. Invasive Plant Sci Manag 2, 191–199. https://doi.org/doi.org/10.1614/IPSM-08-125.1 Najmanova, L., Adamik, P., 2009. Effect of climatic change on the duration of the breeding season in three European thrushes. Bird Study 56, 349–356. https://doi.org/10.1080/00063650902937305 Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proceedings of the Royal Society B: Biological Sciences 280. https://doi.org/10.1098/rspb.2012.2131 Ogée, J., Walbott, M., Barbeta, A., Corcket, E., Brunet, Y., 2024. Decametric-scale buffering of climate extremes in forest understory within a riparian microrefugia: the key role of microtopography. Int J Biometeorol 1–15. https://doi.org/doi.org/10.1007/s00484-024-02702-9 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Wagner, H., Oksanen, M.J., Stevens, M.H.H., 2013. Package 'vegan'. Community ecology package, version. Ortega, Y.K., Capen, D.E., 2002. Roads as edges: effects on birds in forested landscapes. Forest Science 48, 381–390. https://doi.org/10.1093/forestscience/48.2.381 Palomino, D., Carrascal, L.M., 2007. Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. Biol Conserv 140, 100–109. https://doi.org/10.1016/j.biocon.2007.07.029 Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peters, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C., Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187–191. https://doi.org/10.1038/nature24457 Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J Theor Biol 13, 131–144. Polo, V., Carrascal, L.M., 1999. Shaping the body mass distribution of Passeriformes: habitat use and body mass are evolutionarily and ecologically related. Journal of Animal Ecology 68, 324–337. https://doi.org/doi.org/10.1046/j.1365-2656.1999.00282.x Reif, J., Skálová, A.J., Vermouzek, Z., Voříšek, P., 2022. Long-term trends in forest bird populations reflect management changes in Central European forests. Ecol Indic 141, 109137.

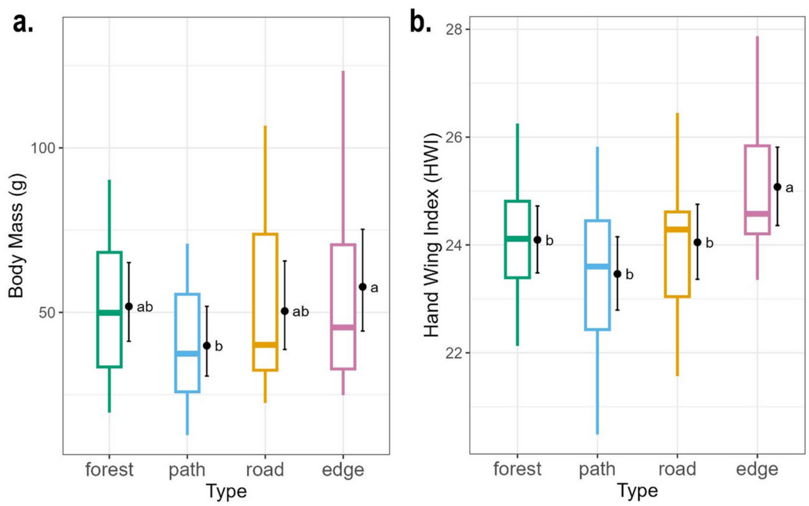
https://doi.org/10.1016/j.ecolind.2022.109137 Reijnen, R., Foppen, R., 2006. Impact of road traffic on breeding bird populations, in: Davenport, J., Davenport, J.L. (Eds.), The Ecology of Transportation: Managing Mobility for the Environment. Springer, Dordrecht, pp. 255–274. Resano-Mayor, J., Korner-Nievergelt, F., Vignali, S., Horrenberger, N., Barras, A.G., Braunisch, V., Pernollet, C.A., Arlettaz, R., 2019. Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change. Biodivers Conserv 28, 2669–2685. https://doi.org/10.1007/s10531-019-01786-9 Rich, A.C., Dobkin, D.S., Niles, L.J., 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. Conservation biology 8, 1109–1121. https://doi.org/10.1046/j.1523-1739.1994.08041109.x Ries, L., Fletcher Jr, R.J., Battin, J., Sisk, T.D., 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu. Rev. Ecol. Evol. Syst. 35, 491–522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148 Riitters, K.H., Wickham, J.D., 2003. How far to the nearest road? Front Ecol Environ 1, 125–129. https://doi.org/doi.org/10.1890/1540-9295(2003)001[0125:HFTTNR]2.0.CO;2 Robertson, O.J., McAlpine, C., House, A., Maron, M., 2013. Influence of Interspecific Competition and Landscape Structure on Spatial Homogenization of Avian Assemblages. PLoS One 8. https://doi.org/10.1371/journal.pone.0065299 Robson, L.E., Blouin-Demers, G., 2013. Eastern hognose snakes (Heterodon platirhinos) avoid crossing paved roads, but not unpaved roads. Copeia 2013, 507–511. Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlahan, J.E., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S., Van der Grift, E.A., 2007. The Rauischholzhausen agenda for road ecology. Ecology and society 12. https://doi.org/10.5751/ES-02011-120111 Šálek, M., Svobodová, J., Zasadil, P., 2010. Edge effect of low-traffic forest roads on bird communities in secondary production forests in central Europe. Landsc Ecol 25, 1113–1124. https://doi.org/10.1007/s10980-010-9487-9 Salisbury, C.L., Seddon, N., Cooney, C.R., Tobias, J.A., 2012. The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. Ecol Lett 15, 847–855. https://doi.org/10.1111/j.1461-0248.2012.01806.x Sander, M.M., Tietze, D.T., 2022. Impacts of Traffic Infrastructure on Urban Bird Communities: A Review. Sustainability 14, 16805. https://doi.org/10.3390/su142416805 Shannon, C.E., 1948. The mathematical theory of communication. The Bell System Technical Journal 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x Sheard, C., Neate-Clegg, M.H.C., Alioravainen, N., Jones, S.E.I., Vincent, C., MacGregor, H.E.A., Bregman, T.P., Claramunt, S., Tobias, J.A., 2020. Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat Commun 11. https://doi.org/10.1038/s41467-020-16313-6 Storch, I., Penner, J., Asbeck, T., Basile, M., Bauhus, J., Braunisch, V., Dormann, C.F., Frey, J., Gärtner, S., Hanewinkel, M., Koch, B., Klein, A.M., Kuss, T., Pregernig, M., Pyttel, P., Reif, A., Scherer-Lorenzen, M., Segelbacher, G., Schraml, U., Staab, M., Winkel, G., Yousefpour, R., 2020. Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of Central Europe using an interdisciplinary, multi-scale approach. Ecol Evol 10, 1489–1509. https://doi.org/10.1002/ece3.6003 Sutherland, W.J., 2006. Ecological census techniques: a handbook. Cambridge university press, New York. Switalski, T.A., Nelson, C.R., 2011. Efficacy of road removal for restoring wildlife habitat: Black bear in the Northern Rocky Mountains, USA. Biol Conserv 144, 2666–2673. https://doi.org/10.1016/j.biocon.2011.07.026Getrightsandcontent Tinker, D.B., Resor, C.A.C., Beauvais, G.P., Kipfmueller, K.F., Fernandes, C.I., Baker, W.L., 1998. Watershed analysis of forest fragmentation by clearcuts and roads in a Wyoming forest. Landsc Ecol 13, 149. https://doi.org/10.1023/A:1007919023983 Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M.H.C., Alioravainen, N., Weeks, T.L., Barber, R.A., 2022. AVONET: morphological, ecological and geographical data for all birds. Ecol Lett 25, 581–597. https://doi.org/10.1111/ele.13898 van der Ree, R., Jaeger, J.A.G., Rytwinski, T., van der Grift, E.A., 2015. Good science and experimentation are needed in road ecology, in: Van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. Wiley Online Library, pp. 71–81. van der Ree, R., van der Grift, E.A., Estacio, C.M., Suarez, F., 2007. Overcoming the Barrier Effect of Roads-How Effective Are Mitigation Strategies?, in: Leroy Irwin, C., Nelson, D., McDermott, K.P. (Eds.), Proceedings of the 2007 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, pp. 423–431. van Rossum, G., Drake, F.L., 2009. PYTHON 2.6 reference manual. CreateSpace. van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R.S.E.W., Van Strien, A., Siepel, H., 2010.

Life-history and ecological correlates of population change in Dutch breeding birds. Biol Conserv 143, 173–181. https://doi.org/doi.org/10.1016/j.biocon.2009.09.023 Vepakomma, U., Kneeshaw, D.D., De Grandpre, L., 2018. Influence of natural and anthropogenic linear canopy openings on forest structural patterns investigated using lidar. Forests 9, 540. https://doi.org/doi.org/10.3390/f9090540 Villard, M.-A., Foppen, R., 2018. Ecological Adaptations of Birds to Forest Environments, in: Mikusiński, G., Roberge, J.-M., Fuller, R. (Eds.), Ecology and Conservation of Forest Birds. Cambridge University Press, Cambridge, p. 51. https://doi.org/10.1017/9781139680363 Wang, X., Wang, C., Li, Q., 2014. Wind regimes above and below a temperate deciduous forest canopy in complex terrain: Interactions between slope and valley winds. Atmosphere (Basel) 6, 60–87. https://doi.org/doi.org/10.3390/atmos6010060 Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251. https://doi.org/doi.org/10.2307/1218190 Wu, N., Hu, B., Wang, Y., Qin, Y., Ma, G., He, H., Zhou, Y., 2023. Even minor logging road development can decrease the functional diversity of forest bird communities: Evidence from a biodiversity hotspot. For Ecol Manage 534, 120865. https://doi.org/10.1016/j.foreco.2023.120865 Yahner, R.H., 1988. Changes in wildlife communities near edges. Conservation biology 2, 333–339. Zar, J.H., 2010. Biostatistical Analysis, 5th edition. ed. Prentice-Hall, Englewood Cliffs. Zhou, T., Luo, X., Hou, Y., Xiang, Y., Peng, S., 2020. Quantifying the effects of road width on roadside vegetation and soil conditions in forests. Landsc Ecol 35, 69–81. https://doi.org/10.1007/s10980-019-00930-8




a.
Species Richness
0
5
10
15
forest
path
road
edge
Type
a
a
a
a
b.
Shannon Index
0
1
2
3
forest
path
road
edge
Type
ab
b
b
a


NMDS2
NMDS1
0.5
0.0
-0.5
-0.4
0.0
0.4
Type of plot
forest
path
road
edge



Hosted file

`Table_1.docx` available at https://authorea.com/users/919694/articles/1291967-effects-of-linear-openings-in-forest-canopy-on-temperate-bird-communities

Hosted file

`Table_2.docx` available at https://authorea.com/users/919694/articles/1291967-effects-of-linear-openings-in-forest-canopy-on-temperate-bird-communities