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Landscape composition and life-history traits influence bat movement and space use: Analysis of 30 years of published telemetry data

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► To cite this version:

Alexis Laforge, Frédéric Archaux, Aurélie Coulon, Clélia Sirami, Jérémy Froidevaux, et al.. Landscape composition and life-history traits influence bat movement and space use: Analysis of 30 years of published telemetry data. *Global Ecology and Biogeography*, 2021, 30 (12), pp.2442-2454. 10.1111/geb.13397 . hal-03435073

HAL Id: hal-03435073

<https://hal.inrae.fr/hal-03435073v1>

Submitted on 30 Sep 2024

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1 **Accepted version of the manuscript published in Landscape and Urban Planning**

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3 **Road density and forest fragmentation shape bat communities in temperate**
4 **mosaic landscapes**

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17 **HIGHLIGHTS**

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19 · Bat diversity peaked in landscapes with intermediate forest fragmentation levels.
20 · Road density had negative effects on functional and phylogenetic bat diversity.
21 · Road density impacted bat activity differently between forest edges and interiors.
22 · Forest fragmentation mediated road density effects on bats at landscape scale.
23 · Our study advocates for more holistic approaches in fragmentation studies.

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26 *Keywords:* Chiroptera Edge effects

27 Habitat fragmentation Matrix quality Multidimensional diversity Road network

28

29 ABSTRACT

30 Road construction is expanding worldwide, exacerbating both direct mortality by road-
31 kills and habitat frag- mentation, especially for mobile vertebrates such as bats.
32 Understanding how road density affects bat commu- nities in mosaic landscapes of
33 various compositions and configurations is therefore critical. We acoustically sampled bat
34 communities in 172 landscapes of southern France to: (i) disentangle the relative and
35 interacting effects of road density and forest fragmentation by farmland on the activity of
36 bat communities; (ii) investigate how road density affects different aspects of bat
37 diversity (taxonomic, functional and phylogenetic) and species activity according to their
38 life-history traits; and (iii) assess whether road density effects on bats change with the
39 level of forest fragmentation. Forest amount and patchiness were more important than
40 road density for all components of bat diversity, except for functional evenness. Bat
41 diversity peaked in landscapes with intermediate levels of forest fragmentation, while
42 road density had negative effects on functional and phylogenetic diversity. The effect of
43 road density on the activity of *R. ferrumequinum*, *R. hipposideros*, *N. leisleri* and *P.*
44 *pipistrellus* was only negative in landscapes with either a low forest amount or a low
45 number of forest patches. By better under- standing interactions between forest
46 fragmentation and road density, our study will contribute to a more adequate
47 landscape planning that will improve the resilience of bat communities to both road
48 expansion and forest fragmentation. Moreover, the complex landscape-level
49 interactions between habitat fragmentation and matrix quality on bats advocate for the
50 use of a more holistic view in future fragmentation studies.

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1. Introduction

Habitat fragmentation at the landscape level is a major ongoing process in temperate landscapes, leading animals – and especially mobile vertebrates - to deeply change their movements and habitat use (Pfeifer et al., 2017; Tucker et al., 2018). The process of habitat fragmentation primarily may refer to a reduction in habitat amount leading to an altered spatial configuration and reduced connectivity (Carr et al., 2002), although its definition may also be restricted to fragmentation per se, i.e. to changes in habitat configuration without changes in habitat amount (Fahrig, 2017). However, both definitions agree in considering fragmentation as multifactorial and leading to both positive and negative responses of vertebrates to several underlying mechanisms including enhanced or reduced functional connectivity, positive or negative edge effects, changes in matrix quality or habitat diversity, and increases or decreases in the magnitude of biotic interactions such as predation, parasitism or competition (Fahrig, 2017; Pfeifer et al., 2017; Fahrig, 2019). Among the factors strongly interacting with habitat fragmentation in temperate landscapes, road density is key, through its potential large-scale effects on population persistence (Carr et al., 2002; Fahrig & Rytwinski, 2009).

Road networks have expanded by 12 million km worldwide since 2000, and 25 million km of additional roads are expected by 2050 (Laurance et al., 2014). Road expansion is a complex phenomenon with cumulative negative impacts on bats beyond habitat fragmentation, including a barrier effect (Claireau et al., 2019), mortality due to collisions with vehicles (Medinas et al., 2021), and light and noise pollution, which disturb bats while commuting and foraging (Bennett & Zurcher, 2013; Stone et al., 2015). In light of the rapid increase in road infrastructure, we need a better understanding of how road density affects bat communities compared to habitat fragmentation by other land use changes. In particular, we lack studies that would allow to better assess the relative importance of road effects at the landscape level, especially given that researchers often underestimate the effects of direct road-kills compared to habitat mitigation (Zimmermann Teixeira et al., 2017; Medinas et al., 2021). While no studies to date have specifically focused on estimating the relative effects of road density and habitat fragmentation on temperate forest bats, a previous study found both negative and positive effects of roads on forest insectivorous birds (Khamcha et al., 2018). Although temperate forests are key roosting and foraging habitats for bats, the relative effects of forest amount and configuration on bats at the landscape level have been studied mostly in tropical zones (Presley et al., 2019). Overall, forest amount in a landscape is generally considered as a more important predictor of bat diversity and activity than forest configuration (Ethier & Fahrig, 2011; Arroyo-Rodríguez et al., 2016). Previous studies also found that landscapes with moderately fragmented forests often host the highest functional diversity, species richness or abundance in bats (Klingbeil & Willig, 2009; Fuentes-Montemayor et al., 2013).

The relative importance of forest amount and configuration actually depends on bat life-history traits.

89 For instance, forest amount plays a greater role for frugivorous bat species, while configuration has a
90 higher impact on animal-eating bat species (Klingbeil & Willig, 2009). Bat species with low mobility are
91 more affected by configuration, whereas for more mobile species, the amount of a given habitat in a
92 landscape generally outweighs the pure configuration effect (Fuentes-Montemayor et al., 2017). However,
93 these effects on bat diversity and abundance vary greatly between studies and bioclimatic regions, found
94 to be either positive, negative or both (Gorresen & Willig, 2004; Ethier & Fahrig, 2011). Furthermore,
95 responses of bat species to forest fragmentation depend on landscape contexts, species traits and the
96 spatial scale considered (Klingbeil & Willig, 2009; Fuentes-Montemayor et al., 2017). Recent reviews argued
97 that a more holistic perspective is needed in fragmentation studies to elucidate the potential complex
98 and inter-twined relations between matrix quality and habitat fragmentation, and ultimately to better
99 orientate future conservation efforts in landscape planning (Fahrig, 2017; Presley et al., 2019). Studies
00 aiming to assess the effect of road density alongside habitat fragmentation therefore need to ensure that
01 the effect of changes in matrix quality associated with different amount of roads will not be interpreted
02 as an effect of habitat fragmentation (Fahrig, 2017). Here, we investigated both the effects of matrix
03 quality, including road density, and landscape-level forest fragmentation on bat communities,
04 particularly focusing on the potential role of the former in mediating responses to the latter. To better
05 predict how habitat fragmentation may affect bat communities, we investigated different dimensions of
06 bat diversity, including its functional and phylogenetic components (Cisneros et al., 2015). While
07 taxonomic diversity measures the number of species, functional diversity summarizes the variability in
08 life-history traits among species and therefore provides a mechanistic link to ecosystem resistance,
09 resilience and functioning (Petchey & Gaston, 2006). Phylogenetic diversity represents the long-term
10 evolutionary potential of a community in response to current and future landscape modifications
11 (Cisneros et al., 2015).

12 In the present work, we specifically aimed at: (i) disentangling the relative and interacting effects of
13 road density and forest fragmentation (i.e. amount and patchiness) by farmland on the activity of bat
14 communities; (ii) investigating how road density affects different aspects of bat diversity (taxonomic,
15 functional and phylogenetic) and species activity according to their life-history traits; and (iii) assessing
16 whether road density effects on bats change with the level of forest fragmentation.

17 18 **2. Materials and methods**

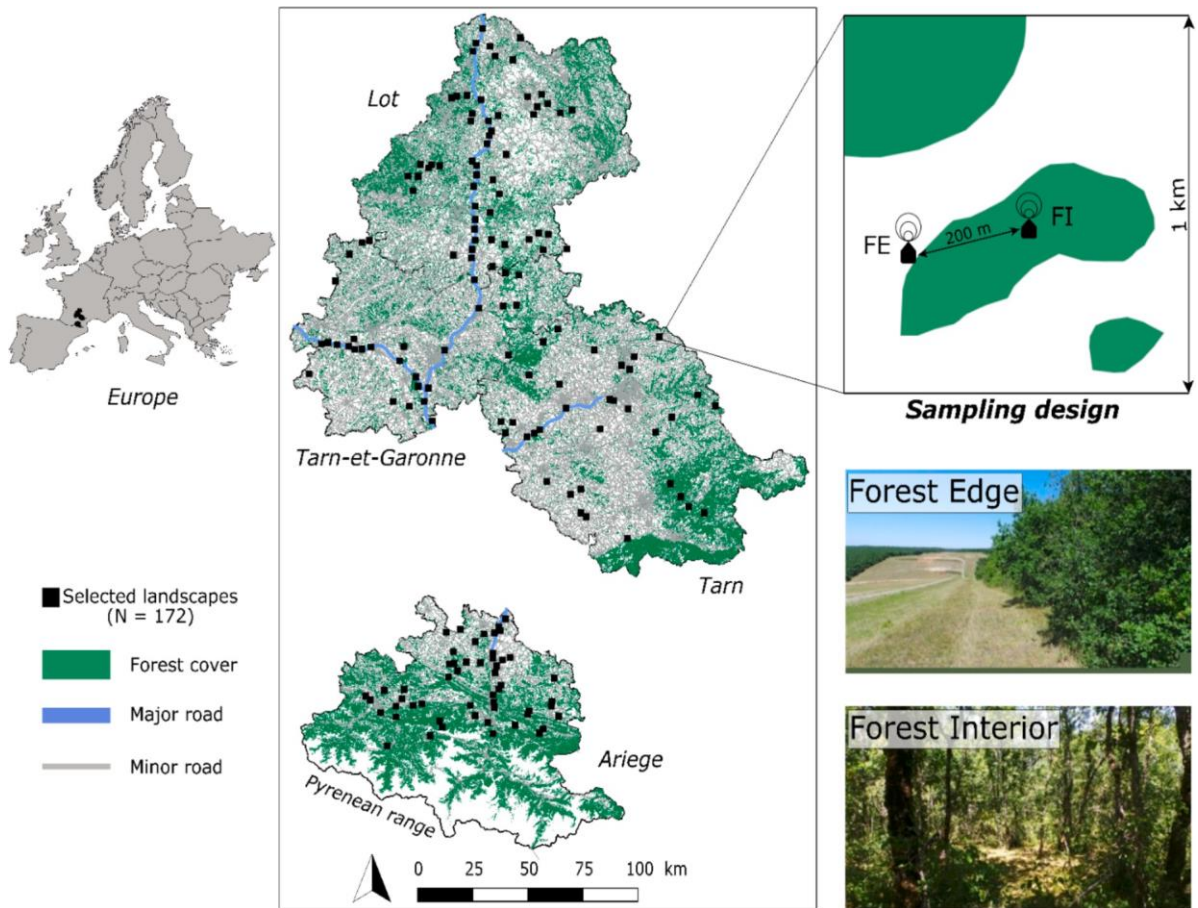
19 *2.1. Study area*

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21 The study was carried out in the region of Occitanie, in southwestern France, in an area spanning 19 583
22 km² (N 43.70, E 1.56) (Fig. 1). The region has a predominantly temperate climate, lying at the
23 intersection of the Atlantic, Mediterranean and Continental climatic zones, with the additional influence

24 of the Pyrenees Mountains to the south (Fig. 1). The study area is below 400 m a.s.l. and is dominated by
25 agriculture (crops, vineyards, pastures), with patches of grasslands and forests of various sizes (mainly
26 mixed woods and deciduous stands), tree-lined hedgerows, rivers, and a large network of both major and
27 minor roads (Fig. 1). The area hosts relatively high bat diversity, with a total of 27 bat species (Bodin et
28 al., 2011). The study was conducted between June and October 2017, with a mean air temperature
29 of 20.8 °C (oscillating between 38.3 °C in June and 1.5 °C in October) and average monthly precipitation
30 of 38.6 mm (varying between 55.2 mm in July and 11.6 mm in October).

32 *2.2. Landscape and site selection*

34 We selected landscapes along a gradient of road density and forest amount in three sub-regions: the
35 Lot (5217 km²), Tarn and Tarn-et-Garonne (9476 km²) and Ariège districts (4890 km²) (Fig. 1). We
36 excluded landscapes with elevations above 1000 m to keep climatic conditions comparable and to limit
37 biases due to complex impacts of elevation on bat activity and richness (McCain, 2006). Within each sub-
38 region, we defined selected 'landscapes' with a square area of 1 km x 1 km (this scale was used only for
39 selecting landscapes). To limit the effect of possible confounding variables, we excluded landscapes
40 with >20 % of impervious surfaces (buildings and parking lots) and/or wetlands (lakes, ponds and
41 watercourses). We calculated the amount of forest and road density in each 1-km² landscape and
42 categorized them according to 8 classes (forest amount in %: 0–12.5, 12.5–25, 25–37.5, 37.5–50, 50–
43 62.5, 62.5–75, 75–87.5, 87.5–100; road density in km/km²: 0–5.5, 5.5–11, 11–16.5, 16.5–22, 22–
44 27.5, 27.5–33, 33–38.5, 38.5–44). We chose this number of classes in order to cover the whole gradient and
45 combination of variables. This resulted in 64 potential combinations of road density and forest amount for
46 which we selected three replicates, one in each sub-region. As a few combinations were not represented
47 in some sub-regions, the final set included 172 landscapes (Fig. 1). All landscape variables were calculated
48 with ArcGis 10 (ESRI, Redlands, CA) based on land cover data obtained from the French Theia Land Data
49 Centre (land use land cover layer OSO based on 2016 data used to quantify forest configuration and
50 amount, (Inglada et al., 2017) and the French National Institute for Geographic and Forestry
51 Information (www.ign.fr/; BD TOPO© layer released in March 2017 used to quantify road density).



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Fig. 1. Land cover map and location of selected landscapes in the study area, showing sampling design with simultaneous recordings of bat activity over one night at the forest edge and interior within each landscape.

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Forest patchiness (i.e., number of forest patches as a proxy of habitat configuration) was not fully independent from forest amount (i.e., forest proportion as a proxy of habitat amount) in our sampling design (see Appendix A), because we focused instead on orthogonal gradients of forest amount and road density at the landscape scale. Although forest amount and patchiness (the two components of fragmentation) were not highly correlated among our landscape levels ($r < 0.7$ and $VIF < 4$), forest proportion and the number of forest patches revealed a typical hump-shaped relationship at 0.5 and 1 km scale but a strict positive relationship at the largest scales (i.e. 2, 3, 4 and 5 km radius). This means that our study did not include the less common combinations of low forest amount with high number of forest patches and high forest amount with low number of forest patches, being naturally the rarest landscape contexts because of intertwined patterns of forest amount and patchiness (Smith et al., 2009).

2.3. Bat community sampling

Within each of the 172 landscapes, we selected the forest patch closest to the landscape centroid for bat sampling (patch size (ha): mean = 600.7; SD = 2813.3; min = 0.1; max = 25629.7). We deployed two automatic bat ultrasound recorders (Batlogger A, Elekon AG, Lucerne, Switzerland), one in the centre of the forest patch (i.e. forest interior) and the second at the interface between the forest and the semi-natural agricultural matrix (i.e. forest edge; Fig. 1), resulting in 344 recording points. The recorders were at least 200 m away from each other (mean distance: 412.3 ± 183.8 m) to avoid simultaneous recordings of the same bat calls. Microphones were placed 1.50 m above the ground and oriented upwards on a vertical axis. Each recorder was calibrated to be automatically triggered by any sound with a signal-to-noise ratio above 6 dB and to start recording ultrasound calls from half an hour before sunset to half an hour after sunrise.

Each landscape was surveyed twice, at two key periods in the annual bat life-cycle: parturition (sampled between 19 June and 27 July) and the dispersion and mating period (sampled between 23 August and 14 October), resulting in 675 full nights of recording (13 failed). We simultaneously surveyed eight landscapes at a time (16 deployed detectors) during one full night. The order in which we surveyed landscapes was chosen to limit correlations between landscape variables (forest amount and road density) and the date. Surveys were conducted only when there was no rain, the wind speed was below 30 km/h, and the ambient temperature was above 12 °C.

2.4. Bat call identification and response variables

As it is currently impossible to determine the actual number of individual bats using acoustic data from

02 passive ultrasound recorders, we calculated bat activity as the number of bat passes per night and per
03 species. A bat pass was defined as one or several echolocation calls during a given 5-second interval. This
04 time interval is considered to be the best trade-off to optimize bat pass duration among species with
05 different call lengths and frequencies (Millon et al., 2015). In a first step, echolocation calls were detected
06 and classified to the most accurate taxonomic level, allowing a confidence index to be assigned to each
07 bat pass using the software Tadarida (Bas et al., 2017). The raw data was then divided into two subsets
08 using two confidence index thresholds (see Appendix B – Table B1), corresponding to a predicted
09 maximum error risk of 0.5 (a 0–50% probability of misidentifying a bat pass) or 0.1 (a 0–10% probability).
10 The 0.5 confidence index threshold represented the best trade-off to retain a good quantity of data (in
11 terms of number of bat passes and species occurrences), while the 0.1 threshold limited the number of
12 false positives. To ensure robustness, we performed analyses on these two subsets to verify the
13 consistency of the results (Barré et al., 2019). We conducted analyses at the species level for *Pipistrellus*
14 *pipis-trellus*, *P. kuhlii*, *Barbastella barbastellus*, *Myotis crypticus*, *Rhinolophus ferrumequinum*, *R. hipposideros*,
15 *Nyctalus leisleri* and *N. noctula*, which all produce very distinctive calls (Obrist et al., 2004). We assigned
16 all automatic identifications of *Myotis nattereri* to *M. crypticus*, which has recently been split genetically
17 and geographically from the *M. nattereri* species complex, as our study area is within the range of this
18 newly described species (Juste et al., 2018).

19 From our acoustic data, we measured four diversity indices: species richness, functional dispersion,
20 functional evenness and phylogenetic diversity. Species richness (i.e. taxonomic diversity) considers
21 species as distinct and is insensitive to ecological and evolutionary attributes. Functional dispersion
22 measures the mean abundance-weighted distance of an individual species to the centroid of the more
23 abundant species in a multidimensional trait space (Laliberté & Legendre, 2010). Functional evenness
24 measures the regularity of the distribution of species abundance and dissimilarities in the functional
25 space; it represents the proportion of dominant species in the community, ranging between 1, when the
26 community is perfectly even, to 0, when the community is dominated by one species (Villéger et al.,
2008). These functional indices are complementary (respectively measuring dispersion and regularity in
27 trait space) yet independent, representing two different facets of functional diversity (Laliberté &
28 Legendre, 2010). Lastly, we calculated the mean nearest taxon distance (MNTD), a phylogenetic diversity
29 index that indicates the mean distance between each species in the phylogeny and its most closely
30 related species in the sampled community (Vamosi et al., 2009). The MNTD measures the evolutionary
31 difference between species based on the time since the divergence from a common ancestor (Faith,
32 1992). We calculated FDis and FEve using the dbFD function in R (R package 'FD'; (Laliberté & Legendre, 2010),
33 based on a dataset of 11 traits that we are confident to influence bat responses to forest fragmentation
34 and road density (Santos et al., 2016; see Appendix B – Table B2). We computed MNTD using a tree-based
35 method implemented in the *ses.mntd* function (R package 'Picante') and a phylogenetic tree obtained

from <https://www.treebase.org/>. Finally, we integrated species abundance variations in the phylogenetic and functional diversity calculations to better reflect finer variations in community structure and composition (Devictor et al., 2010).

2.5. Calculation of local and landscape-level variables

Within each landscape, we calculated road density, the proportion of forest, the number of forest patches, the Euclidean distance to the nearest paved road (whatever its width) and the Shannon diversity index calculated from all types of land cover (except forest habitat; $n = 8$, i.e. cropland, grassland, orchard, pasture, road, urban, vineyard and waterbody) in the landscape matrix (see Appendix C – Fig. C1) using updated land use land cover data (OSO 2017, Inglada et al., 2017). As different bat species respond to the landscape at different spatial scales, we quantified landscape variables at six spatial scales (a radius of 0.5, 1, 2, 3, 4 and 5 km from each landscape centroid) to identify the strongest biologically relevant ‘scale of effect’ (Jackson & Fahrig, 2012). The mean spatial overlap of our landscapes for each scale was 1% for 0.5 km, 3% for 1 km, 11.2% for 2 km, 23% for 3 km, 34.4% for 4 km and 44% for 5 km. Overlapping landscapes do not themselves represent a violation of independence and thus are distinct from the concerns of pseudo-replication (Zuckerberg et al., 2020). Furthermore, both empirical results and simulations have demonstrated that overlapping landscapes do not necessarily induce more residual spatial autocorrelation (Zuckerberg et al., 2020).

To statistically control for local habitat quality effects known to influence bat activity (Langridge et al., 2019), we measured the width and the height of each forest edge as well as the proportion of space between understory and canopy levels relative to the total height (Andrieu et al., 2018). For forest interiors, we measured the basal area (using a relascope) and mean vegetation clutter (proportion in four vertical height bands: 0–2 m, 2–10 m, 10–20 m and >20 m; see Table C1) within a circular area plot measurement (25 m radius) centered on the bat recorder location. To avoid collinearity in model predictors, we used a principal component analysis (PCA) to aggregate into axes local edge (PCA1) and forest interior (PCA2) attributes as two new variables (details in Appendix C – Fig. C2).

2.6. Statistical analysis

To assess how road density, forest amount and patchiness influenced bat activity and diversity, we used generalized linear mixed models (GLMM, R package ‘glmmTMB’). Models were fitted using a Gaussian distribution for the bat diversity variables (richness, FDis, FEve and MNTD) and a negative binomial error distribution for bat activity (the number of bat passes per night for each species) with a log link function to take into account overdispersion in our data. Potential non-linear effects of each landscape

262 predictor were visually checked on biplots from generalized additive mixed models (GAMM, R package
263 'mgcv'). We detected non-linear relationships for richness, FDis, FEve and MNTD with forest amount, and
264 for FDis and MNTD with the number of patches (Appendix D – Fig. D1). In those cases, we added a
265 quadratic effect for these two predictors in the models. We included the first two PCA axes (the local
266 predictors being potential confounding factors to be taken into account) and the five landscape covariates
267 (Table C1; our factors of interest) as fixed effects in the full models, while 'landscape' and 'date' were
268 included as random effects to account for the non-independency of our paired recording points (i.e. at
269 both forest edge and interior) and for the same weather conditions between all landscapes sampled
270 during a given night, respectively. The seven continuous fixed effects were scaled so that the associated
271 regression coefficients were comparable in magnitude and their effects were biologically interpretable
272 (Schielzeth, 2010). Forest amount and patchiness are not fully independent ($R^2=0.37, 0.45, 0.68, 0.65,$
273 $0.69, 0.7$ at 0.5, 1, 2, 3, 4 and 5 km scales, respectively) but they were both included as predictors in the
274 models because they can be seen as proxies of distinct ecological processes related to bat responses to
275 fragmentation (Fahrig, 2017). Furthermore, Smith et al., (2009) found by simulations that if forest amount
276 and number of forest patches are controlled for, even when highly correlated (i.e. as potential con-
277 founding predictors), then standardized partial regression coefficients are unbiased estimates. Because
278 forest proportion and number of forest patches have a suppressor relationship in our study, i.e., opposite
279 qualitative effects (see results) and a positive correlation (Appendix A), removing one would
280 underestimate the effects of our remaining predictors and would decrease the explanatory power of our
281 models. Furthermore, despite using an urban filter during landscape selection, the road network was
282 still correlated (Spearman's correlation > 0.7) with urban cover and average radiance (i.e. light
283 pollution). Consequently, we carried out a complementary analysis to test whether urban cover or light
284 pollution better explained the data compared to road density at the best scale for each response variable
285 (Appendix D). We also checked the correlation between local forest variables (i.e. PCA axes) and
286 landscape forest variables (Table C.2 in Appendix C). Considering both the low Pearson's R values
287 ($< |0.28|$ for PCA1 and $< |0.10|$ for PCA2) and the low VIF values associated with PCA1 and PCA2 in models
288 ($VIF < 1.31$ in Table D.2 in Appendix D), we considered both local and landscape variables related to forests
289 in our full models (see below).

290 To take into account expected differences in bat activity and di- versity between forest edges and
291 interiors, we used a two-level factor related to the location of the bat recorder at each forest patch: forest
292 interior (FI) versus forest edge (FE). To explore the potential interacting effects of road density and forest
293 fragmentation by farmland on bat communities (objectives i and iii), we also included three interaction
294 terms in the models, i.e. between edge/interior location and road den- sity, between road density and
295 forest amount, and between road density and forest patchiness. For each of our 12 response variables, six
296 full single-scale models were built with all 11 predictors, as follows: significantly different responses to

road density between forest edges and interiors (Fig. 4). The effect of road density was positive in forest interiors, but negative for *R. ferrumequinum* and neutral for *P. pipistrellus* at forest edges. For *P. kuhlii*, road density was positive at both forest locations, although this effect was stronger in forest interiors than at forest edges (Fig. 4). For *N. noctula*, activity increased with road density at forest edges, but decreased in interiors. For phylogenetic diversity, we found that road density had no effect at forest edges, but had a negative effect in interiors (Fig. 4). The effect of road density on bats also depended on forest fragmentation (amount and patchiness; Fig. 5).

$$\text{Bat Activity or Diversity} \sim \text{PCA1} + \text{PCA2} + \text{Road_dens} + \text{Forest_prop} + \text{Numb_forestp} + \text{Dist_road} + \text{Matrix_div} + \text{FI/FE} + \text{FI/FE}$$

$$: \text{Road_dens} + \text{Road_dens} : \text{Forest_prop} + \text{Road_dens} : \text{Number_forestp} + 1 | \text{Date} + 1 | \text{Landscape}$$

We calculated multivariate regressions (R-package ‘MuMIn’) for all possible combinations of predictor variables and performed AICc-based model averaging using only the best models within $\Delta\text{AICc} \leq 2$. Model averaging calculates the averaged coefficients and relative variable importance (RVI) for each predictor as the sum of AICc weights of all top models containing that variable (Burnham & Anderson, 2002). This procedure was conducted at all six spatial scales for each response variable, and the best scale was defined by the highest R^2 among the six models (Appendix D - Table D1). We considered effects to be significant when RVI values were 0.6 or above (as Dencker et al., 2017). We checked for multicollinearity by conserving only variables with Spearman’s correlation < 0.7 and a VIF value < 4 (Appendix D - Table D2). We checked for spatial autocorrelation in the residuals of the best models using the *dnearneigh* and *sp.correlogram* functions in R package ‘spatial’ and found no significant spatial autocorrelation. We did not detect any overdispersion in the best models (ratio < 1) by visual examination of residual plots (Zuur et al., 2009). We performed all analyses in R version 3.3.1. (R Core Team, 2018).

3. Results

In total, 263 463 passes of 21 bat species were recorded at the 675 recording points spread over 172 landscapes (Table B1). The best models from multi-model averaging showed model fits (*conditional* R^2) of 0.19–0.48 for bat activity (with the highest variance for *P. kuhlii*) and of 0.07–0.29 for bat diversity (with the highest variance for species richness; see Figs. 2 and 3 and Table D1). Overall, forest amount or its

331 patchiness (i.e. the number of forest patches) were always more important than road density for bat
332 diversity, except for functional evenness (Fig. 2). In contrast, at the species level, forest amount or its
333 patchiness were more important than road density for only two of the eight studied species, while it was
334 equally important for the six other species (Fig. 3). Results were similar for both confidence thresholds, so
335 we only present outcomes for the 0.5 threshold of maximum error risk tolerance (Fig. 2).

337 3.1. Effect of road density on bat communities

338 Road density had a significant effect ($RVI > 0.6$) on all bat species and diversity metrics, except for *B.*
339 *barbastellus*, which responded more strongly to the distance to the nearest road (Figs. 2 and 3). The effect
340 of road density was negative for functional and phylogenetic diversity and for the activity of *M. crypticus*
341 and *R. hipposideros*, but positive for the activity of *N. leisleri*, *N. noctula*, *P. kuhlii*, *P. pipistrellus*
342 and *R. ferrumequinum* (Figs. 2 and 3). For four of these five species, we found significant positive effect of
343 road density on *P. pipistrellus* occurred only in landscapes with a high number of forest patches at the 0.5
344 km scale. For *R. ferrumequinum* and *R. hipposideros*, the negative effect of road density was significant
345 only in landscapes with low, or both low and intermediate numbers of patches, respectively. Finally, road
346 density had a significant negative impact on *N. leisleri* only in landscapes with a low amount of forest.

348 3.2. Relative effects of forest amount and patchiness on bats

349
350 For seven out of eight species, forest patchiness was more or equally important than forest amount,
351 while the reverse was only true for *N. noctula* (Fig. 3). More precisely, a higher number of patches had
352 a positive effect on the activity of five species, but a negative one on the two *Pipistrellus* species. In
353 contrast, we did not find any positive effects of forest amount on bat activity. The effect of forest amount
354 on functional diversity (FDIs) was also negative, whereas species richness showed a hump-shaped
355 response (quadratic term), with maximum taxonomic diversity in landscapes with 40–50% of forest cover
356 (Fig. 6). The effect of forest patchiness on functional and phylogenetic diversity also showed a hump-
357 shaped response, with a maximum occurring at an intermediate number of patches (Fig. 6). Moreover,
358 we found that the activity of six species and two diversity metrics were significantly higher at forest edges
359 compared to interiors, while no significant differences were found for *M. crypticus*, *N. noctula* nor
360 phylogenetic diversity. In contrast, only functional evenness was significantly higher in forest interiors
361 (Fig. 7).

362 Finally, landscape matrix diversity was important ($RVI > 0.6$) for three species (*N. noctula*, *P. kuhlii* and *R.*
363 *ferrumequinum*) and for phylogenetic diversity (MNTD), with both positive and negative effects (Figs. 2 and 3;
364 see Appendix C – Fig. C1 for interpretation).

366 4. Discussion

367 Forest amount and patchiness were more important than road density for all bat diversity components
368 but functional evenness. Bat diversity was highest in landscapes with intermediate levels of forest
369 fragmentation, while functional and phylogenetic diversity decreased with increasing road density. This
370 negative effect of road density on the activity of *R. ferrumequinum*, *R. hipposideros*, *N. leisleri* and *P.*
371 *pipistrellus* was only found in landscapes with either a low forest amount or a low number of forest
372 patches. While models explained a good proportion of data variance for species richness (conditional R^2
373 0.29) and individual species (from 0.26 to 0.41), this proportion was noticeably lower for three other
374 diversity metrics (between 0.7 and 0.11). As a result, detailed results reported below for taxonomic,
375 functional and phylogenetic diversity should be carefully interpreted.

376 In our temperate study area, forest amount and patchiness (i.e. forest fragmentation) were more
377 important drivers for shaping bat communities than road density in regard to taxonomic, phylogenetic and
378 functional diversity. Only functional evenness was more negatively affected by road density and edge
379 effects than forest amount and patchiness. However, we found that most bat responses to road density
380 were both species-specific and context dependent. Taxonomic diversity of bat communities was best
381 explained by forest amount, while functional and phylogenetic diversity were best explained by a
382 combination of forest amount and patchiness (i.e. number of patches). We found that bat species richness
383 peaked at intermediate forest amounts, while functional and phylogenetic diversity peaked at
384 intermediate levels of forest patchiness. This suggests that landscapes with forest habitat moderately
385 fragmented (in terms of both amount and number of patches) mixed with other land uses would produce
386 the best environmental conditions for maintaining the highest bat diversity (Bailey et al., 2019). At the
387 landscape level, these environmental conditions may be optimal by providing sufficient resources for both
388 foraging and roosting to the widest range of bat species and life-history traits (Klingbeil & Willig, 2009).

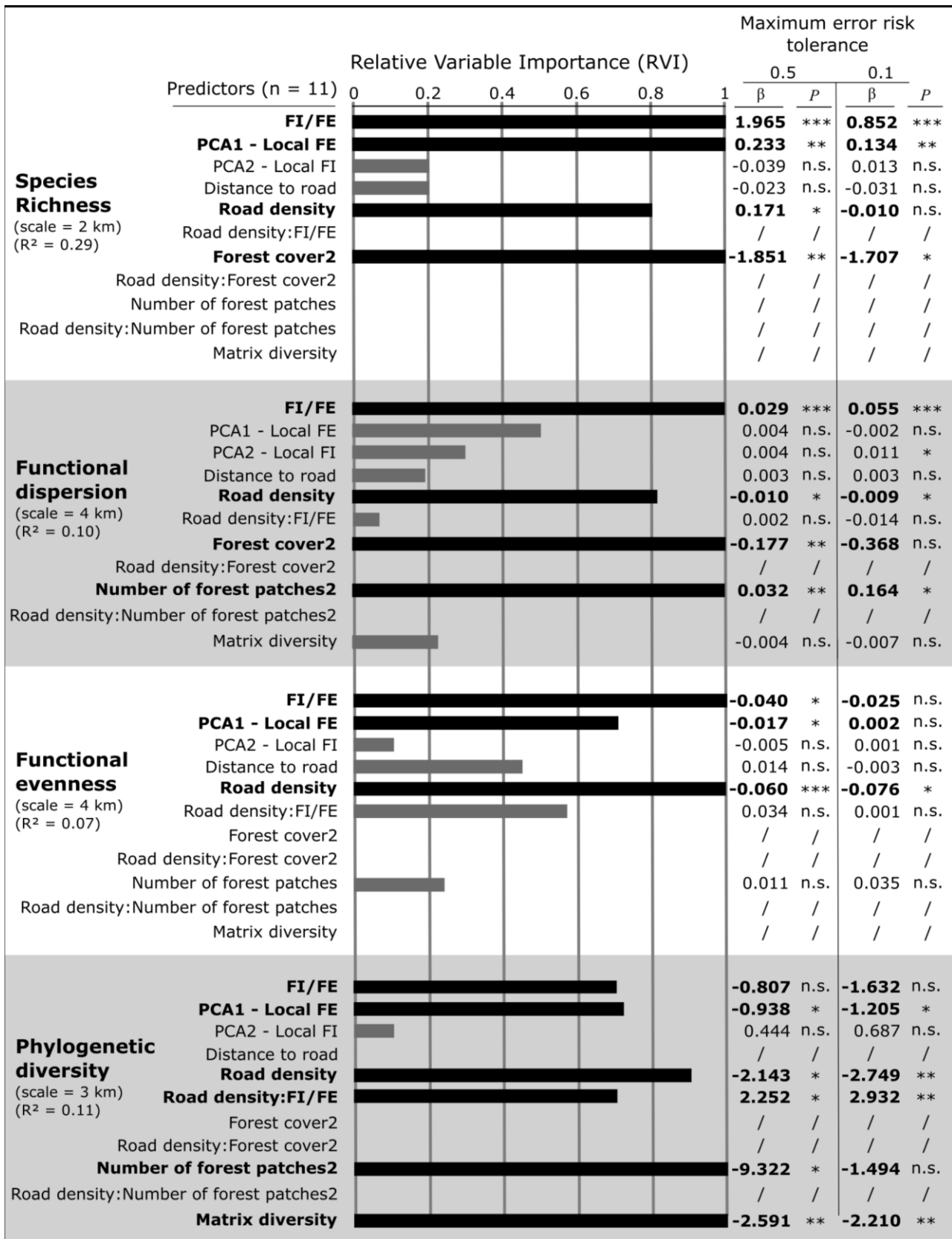
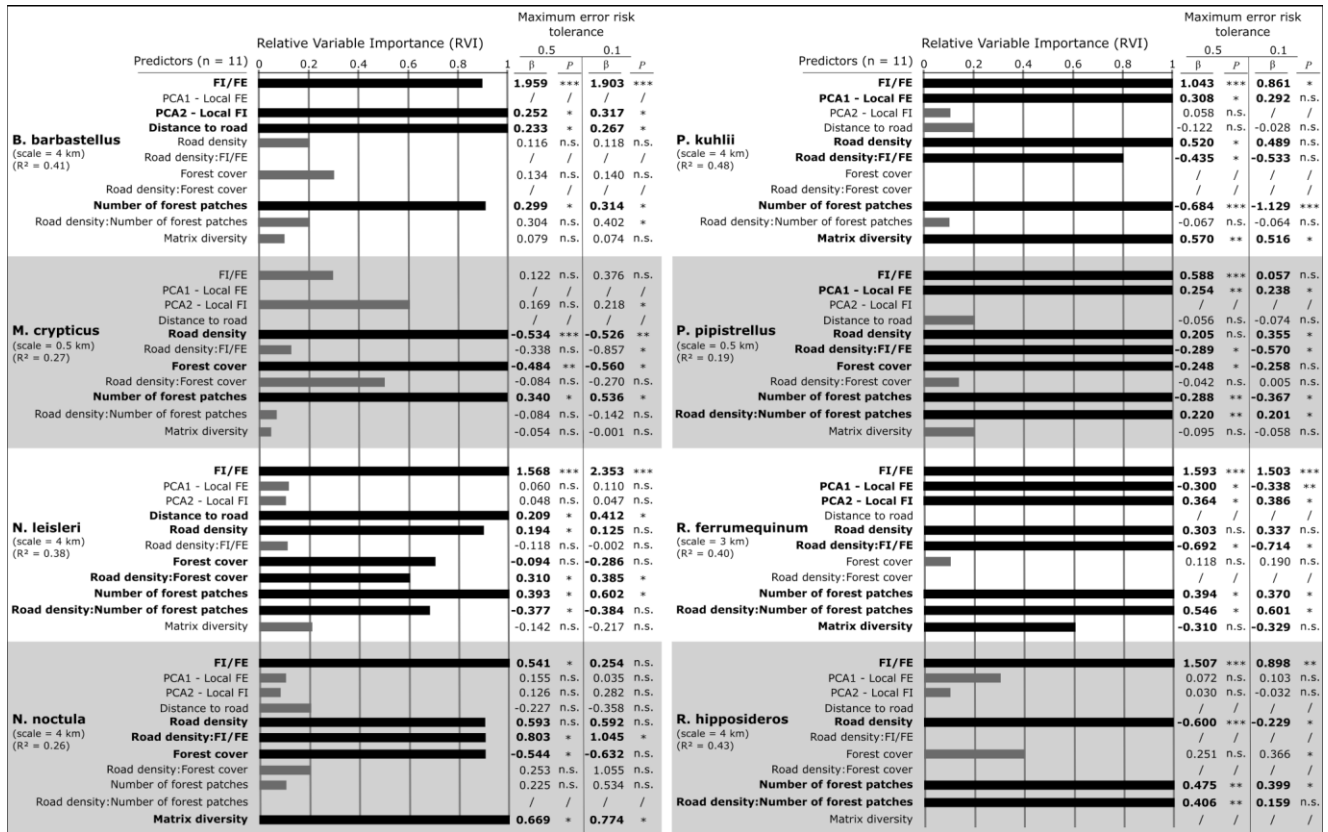


Fig. 2. Relative importance (bar length), estimates (β) and significance ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$; n.s. not significant) of model-averaged multiple regressions for the four bat diversity indices at their best scale (highest R² of the best model). The relative importance of predictor variables indicates the individual contribution of the variable to the explanatory power of the models (a value of 1 indicates

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its presence in all top models; bar is black if > 0.6). *P*-values are only provided for comparison of the model averaging approach with null hypothesis testing. Forest interiors were used as the reference (i.e. intercept) in each model. A predictor followed by the number 2 indicates quadratic terms.



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Fig. 3. Results from model-averaged multiple regressions for the activity of 8 bat species (i.e. number of bat passes per night). See details in caption of Fig. 2.

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Taxonomic, functional and phylogenetic diversity as well as the eight bat species responded to road density and forest fragmentation at multiple spatial scales (from 0.5 to 4 km radii; see Figs. 2 and 3). We note that our ‘scales of effect’ for both bat diversity and activity were not equal to the smallest or largest scale evaluated (except for two species), suggesting that our range of scales was relevant and that our diversity/ species–landscape relationships are estimated at the most biologically relevant scale (Jackson & Fahrig, 2015). However, our ‘scales of effect’ for bats’ activity were not consistent with species home range size (i.e. mobility; see Table B2) and previous studies (Boughey, Lake, Haysom, & Dolman, 2011; Ducci et al., 2015; Fuentes-Montemayor, Goulson, Cavin, Wallace, & Park, 2013; Fuentes-Montemayor, Goulson, & Park, 2011). Across-study comparisons of the ‘scale of effect’ is difficult since (i) the ‘scale of effect’ may simultaneously depend on multiple biological factors (e.g. dispersal distance, reproductive rate, population density); and (ii) the estimated ‘scale of effect’ for a given species or group may vary

15 among studies depending on many methodological choices (e.g. land-
16 scape variables measurement, range of spatial scales considered, statistical approach and selection criteria used to identify the 'scale of
17 effect') but also on the regions where the studies were carried out (Miguet et al., 2016).
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19 *4.1. Effects of road density on three-dimensional bat diversity*

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21 Beyond effects of forest fragmentation, the density of the road network had a significant negative
22 influence on bat functional and phylogenetic diversity, but not on taxonomic diversity. We thus
23 demonstrate that considering only taxonomic species richness may be limited for conservation purposes,
24 as it could mask losses of key ecological or evolutionary attributes of bat assemblages, likely involving a
25 decreased resilience to landscape modification due to road network densification (Cisneros et al., 2014).
26 Moreover, positive or non- significant effects of roads on taxonomic diversity may be coupled with
27 significant decreases in functional and phylogenetic diversity, which would suggest that roads act as
28 environmental filters and could lead to a biotic homogenization of bat communities at the landscape level
29 (Monnet et al., 2014). Lower variations in functional diversity, compared to other aspects of diversity,
30 along environmental gradients have been actually documented in a variety of taxa, including tropical bats
31 (Cisneros et al., 2014). Based on the life-history traits we used to calculate functional diversity indices, we
32 could speculate that road density favours bat species flying at higher height because they are less vulnerable
33 to the risk of road-kills and disturbance related to road traffic (Claireau et al., 2019; Medinas et al., 2019).
34 Since the time spent at height is linked with acoustic performances and wing morphology among bats
35 (Roemer et al., 2019), we could also speculate that (i) spe- cies with sonar adaptations for long-distance
36 perception of their envi- ronment (i.e. low frequency signals, small bandwidths, and long call length) and (ii)
37 species with high wing aspect ratio and loading (which is positively correlated to body mass; Norberg &
38 Rayner, 1987), should be able to better persist within landscapes with a denser road network.

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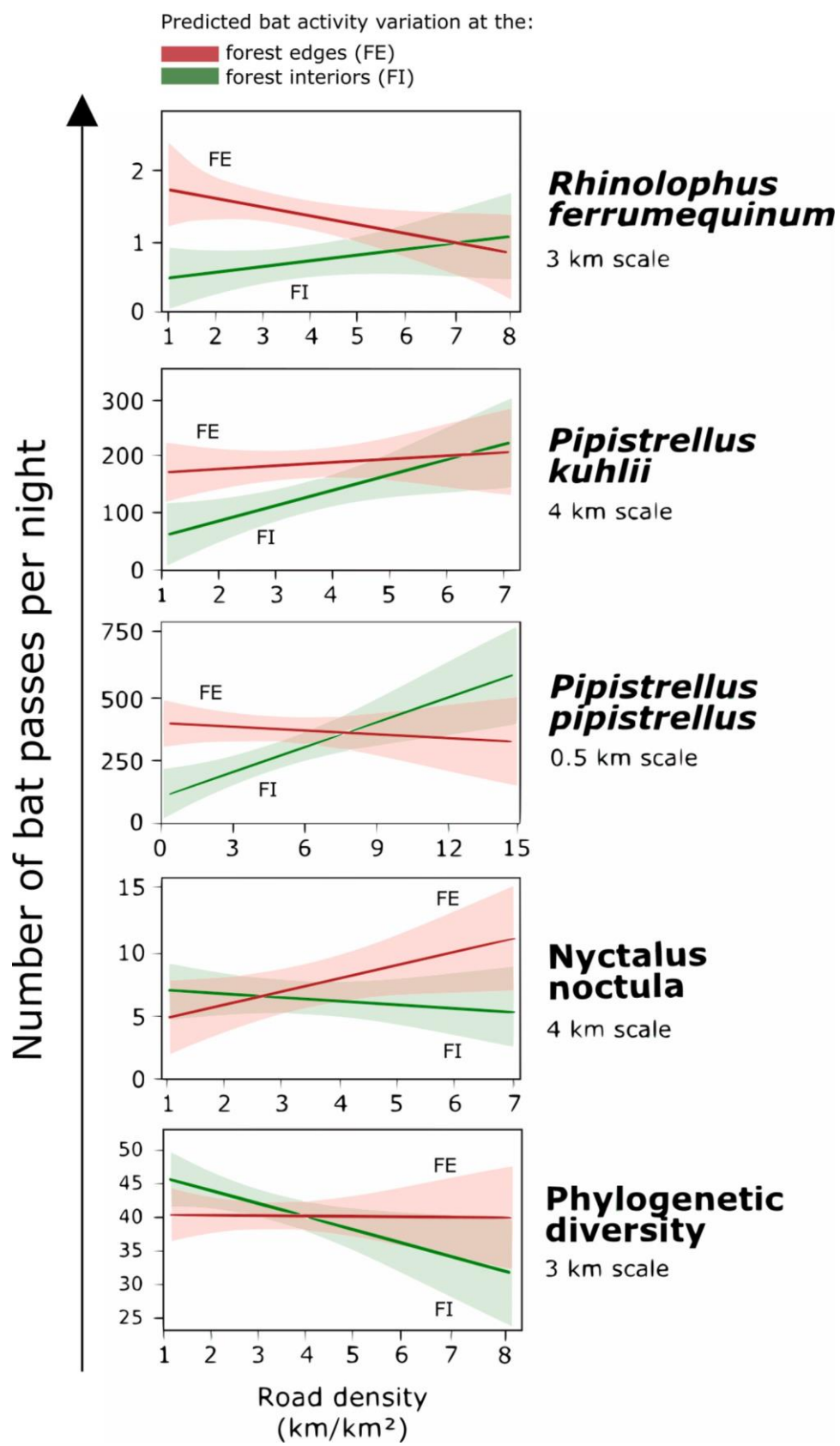
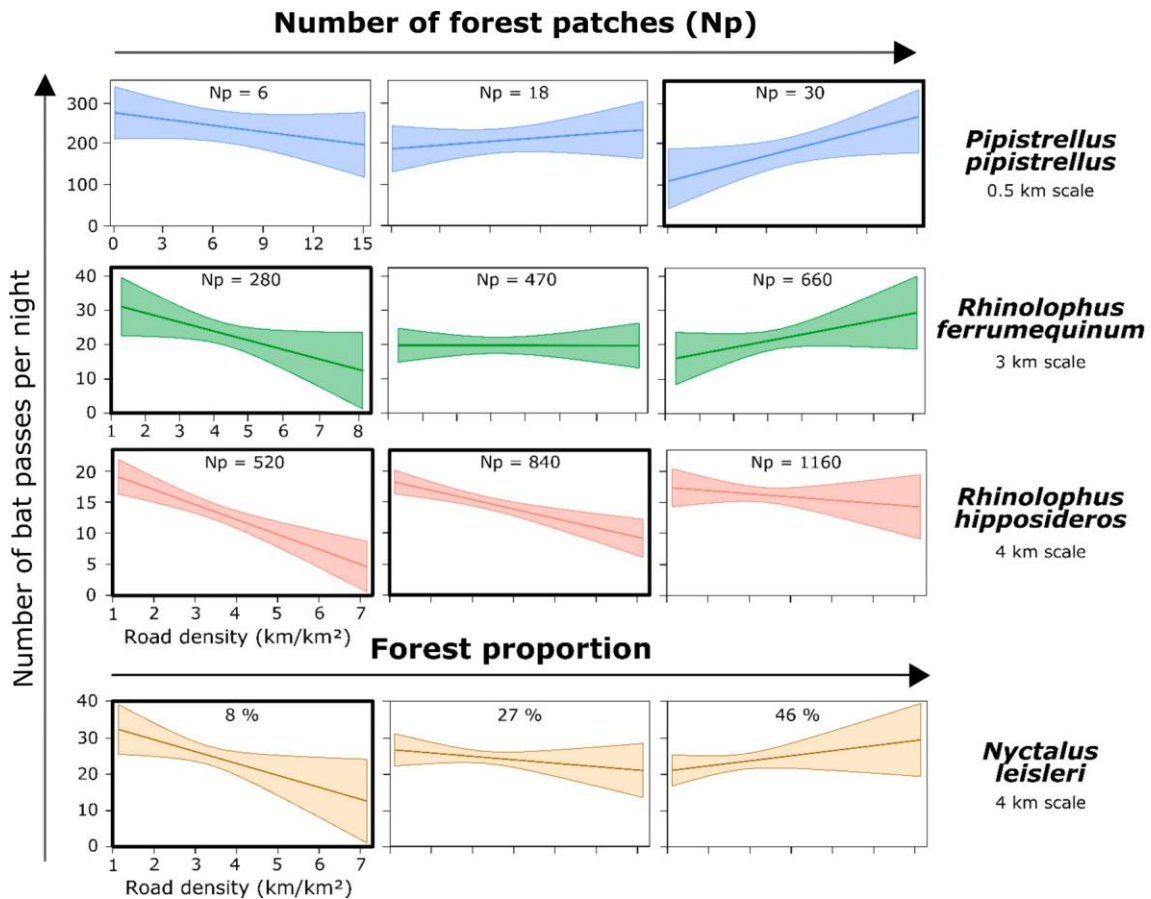


Fig. 4. Predicted bat responses to road density at forest edges versus forest interiors from at the 'scale of effect'. Only selected interactions in the best models are presented (i.e. RVI > 0.6; see Figs. 2 & 3). Values on the y-axis are the number of bat passes per night (i.e. activity). The red and green bands represent the 95% confidence interval for the predicted values at the forest edges and interiors respectively. (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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Fig. 5. Predicted bat responses to road density (with the 95% confidence interval) at three different levels of forest amount and patchiness at the ‘scale of effect’. Only selected interactions in the best models are presented (i.e. RVI > 0.6; see Fig. 3). The three levels have been calculated according to the standard ‘spotlight analysis’ as follows: mean - SD; mean; mean + SD. Values on the y-axis are the number of bat passes per night (i.e. activity). Bold frames represent significant slopes (i.e. 95% confidence interval not containing zero).

Several assembly mechanisms may differently influence the set of bat traits that we used to calculate functional diversity. For instance, a given mechanism could favour one trait and discriminate against another, leading to no change in functional diversity. An increase in functional and phylogenetic diversity could come either from adding more ecological or evolutionary attributes to a bat community, or from a decrease in abundant and/or a loss of redundant species, both of which would enhance the distribution, dispersion and/or regularity of traits in the functional space (Cisneros et al., 2014). Ultimately, changes in functional and phylogenetic diversity observed in our study may reflect a combination of mechanisms for which the species-specific responses, related to life-history traits, can provide further insights.

4.2. Bat activity responses to road density according to life-history traits

Road expansion has cumulative negative impacts on bats: habitat fragmentation (Carr et al., 2002), barrier effect (Claireau et al., 2019), collision with vehicles (Medinas et al., 2021) and diverse pollutions/disruptions (Bennett & Zurcher, 2013; Stone et al., 2015). Furthermore, roads generally develop together with overall urbanization and agriculture intensification and thus correlate with urban cover and light pollution, which is verified in our study. Road network density can be therefore viewed as a proxy of the overall matrix quality for bats, by indicating a global anthropization level of the landscapes (Fahrig, 2017). As expected, road density had a negative effect on the lowest-flying species (*M. crypticus*) and on the most specialized species to forest interiors (*R. hipposideros*). Those species are particularly vulnerable to road effects (Fensome & Mathews, 2016) and anthropogenic pressures on temperate landscapes, known to be the main drivers in the decline of specialist bats at the expense of generalists (Russo & Ancillotto, 2015). Road density had a positive effect on the highest-flying and most generalist species (*Pipistrellus* and *Nyctalus* spp.) and non-forest interior specialists (*R. ferrumequinum*). More precisely, the activity of *R. ferrumequinum*, *P. kuhlii* and *P. pipistrellus* in forest interiors increased with road density, while it tended to decrease at edges. In landscapes with higher road density, the probability that forest edges are closer to roads increases, leading to a behavioural adjustment to road impacts. Furthermore, landscapes with higher road density make the overall matrix less permeable to bat movements, leading to more time spent in forest patches, as refuges, than in the matrix (Carr et al., 2002; Fahrig, 2003). In contrast, the activity of *N. noctula* at forest edges increased with road density, while it tended to decrease in interiors. As a high-flying and open-space species, *N. noctula* may benefit from less hetero-specific competition with other insectivorous bat species more sensitive to urban land cover effects such as the 'road-effect zone' (Claireau et al., 2019; Medinas et al., 2019).

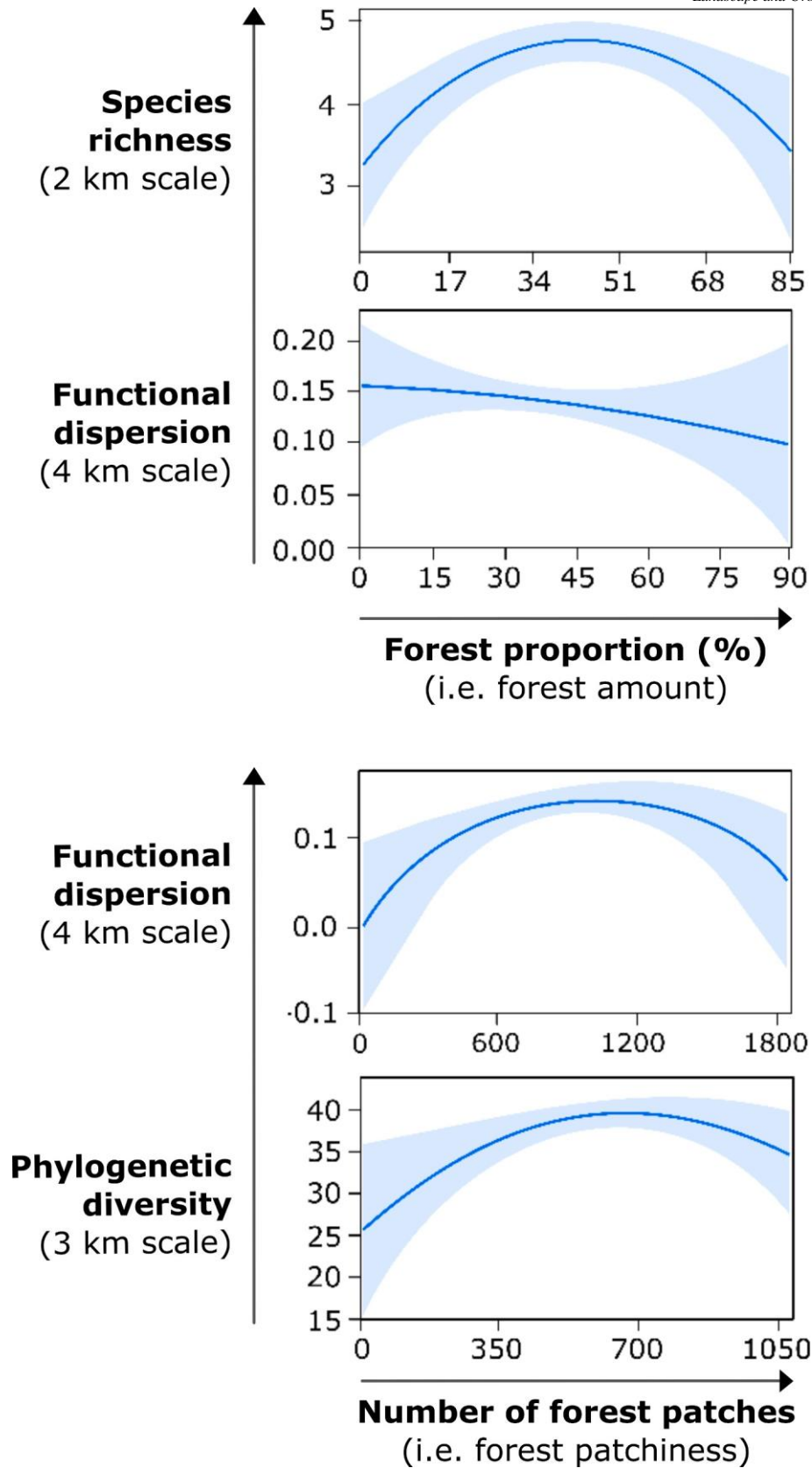


Fig. 6. Variation in the three dimensions of bat diversity predicted (with the 95% confidence interval) in response to forest amount and patchiness at the ‘scale of effect’. Only selected relationships in the best models are presented (i.e. RVI > 0.6; see Fig. 2).

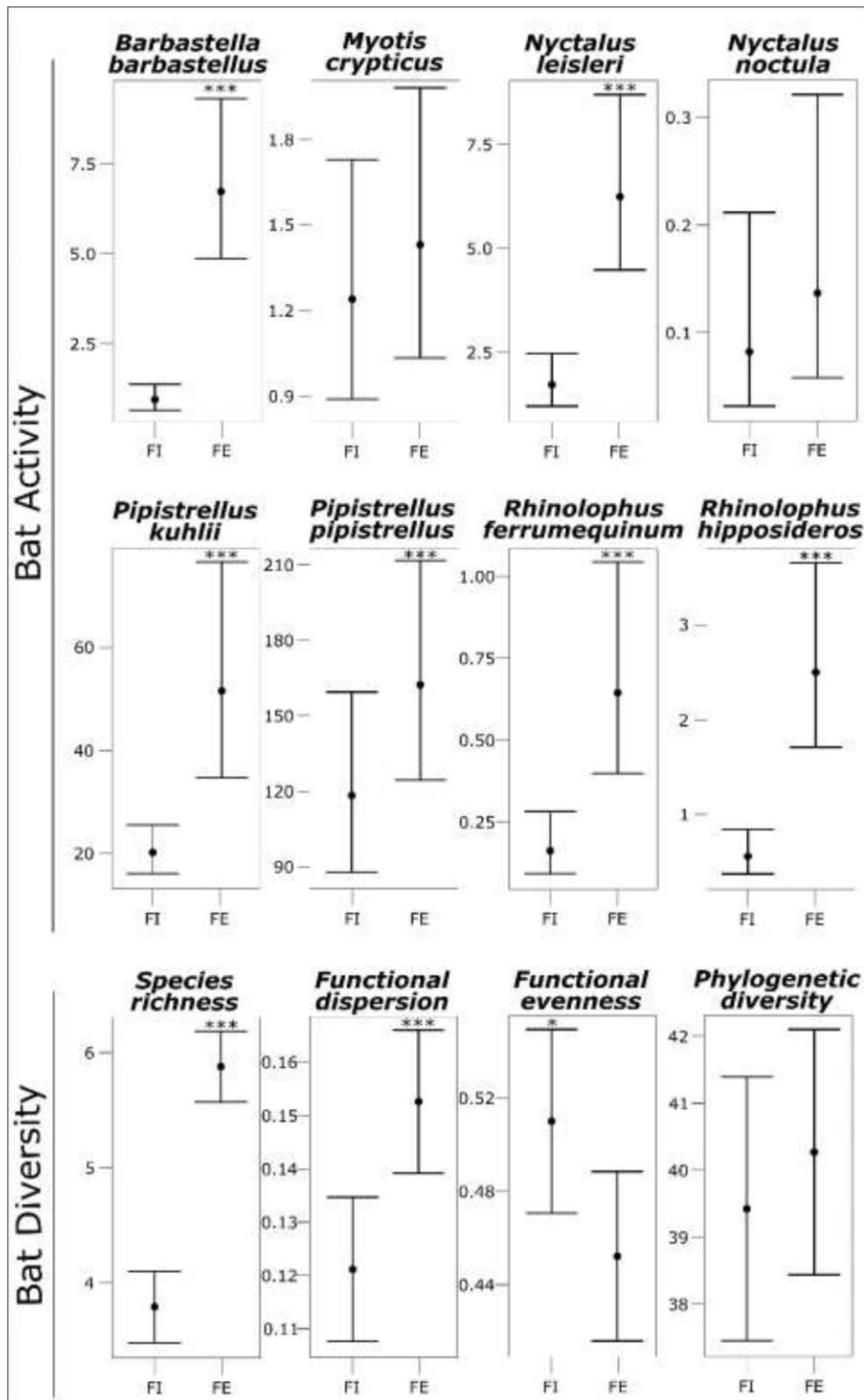


Fig. 7. Boxplots of predicted bat activity and diversity for one night at forest edge versus forest interior. Dots represent means and error bars show 95% confidence intervals. FI = Forest Interior and FE = Forest Edge. Forest interior were used as the reference (i.e. intercept) in each model (*** $P < 0.001$; * $P < 0.05$).

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514 Finally, as bat diversity and species activity did not consistently respond to vegetation structure (i.e. PCA
515 axes) at both forest edge and interior, we suggest that the way bats use forest interiors and their edges for
516 a given patch is mediated by local understorey complexity.

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518 For four out of the eight bat species studied, we found significant interactions between road density
519 and forest amount/patchiness, indicating that landscape context can significantly mediate road density
520 effects. The activity of the two horseshoe bat species decreased with increasing road density only in
521 landscapes with relatively few forest patches, while it increased with road density in landscapes with
522 more forest patches for *P. pipistrellus*. Similarly, road density negatively affected *N. leisleri* in
523 landscapes with a low amount of forest (<8 %), but it tended to be positive in more forested landscapes
524 (>27 %). First, light and noise effects from traffic are likely higher in open areas than in forest-
525 dominated landscapes, potentially resulting in a wider 'road-effect zone' (Medinas et al., 2019). In our
526 study, the probability of being close to a major road was highest in the least forested landscapes, so that
527 lower negative effects of road density in the most forested landscapes could be caused by a dominance of
528 minor roads, probably less impactful. Second, forest patches are increasingly used by bats as road density
529 increases and matrix quality decreases (as previously discussed). Third, in accordance with Ethier & Fahrig
530 (2011), we found that bat activity mainly increased with number of forest patches and decreased with
531 forest amount. Two non-exclusive mechanisms can explain these findings:

532 (i) landscape complementation of non-substitutable resources found by bat in different habitats, since
533 bats tend to forage in a wide range of habitats while most often roosting outside their preferential
534 foraging habitat, as they depend on the availability of potential roosting structures in the landscape
535 (Ancillotto et al., 2014; Downs et al., 2016). The quality of foraging habitats surrounding roosts actually
536 plays a decisive role in roost choice for insectivorous bats (Boughey et al., 2011). An increase in the
537 number of forest patches, with constant forest amount, decreases the mean distance between foraging
538 and/or roosting sites, and therefore facilitate the landscape complementation process (Ethier & Fahrig,
539 2011).

540 (ii) an increase in the number of forest patches also results in increased edge density at the landscape
541 level therefore improving overall landscape connectivity for most bats (Ethier & Fahrig, 2011). Our results
542 confirmed an intensive use of forest edges for foraging and commuting, acting probably as a navigational
543 reference, a source of insect prey, a shelter from wind, and a protection from predators (Morris et al.,
544 2010).

545 Considering all these reasons together, we can thus suggest that an increase of forest patchiness (and
546 amount, depending on species environmental requirements) offsets (at least partially) the negative
547 effects of roads on bat populations at landscape level, improving the persistence of many species within

landscapes of dense road network. Finally, by including habitat fragmentation and matrix quality variables in our analyses, we found that bat response to forest fragmentation was fully consistent with previous studies, suggesting that the confounding effect of matrix quality and road density would not consistently lead to misleading conclusions on the impact of forest fragmentation on bats. For instance, the decreasing bat diversity with increasing forest amount could not be due to hidden road-kill effects since major roads, implying highest bat mortality risk, were located in the least forested landscapes in our study.

5. Conclusions

We conclude that the protection of forest patches within most heavily human-altered landscapes and those having highest road density is critical to bat conservation (Bailey et al., 2019). Landscapes with moderately fragmented forests seem to maintain the highest bat diversity, even in case of high road density, thus reducing the expected magnitude of the wide negative impacts of roads by providing sufficient bat refuges in the landscape. By finding, for the first time, significant interactions between forest fragmentation and road density, our study provides more adequate recommendations towards a landscape planning that will improve the resilience of bat communities to both road expansion and forest fragmentation. Conservation efforts should focus on promoting forest patches within the most opened and road-densified landscapes, with a particular attention to road sections closest to forest where the probability of bat road-kills is higher (Medinas et al., 2021), but where conservation measures to maintain landscape connectivity, such as underpasses, are the most efficient (Laforge et al., 2019). Further research would help to clarify the impact of these interactive effects on long-term bat population persistence and shifts in community composition. Future road expansion will likely alter long-term species interactions, generating a loss of future options in evolutionary history for bat communities. We advocate for more research contributing to an improved understanding of the complex interactions between habitat fragmentation and matrix quality in mosaic landscapes, and valuing more holistic approaches in fragmentation studies.

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.

Acknowledgements

We would like to thank the following for their assistance in collecting field data: Richard Auriol, Julien Blanco, Jean-Philippe Choisis, Rémi Duflot, Jerome Molina, Clémence Moreau, Nirina Ratsimba, Nicolas Salliou and Magali San-Cristobal. We are also grateful to Wilfried Heintz and Florent Blaise for their dataset and IT help with the automatic sound identification and statistical analysis. We thank Kevin Barré for

583 statistical advices and the Reviewers for their constructive comments. We also thank the IN2P3 Computing
584 Centre for providing the facilities to process
585 and archive the recordings, in particular Didier Bas. Funding was provided by 'Direction régionale de
586 l'environnement, de l'aménagement et du logement' of Occitanie region (DREAL) and the French
587 National Research and Technology Agency (ANRT) (CIFRE grant number: 2016/ 1063).
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589 Appendix A. Supplementary data

590 Supplementary data to this article can be found online at [https://doi.](https://doi.org/10.1016/j.landurbplan.2022.104353)
591 [org/10.1016/j.landurbplan.2022.104353](https://doi.org/10.1016/j.landurbplan.2022.104353).
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