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1 **Landscape composition drives the impacts of artificial** 2 **light at night on insectivorous bats**

3

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23

24 Running head: Landscape-dependent effects of ALAN on bats

25 **Abstract**

26 Among the most prevalent sources of biodiversity declines, Artificial Light At Night (ALAN)
27 is an emerging threat to global biodiversity. Much knowledge has already been gained to
28 reduce impacts. However, the spatial variation of ALAN effects on biodiversity in interaction
29 with landscape composition remains little studied, though it is of the utmost importance to
30 identify lightscapes most in need of action. Several studies have shown that, at local scale,
31 tree cover can intensify positive or negative effects of ALAN on biodiversity, but none have –
32 at landscape scale – studied a wider range of landscape compositions around lit sites. We
33 hypothesized that the magnitude of ALAN effects will depend on landscape composition and
34 species' tolerance to light. Taking the case of insectivorous bats because of their varying
35 sensitivity to ALAN, we investigated the species-specific activity response to ALAN. Bat
36 activity was recorded along a gradient of light radiance. We ensured a large variability in
37 landscape composition around 253 sampling sites. Among the 13 bat taxa studied, radiance
38 decreased the activity of two groups of the slow-flying gleaner guild (*Myotis* and *Plecotus*
39 spp.) and one species of the aerial-hawking guild (*Pipistrellus pipistrellus*), and increased the
40 activity of two species of the aerial-hawking guild (*Pipistrellus kuhlii* and *Pipistrellus*
41 *pygmaeus*). Among these five effects, the magnitude of four of them was driven by landscape
42 composition. For five other species, ALAN effects were only detectable in particular
43 landscape compositions, making the main effect of radiance undetectable without account for
44 interactions with landscape. Specifically, effects were strongest in non-urban habitats, for
45 both guilds. Results highlight the importance to prioritize ALAN reduction efforts in non-
46 urban habitats, and how important is to account for landscape composition when studying
47 ALAN effects on bats to avoid missing effects.

48

49 Key words: Chiroptera, land-cover, landscape-dependant responses, light pollution, outdoor
50 lighting, urbanization
51

52 **1. Introduction**

53 The loss and fragmentation of habitats constitute two of the main threats to global biodiversity
54 (Monastersky, 2014). Therefore, both amount of semi-natural habitats and their spatial
55 organization in landscapes drives species' habitat use and movements at multiple spatial
56 scales (Ancillotto et al., 2019; Benton et al., 2003; Rybicki and Hanski, 2013; Sahraoui et al.,
57 2021). For example, farming intensification and urbanization processes are widely recognized
58 as strong pressures negatively affecting biodiversity by decreasing the amount of favourable
59 habitat in landscapes (Peng et al., 2020; Salinas-Ramos et al., 2021). Such drivers can act as
60 additive or synergistic pressures on biodiversity (Brook et al., 2008). Thus, the magnitude of
61 pressures that affect biodiversity can depend on the heterogeneity in landscape composition or
62 landscape structure (e.g. Caryl et al., 2016; Tamburini et al., 2016).

63 Artificial Light At Night (ALAN) is also an emerging threat to global biodiversity (Koen et
64 al., 2018; Falchi et al., 2016; Kyba et al., 2017). ALAN affects biological rhythms (Gaston et
65 al., 2017), fitness (e.g. de Jong et al., 2015), species movements (e.g. Doren et al., 2017) and
66 has cascade effects on ecosystems (Bennie et al., 2018; Knop et al., 2017). All these ALAN
67 effects are particularly well-known for insectivorous bats (Boldogh et al., 2008; Mathews et
68 al., 2015; Rydell et al., 2017), and ALAN is even proposed as one of the main global threats
69 to bats (Voigt and Kingston, 2016).

70 Studies have shown that ALAN reduced bat movements through barrier effects, thus
71 generating habitat fragmentation and loss (Hale et al., 2015). Such effects can ultimately
72 decrease habitats connectivity for bats within landscape (Laforge et al., 2019), connectivity
73 being a key driver of bat activity and populations' health status (Frey-Ehrenbold et al., 2013;
74 Froidevaux et al., 2017). However, how ALAN effects vary across landscape composition,
75 remains little studied. It was recently shown that increasing tree cover 100-500 m around
76 streetlights intensified negative and positive responses of bats to light (Straka et al., 2019).

77 These authors also showed that tree cover can mitigate negative impacts of streetlights on
78 open space foraging bats. Two other studies drew similar conclusions: in case of low tree
79 cover proportion, ALAN had a negative impact on bat activity, while effects tended to be
80 positive under high proportions (Mathews et al., 2015; Pauwels et al., 2019). Thus,
81 accounting for spatial variations of ALAN effects according to landscape composition is of
82 high importance to build efficient conservation strategies aiming to limit landscape
83 functionality losses concerning bats.

84 Two deeply linked pressures can drive bat responses when studying the spatial variation of
85 ALAN effects on insectivorous bats: (i) a decrease in the amount of habitats through their
86 degradation or urbanisation, which in turn reduces food resource for bats (i.e. arthropods;
87 Sánchez-Bayo and Wyckhuys, 2019), and (ii) the artificial light level with its behavioural-
88 induced changes (e.g. increased perceived predation risk and flight speed; Jones and Rydell,
89 1994; Polak et al., 2011) and its ‘vacuum cleaner’ effect, which aggregates arthropod preys
90 around light sources while decreasing their amount in unlit areas (Eisenbeis, 2006; Owens and
91 Lewis, 2018). Thus, bats are potentially constrained by the cost-benefit ratio of foraging at a
92 given place driven by both habitat suitability and artificial light levels. In addition, bats’
93 response to light likely depends on their flight strategy: aerial-hawking species (i.e. from
94 genera such as *Eptesicus*, *Nyctalus* and *Pipistrellus*) appear to be less locally affected by
95 ALAN by being able to exploit insects under light sources, while slow-flying gleaner species
96 (i.e. from genera such as *Myotis* and *Plecotus*) avoid streetlights, potentially due to perceived
97 predation risk (Stone et al., 2015a). In addition, one aerial-hawking species, *P. pipistrellus*,
98 although described as less affected by light at local scales (Azam et al. 2015, 2018), was
99 found as negatively affected at regional (Pauwels et al., 2019) and national (Azam et al.,
100 2016) scales. We thus specifically expected the global activity (i.e. not differentiating
101 foraging from commuting) of *P. pipistrellus* to decrease with increasing ALAN.

102 As a consequence, we hypothesized that global activity of slow-flying gleaner species should
103 decrease with ALAN, and this more strongly in non-urban habitats (areas composed of any
104 land-use types other than impervious surfaces – such as housing, industrial areas or roads –,
105 i.e. farmlands, forests, hedgerows and wetlands). This could be caused by an additive effect
106 between (i) light sources repulsive effects (e.g. related to their intrinsic perception of
107 increased predation risk; Jones and Rydell, 1994), and (ii) an increasing prey density in non-
108 urban habitats irrespective of light as insects complete their life cycle on vegetation or in
109 water (Lagucki et al., 2017). Thus, given that all bat species are expected to be more abundant
110 in areas with more preys, artificial light sources at such places would have stronger repulsive
111 effects on light-shy species such as slow-flying gleaners compared to places less attractive for
112 these species in terms of prey (Fig. 1a). In contrast, we expect that global activity of aerial-
113 hawking bat species would be less affected or even positively affected by ALAN, and this
114 more strongly when the amount of non-urban habitats increases, thanks to an additive effect
115 between (i) their ability to exploit insects around light sources (Azam et al., 2018) and (ii)
116 higher insect density in non-urban habitats (Fig. 1b).

117 Focusing on a study area with a diversified landscape composition (i.e. the amount of each
118 land-use/habitat) along a wide ALAN gradient, we aimed to investigate (i) the species-
119 specific response to ALAN at landscape scale using satellite-based radiance as an indicator of
120 artificial lighting for 10 bat species and three bat species groups, and (ii) response variations
121 according to landscape composition around sampling sites (i.e. a few hundred meters around
122 sampling sites). To achieve this goal, we selected sample sites (i) within a gradient of
123 radiance, (ii) while accounting for all possible landscape contexts from the combination of
124 three land-uses (forest, urban, wetland), and (iii) making sure that land-uses were not
125 correlated with each other or with the radiance.

126

127 **2. Materials and methods**

128 *2.1. Study area*

129 We carried out the study over a 33,468 ha area around a highly urbanized city in France:
130 Valence (Fig. 2). This area exhibits a wide radiance gradient (i.e. a measure of ALAN defined
131 as the radiant flux reflected or emitted by surfaces) from 0 to 94 nW/cm²*sr. Land-use types
132 in the study area were largely agricultural (54%), urban (21%), and forest (21%), while
133 wetlands cover only 4% (Fig. 2; see Environmental variables section for information source).
134 Note the agriculture land-use in the study area: 86% annual crops (mainly cereals and market
135 gardening), 7% perennial crops (orchard and vineyard) and 7% grasslands, with an average of
136 20 m of hedgerows per hectare.

137

138 *2.2. Sampling design*

139 The study aimed to investigate the radiance effects on bat activity (i.e. not differentiating
140 foraging from commuting) according to landscape composition. For that we sampled bat
141 activity at 253 sampling sites covering a wide range of radiance (from 0 to 57 nW/cm²*sr
142 used as an indicator of artificial lighting (Azam et al., 2016); Fig. S1, higher than 57 radiance
143 values were too scarce in the study area to be included in the sampling design). Within this
144 radiance range we sought to include a high variability in land-use variables (see
145 Environmental variables section) while minimising correlations between radiance and land-
146 use variables (Figs. S2 & S3; Table S1). Accordingly, we selected sampling sites following
147 the Laforge et al., (2019) approach. We first divided the whole study area into 250x250 m
148 quadrats, whose mean radiance, forest areas proportion, urban areas proportion and distance
149 from the center of quadrats to wetland were calculated. We used these four variables only to
150 select sites, in order to limit the number of possible combinations while maximising
151 variability in landscape contexts. We then categorized each of these variables into four values

152 classes, maximising the inter-class variance and minimising the intra-class variance, using the
153 Jenks Algorithm (Jenks, 1977). On the study area, 133 combinations of four classes (i.e. each
154 derived from the radiance, forest proportion, urban proportions or distance to wetlands) were
155 available (see Supporting information S1). Thus, each combination was composed of a given
156 class of radiance, forest proportion, urban proportion and distance to wetland. We randomly
157 selected three quadrats per combination whenever possible (i.e. 253 quadrats selected in total;
158 see Supporting information S1 for details on this quadrat selection method). The selected
159 quadrats central points were defined as the location of sampling sites, or it was slightly moved
160 when inaccessible.

161

162 *2.3. Bat monitoring*

163 Recordings were carried out from the 3 May to 3 July 2017, during 27 nights in the seasonal
164 peak of bat activity according to the French national bat monitoring program “Vigie- Chiro”
165 (<http://www.vigienature.fr>), under favourable weather conditions: no rain; <5 m/s wind
166 speeds, and > 12°C temperatures. The average nighttime cloud cover varied from 17 to 70 %
167 (47 % in average; see Table S2).

168 We sampled on average nine sites per night simultaneously, covering a wide range of
169 radiances (Table S2), with at least 750 m between each of them. Bats were recorded
170 throughout the entire night, from 30 min before sunset to 30 min after sunrise, and only once.
171 Echolocation calls were recorded using one SM4BAT (Wildlife Acoustics Inc., Concord,
172 MA, USA) recorder per site (Supporting Information S2 for details about standardized
173 settings).

174 Since it is impossible to determine the number of individual bats from their echolocation
175 calls, we calculated an activity metric commonly used in Europe, hereafter named ‘bat
176 passes’, calculated as the number of bat passes per night (Kerbiriou et al., 2019, 2018;

177 Stahlschmidt and Brühl, 2012). A bat pass was defined as a single or greater echolocation call
178 separated by at least a 2-second gap without calls, and a maximum duration of 15 seconds.
179 We did not separated foraging from commuting bat passes. We then automatically identified
180 bat passes to the most accurate taxonomic level possible, using the SonoChiro© software
181 (Biotope, France).

182 To account for potential errors in automated identifications, we followed the Barré et al.
183 (2019) approach proposing a cautious method to ensure results robustness against automated
184 identification errors in acoustic surveys. The method allows, resorting to random manual
185 checking of automated identifications (by combining measurements of energy peak, final
186 frequency, call duration, band width and time between calls, as discussed in Barataud (2015)),
187 to model the error rate for each species or group, according to confidence scores provided by
188 the software (Supporting Information S3, Table S3 and Fig. S4). This method allows
189 presenting results based on a maximum error rate tolerance of 0.5 (MERT), above which data
190 were discarded. This keeps the number of bat passes for all species and species groups great
191 enough for analysis, while limiting false positives. Then results are confirmed on a more
192 restrictive 0.2 MERT, in order to permit conclusive interpretation only when both MERT
193 thresholds are consistent (Barré et al., 2019; see Supporting Information S3, Tables S3 & S4
194 and Fig. S4 for more details).

195 Two species groups (i.e. *Myotis* spp. and *Plecotus* spp.) were constructed, because species
196 within these groups were difficult to distinguish from each other, based on their echolocation
197 calls (Obrist, Boesch & Fluckiger, 2004). We also constructed a third species group,
198 *Rhinolophus* spp., including *Rhinolophus ferrumequinum* and *R. hipposideros*, because of
199 their very low abundances and occurrences (Table S4).

200

201 *2.4. Environmental variables*

202 Since the effects of environmental variables on bat activity can change according to the
203 spatial scale considered and are very context-dependent and difficult to predict, we calculated
204 their metrics regarding average, proportion or length at five different buffer sizes used in
205 previous studies (200, 400, 600, 800 and 1000 m; Kalda et al., 2015; Lacoeuilhe et al., 2016),
206 using the QGIS software.

207 For each sampling site and each buffer size, we first extracted the average radiance in buffers
208 from VIIRS night-time lights. Then, to characterize landscape composition, we computed 11
209 land-use variables (either distances or length/proportion in buffers) varying across sites (Table
210 S5), which are well-known good bat activity predictors: the proportion of, and distance to
211 urban (e.g. Azam et al., 2016), forest (e.g. Boughey et al., 2011), farmland (e.g. Roeleke et al.,
212 2016) and wetland areas (e.g. Amorim et al., 2018; De Conno et al., 2018); hedgerow length
213 (e.g. Froidevaux et al., 2017; Lacoeuilhe et al., 2016), road (e.g. Berthinussen & Altringham,
214 2012) and wooded edges (Heim et al., 2017).

215 Radiance was extracted from VIIRS night-time lights, which is a yearly and cloud-free
216 composite raster (2016) with a 450-m pixel size produced by the Earth Observation Group
217 and NOAA National Centres for Environmental Information (NCEI)
218 (https://ngdc.noaa.gov/eog/viirs/download_dnb_composites.html). Environmental variables
219 (2016) were provided by the National Institute of Geography in a vectorial shapefile with a
220 2.5-m spatial accuracy (from BD TOPO for data on forests, hedgerows and urban areas, from
221 BD Carthage for wetland data, from BD ORTHO and Graphical Parcel Register for farmland
222 data).

223

224 *2.5. Statistical analyses*

225 We examined the radiance effects on bat activity according to land-use variables around
226 sampling sites (i.e. landscape composition). A summary of the statistical analysis steps

227 presented below is shown in Figure S5. We ran Generalized Linear Mixed Models (GLMMs,
228 R package *lme4*; Bates et al., 2015) for each species or species group separately, using the
229 number of bat passes per site as response variable. We used a negative binomial error
230 distribution to keep low overdispersion ratios in models (<1.50 ; Table S5; Zuur et al., 2009).
231 For two rare taxa (*Barbastella barbastellus*, *Rhinolophus* spp.; Table S3), information relative
232 to bat activity variation were too scarce, thus we used the presence-absence per site as
233 response variable associated with a binomial error distribution. To build full models, we
234 included the radiance and land-use variables as fixed effects. In order to assess the
235 dependence on landscape composition of potential radiance effects on bat activity, we
236 included all possible simple interactions between radiance and land-use variables. All
237 variables used as fixed effects were scaled (i.e. by subtracting the mean and dividing by the
238 standard deviation). To control for inter-night variation in bat activity (e.g. due to weather
239 conditions) and according to our sampling design based on simultaneous recordings each
240 night along a radiance-landscape gradient, we included the date as random effect in models.
241 For each variable included in the full models presented above, except where distances are
242 concerned, we selected the best buffer size for each species. To do this, we ran one univariate
243 model per variable per buffer size for each species, and selected the one with the smallest
244 Akaike Information Criteria (AIC). Thus, each full model can contain different optimal buffer
245 sizes between variables (Tables S6 & S7). Full models were constructed by excluding any
246 explanatory variable responsible for multicollinearity with a < 2 variance inflation factor
247 (VIF) value using the *vif* function (R package *car*; Fox and Weisberg, 2019; see Supporting
248 information S4 and table S6 for full models composition). Thus, removing variables
249 responsible for multicollinearity restrained the number of predictors (ranging from 8 to 17) in
250 full models, depending on species (Table S6). We also assessed potential non-linear effects
251 for all variables by visual inspection of plots from Generalized Additive Mixed Models

252 (GAMM, R package *mgcv*; Wood, 2011). Seven quadratic relationships were observed for *B.*
253 *barbastellus*, *Miniopterus schreibersii*, *Myotis* spp., *Pipistrellus kuhlii*, *Pipistrellus nathusii*
254 and *Plecotus* spp. To account for these non-linear relationships, we added quadratic effects on
255 these variables in full GLMMs (Table S6). We also checked for potential spatial
256 autocorrelation in model residuals using the *Moran.I* function to test significance (R package
257 *spatial*; Venables and Ripley, 2002). We found significant spatial autocorrelation for
258 *Eptesicus serotinus*, *Myotis* spp., *Nyctalus leisleri*, *Nyctalus noctula* and *P. pipistrellus*. To the
259 full models, we added a distance-weighted variable in addition to other explanatory variables,
260 to account for spatial autocorrelation (Table S6; Bardos et al., 2015), using the *autocov_dist*
261 function (R package *spdep*; Bivand and Wong, 2018).

262 Then, following a multi-model inference approach (Grueber et al., 2011), we generated –
263 from the full model for each species and species groups – a set of candidate models
264 containing all possible variable combinations ranked by corrected AIC (AICc). Using all
265 models with a delta AICc < 2 (and a delta AICc < 6 for comparison; Grueber et al., 2011), we
266 averaged regression coefficients for each fixed effect, using the *model.avg* function (R
267 package *MuMIn*; Barton, 2015). Fixed effects were averaged only over models in which that
268 fixed effect appeared (i.e. the so-called natural average method; Grueber et al., 2011). From
269 the model averaging procedure, we were also able to extract the relative importance of each
270 variable (estimated by summing the weights of models in which the variable appeared) and
271 the percentage of explained variance by full and best models (i.e. r squared), using the
272 *rsquared* function (R package *piecewise SEM*; Lefcheck, 2016). As it is not possible to run
273 the *rsquared* function on averaged models, we computed it for best and full models in order to
274 provide a global view of the goodness-of-fit.

275 All analyses were performed in the R software v.3.5.1 (R Core Team, 2020).

276

277 **3. Results**

278 *3.1. Bat monitoring*

279 At the 253 sampling sites, we recorded 79,661 bat passes in total, including 10 species and
280 three species groups, where the most abundant species was *P. kuhlii*, representing 71% of
281 passes and present in 100% of sites (Table S3). The least common species were *E. serotinus*
282 (43 passes), *Rhinolophus* spp. (32 passes) and *B. barbastellus* (208 passes), which were
283 recorded respectively in 9%, 13% and 5% of sites (Table S3).

284

285 *3.2. Radiance effects on bat activity*

286 The radiance variable had a significant effect on the activity of five species or species groups
287 (Table 1), with high relative importance (Table S8), and these were selected in all top
288 candidate models with a < 2 AICc delta for nine species or species groups, and in a minimum
289 of 50% of top candidate models for the four remaining ones. We detected significant decrease
290 in activity of *Myotis* spp., *Plecotus* spp. and *P. pipistrellus* due to radiance (Table 1; Fig. 3).
291 We also detected significant increase in activity of *P. kuhlii* and *P. pygmaeus* due to radiance
292 (Table 1; Fig. 3).

293

294 *3.3. Interaction between radiance and landscape composition*

295 Depending on species, best models (i.e. with the lowest AICc) explained a percentage of
296 variance ranging between 7% and 34%, except for those from *E. serotinus* and *N. noctula*,
297 which explained very low variance (i.e. 1 and <0.1 %, respectively; Table S6).

298 We found a significant interaction effect between radiance and land-use variables for 8
299 species or species groups (Table 1). The results of these interactions as a whole show that the
300 positive or negative effects of light on bats, depending on species, mainly occurred in non-
301 urban habitats. Specifically, bat activity becomes increasingly higher under high radiances

302 with the increasing proportion of farmland areas for *P. pygmaeus*, while for *N. noctula*
303 activity it is higher under low radiances with low proportions of farmland; and higher under
304 high radiances with high farmland proportions (Table 1; Fig. 4). We found a similar result
305 concerning *H. savii* and *P. nathusii*, whose activity increased with increasing radiance only
306 when proportion of forests became high (Table 1; Fig. 4). However, we found higher activity
307 of *N. leisleri* under high radiances far from forests (Table 1; Fig. 4). We also found higher *H.*
308 *savii* activity under high radiances far from wetlands, while *M. Schreibersii* was positively
309 affected by radiance below 700 m from wetlands and negatively affected above (Table 1; Fig.
310 4). We found the opposed pattern for *N. noctula* and *N. leisleri*, whose activity became higher
311 under high radiances along with the increasing proportion of wetlands, although sampled
312 gradients were less extensive (Table 1; Fig. 4).

313 Concerning urban variables, we found an increasing *M. schreibersii* activity with increasing
314 radiance, which mainly occurred in non-urban habitats (Table 1; Fig. 4). We found the same
315 pattern for *Myotis* spp., for which the decrease in activity due to radiance became much higher
316 with increasing distance to urban areas, as well as the increase in *P. kuhlii* activity due to
317 radiance, which became increasingly higher with increasing distance to urban areas (Table 1;
318 Fig. 4). For these three species or group, radiance was positively associated with the
319 increasing proportion of, or the decreasing distance to urban areas (Fig. S6), even though this
320 did not result in any collinearity issue.

321 Results were qualitatively very similar and little changes were found after we re-ran analyses
322 at the 0.2 maximum error rate threshold (see Table S9). However, two new significances were
323 found for *P. pipistrellus*. Specifically, we found an increasingly negative effect of radiance on
324 *P. pipistrellus* activity, with an increasing length of hedgerows and a decreasing distance to
325 wetlands (Table S9; Figs. 4 & 5). Finally, averaging candidate models in a delta AICc < 6
326 instead of 2 did not change results (Table S10).

327 **4. Discussion**

328 We show that for 9 bat taxa out of the 13 tested, ALAN affects bat activity (i.e. not
329 differentiating foraging from commuting) especially in non-urban habitats. We also show
330 that, as expected, the responses depend on the species. For five species, the intensity of
331 ALAN (i.e. apart from its interactions with landscape variables) increased the activity of *P.*
332 *kuhlii* and *P. pygmaeus* and decreased the activity of *Myotis* spp., *Plecotus* spp. and *P.*
333 *pipistrellus*, and these effects were significantly driven by landscape composition. More
334 notably, for five species, the ALAN effects on activity were only significant in particular
335 landscape compositions (*H. savii*, *M. schreibersii*, *N. leisleri*, *N. noctula* and *P. nathusii*),
336 which make such effects undetectable without exploring ALAN-landscape composition
337 interactions. Specifically, both positive or negative ALAN effects on bat activity occur much
338 more often in non-urban habitats. All these results highlight (i) the need to prioritize ALAN
339 reduction efforts in non-urban habitats, (ii) how important is to account for landscape
340 composition when studying ALAN effects on bats to avoid missing effects, and (iii) the need
341 to consider both ALAN and landscape composition when designing and implementing green
342 infrastructures (i.e. strategically planned European network of natural and semi-natural areas)
343 (European Commission 2009).

344

345 *4.1. Radiance effects on bat activity*

346 Overall responses of bat species to radiance were consistent with the literature for slow-
347 flying/gleaner species (i.e. *Myotis* and *Plecotus* species) widely known to be negatively
348 impacted by artificial lighting (e.g. Azam et al., 2018; Lacœuilhe et al. 2014). Possible
349 explanations could be the relative high sensitivity of the bat eye to the blue part of light
350 spectrum (Müller et al., 2009), the increase in abundance of less light-shy species at the
351 expense of slow-flying gleaner species (Arlettaz et al., 2000), or the increased predation risk
352 due to their slow flight (Jones and Rydell, 1994). Positive effects of radiance detected for *P.*

353 *kuhlii* and *P. pygmaeus* (i.e. the aerial-hawking species guild) were consistent with literature
354 based on local measures of ALAN (i.e. a street lamp level, e.g. Azam et al., 2015), likely due
355 to increased insect density close to lights (Rydell, 1992). However, our results were opposed
356 to those found by Azam *et al.*, (2016) carried out at national scale. The negative effect
357 detected on *P. pipistrellus* was consistent with studies carried out at national (Azam et al.,
358 2016) or agglomeration scales (Pauwels et al., 2019). However, positive effects on *P.*
359 *Pipistrellus* species are also reported at street light scale (e.g. Azam et al., 2018). Such
360 opposed pattern could be explained by the scale effect and light variable used: (i) studies
361 carried out at local scale involved ground-based data measurements at very small scales (a
362 few meters) and focus on street light contexts, highlighting likely attractiveness of streetlight
363 lamp for insects and, in turn, a number of bats, while (ii) studies carried out on a large scale
364 (countries or cities) have more chances to involve more sampling of unlit areas close to and
365 far from lit ones, which allows for detecting insects depletion due to the “vacuum cleaner”
366 effect in unlit areas close to lit ones (Eisenbeis, 2006; Owens and Lewis, 2018).

367

368 *4.2. Interaction between radiance and landscape composition*

369 First, we found that radiance effects on bat vary among landscape compositions in bat-
370 friendly non-urban habitats (i.e. farmland – including non-negligible amount of perennial
371 crops and grasslands in the study area–, forest, hedgerow and wetland). Radiance had higher
372 effects on bat activity with increasing non-urban habitats (i.e. an increasing amount of, or
373 proximity to, land-uses other than impervious surfaces, or a decreasing amount of or
374 proximity to urban areas). These results are in accordance with a recent study conducted at
375 agglomeration scale, which showed that dense tree cover amplified positive or negative
376 effects of street light for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp. (Straka et al., 2019).
377 Two other studies showed that high tree cover mitigated the negative effects of streetlights on

378 bats (Mathews et al., 2015, Pauwels et al., 2019). One proposed explanation for positive
379 effects is that tree cover could reduce the predation risk linked to light and could also,
380 combined with streetlights, attract more insects and therefore constitute advantageous
381 foraging grounds. Alternatively, close to trees, flying bats could also benefit from favourable
382 microclimate or more structured flightpaths, which offset lighting-generated disadvantages. In
383 our study, we found such mitigating of radiance effects only from increasing proportion of
384 farmland areas and from decreasing distance to wetlands, for *N. noctula*, and *M. schreibersii*,
385 respectively.

386 For species found to be negatively impacted by radiance in our study, we found *P. pipistrellus*
387 to be more impacted at sites with highest length of hedgerows and closest to wetlands, and
388 *Myotis* spp. to be more impacted at highest distances to urban. As hedgerows constitute a key
389 landscape element for bat commuting (Pinaud et al., 2018), lighting at such linear landscape
390 elements may disconnect foraging habitat and even limit their accessibility for bats (Laforge
391 et al., 2019). In addition, we should be cautious about results for *P. pipistrellus* and confirm
392 them in further studies, given that these were only significant at the most restrictive threshold
393 of maximum error rate tolerance (MERT) in acoustic data (Barré et al., 2019). Wetlands also
394 play an important role for foraging and for drinking for most bat species (De Conno et al.,
395 2018; Roeleke et al., 2016), and light sources close to wetlands particularly attract aquatic
396 insects (Manfrin et al., 2017) and in turn potentially induce an insects depletion around due to
397 the “vacuum cleaner” effect. Thus, negative effects of ALAN on slow-flying gleaner species
398 would be stronger close to wetlands. Finally, given that an increasing proportion of urban
399 areas reduce the amount and complexity of available vegetation and in turn of arthropod food
400 resource (Sánchez-Bayo & Wyckhuys, 2019), and since insectivorous bat species strongly
401 depend of high levels of vegetation complexity (Suarez-Rubio et al., 2018) and arthropods
402 amounts (Charbonnier et al., 2014), it is not surprising to find mainly higher negative impacts

403 of radiance in non-urban habitats. Laforge et al., (2019) draw similar conclusions showing
404 that lighting reduction was more efficient to restore bat presence in vegetated areas than in
405 cities.

406 *P. pygmaeus* activity increase with illumination, especially on farmland. Despite a sampling
407 design elaborated for minimising correlations between land-use variables, we observed an
408 opposition between urban and farmland cover in our study sites (correlation coefficient: -0.59;
409 Table S8). Thus, found effects of radiance according to the farmland variable could mirror
410 that non-urbanized areas are more attractive than urbanized areas (Border et al., 2017).
411 Further studies remain needed to investigate why *P. pygmaeus* is especially active in lit more
412 than dark farmland. *H. savii* and *P. nathusii* were also found to be more affected at sites with
413 high forest proportions. Forest edges can drive activity and foraging of *P. nathusii* more than
414 other habitats as hedgerows (Heim et al., 2017), while, to our knowledge, no similar studies
415 have tested the same for *H. savii*. We hypothesize that the interest of forest edges coupled
416 with lighting attracting arthropod prey (Owens & Lewis, 2018) could enhance the
417 attractiveness of such habitat for these species. We also found *M. schreibersii* to be more
418 affected by radiance at the lowest urbanized sites, and *P. kuhlii* to be increasingly affected
419 with increasing distance to urban. Such a result is also consistent with the hypothesis we
420 discussed above for aerial-hawking flying species: increasing amount of urban areas leads to a
421 decreasing amount of other land-uses, which in turn reduces arthropod prey availability for
422 bats, artificial light attractivity being therefore less efficient in such a landscape.

423

424 *4.3. Limitations and perspectives*

425 Most effects found were robust against error rates in acoustic data and the presented
426 interactions did not suffer from any confounding effects between radiance and land-use
427 variables. However, results validity could not be checked at the 0.2 MERT threshold for *E*.

428 *serotinus*, *N. noctula* and *P. nathusii*, potentially because of too low remaining numbers of bat
429 passes, given that such thresholds discarded a lot of data (Table S11; Supporting information
430 S5).

431 Satellite-based data used in this study were calculated using cloud-free images, which
432 potentially underestimate impacts for weather conditions promoting a skyglow caused by
433 upwardly emitted artificial light being scattered in the atmosphere (Kyba et al., 2015). Our bat
434 monitoring was carried out under non-negligible cloud covers which varied from 17 to 70 %
435 (47 % in average; Table S2) over the 27 nights studied, which could significantly increase
436 skyglow. Since a skyglow can be comparable to late twilight and moonlight (Gaston et al.,
437 2017), we could expect it to affect the use of space by bats (Roeleke et al., 2018) and in turn
438 the ALAN effects-landscape relationship. Further studies could thus assess how the skyglow,
439 and more generally less favourable weather conditions, would impact results we report in this
440 study. In addition, further studies should compare such results from the VIIRS raster with
441 ones from more local light intensity measurements to study finer-scale factors, as performed
442 in Straka et al. (2019), Pauwels et al. (2019) and Hale et al. (2015). Indeed, given that our
443 explanatory variable was a radiance pixels averaging in a given radius around sites, there is
444 undeniably an inaccuracy in the real distances of impact. Accurate distances of impact are
445 nevertheless essential for concrete recommendations in local lighting management. In
446 addition, although land-uses used in this study to describe landscape composition were the
447 most accurate information we had, future studies could assess ALAN effects on bats
448 according to landscape composition using (i) more accurate spatial resolution of ALAN data
449 and (ii) finer habitat descriptors, for example by differentiating different types of farming in
450 the farmland category, or by measuring structure of woody habitats.

451 Although we found some positive effects of radiance, artificial lighting is expected to induce
452 negative effects on a larger scale (Azam et al., 2016), likely due to prey accumulation and
453 ‘vacuum cleaner effect’ around light sources decreasing prey availability on larger scales
454 (Eisenbeis, 2006; Owens and Lewis, 2018). As a consequence, positive relationships at local
455 scale between bat activity and ALAN should be interpreted with caution. Finally, one group
456 (*Plecotus* spp.) remains strongly negatively affected by ALAN effects irrespective of
457 landscape composition, which in turn involves thinking of reduction possibilities everywhere
458 for this group.

459

460 **5. Conclusions**

461 Artificial light effects on bats were predicted to vary according to landscape composition, but
462 had so far not received attention at a regional scale for a large number of landscape predictors
463 and bat taxa. We show that the magnitude of most ALAN effects on bats is driven by
464 landscape composition. Some ALAN effects were even only detectable in particular
465 landscape compositions, making the main effect of ALAN undetectable without account for
466 interactions with landscape. This underpins the great importance to prioritize ALAN
467 reduction schemes for bat conservation in non-urban habitats, and how important is to account
468 for landscape composition when studying ALAN effects on bats to avoid missing effects.
469 Indeed, most found effects occurred in non-urban habitats, thereby highlighting the
470 importance of minimizing lighting close to these areas.

471

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479

480 **Author's contribution**

481 KB conceived the ideas; KB, AV, AD and SV designed the methodology; AD and AV
482 collected the data; AD, AV and TD manually checked bat passes; KB and AV analysed the
483 data; KB with the support of CK, CA, AV and IL led writing of the manuscript. All authors
484 critically contributed to the drafts and gave their final approval for publication.

485

486 **Data accessibility**

487 Dataset used will be available in a dedicated platform.

488 **References**

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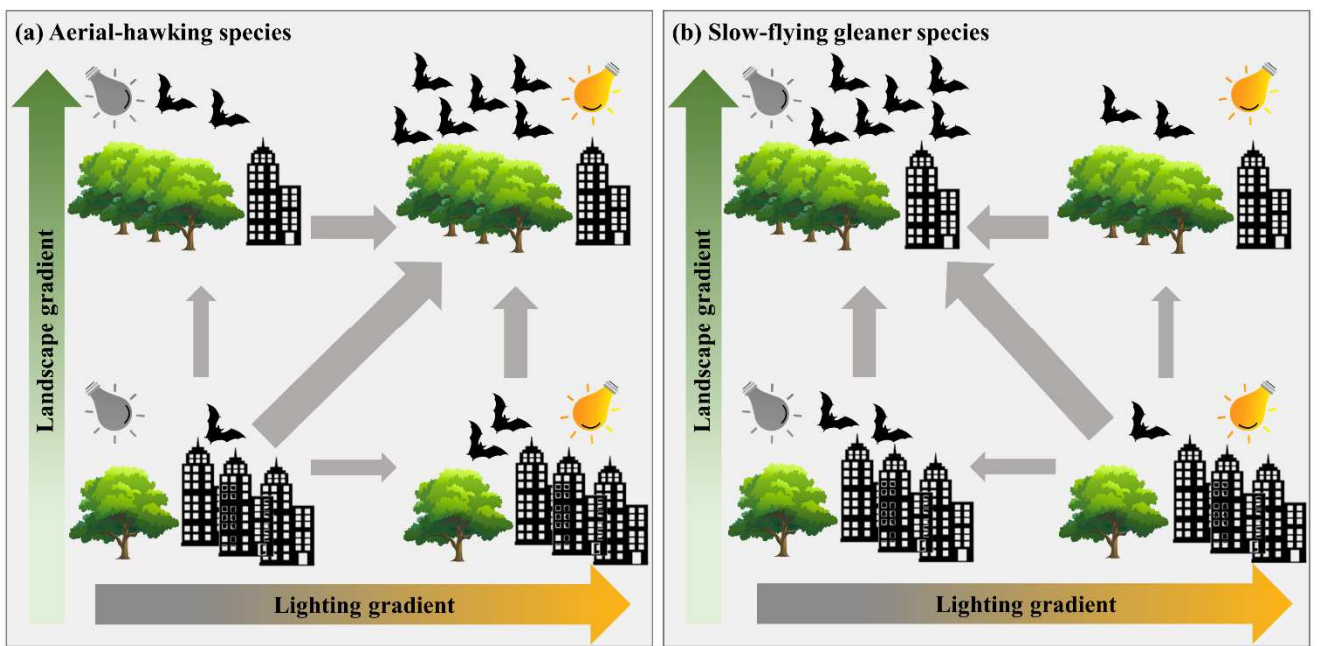
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734 Figure 1. Schematic representation of the tested hypothesis showing the expected variation of
735 artificial light effects on bat activity according to landscape composition for slow-flying
736 gleaner (a; e.g. *Myotis* and *Plecotus* groups) and aerial-hawking (b; e.g. *Eptesicus*, *Nyctalus*
737 and *Pipistrellus* species) bats. The direction of the grey arrows shows the expected ways of
738 increasing bat activity in term of light-landscape combinations, and the grey arrows width
739 shows expected the magnitude of changes.

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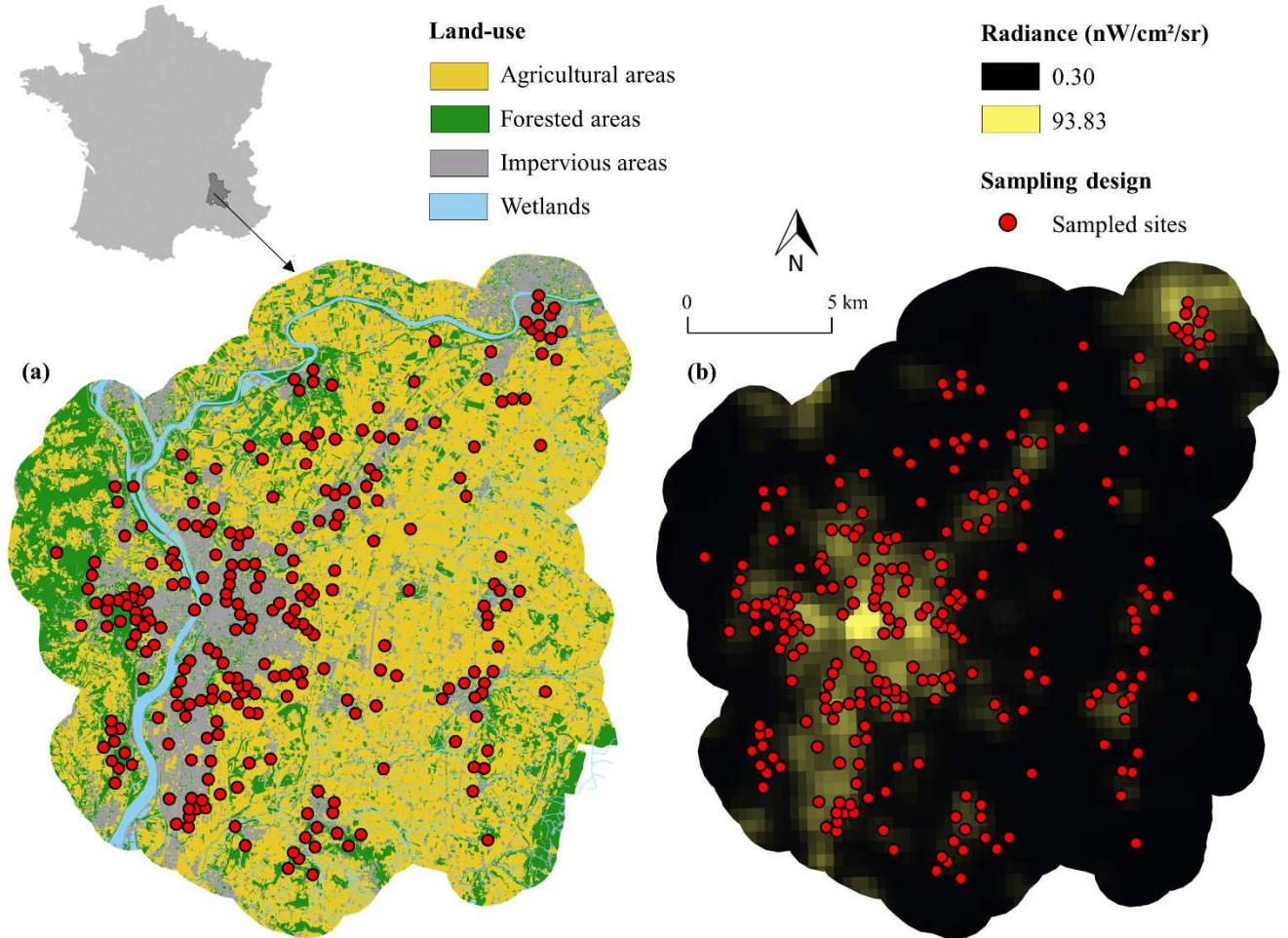


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743 Figure 2. Map of the study area in France and the 253 sampling sites, according to the main
744 land-use (a) and radiance gradient (b).

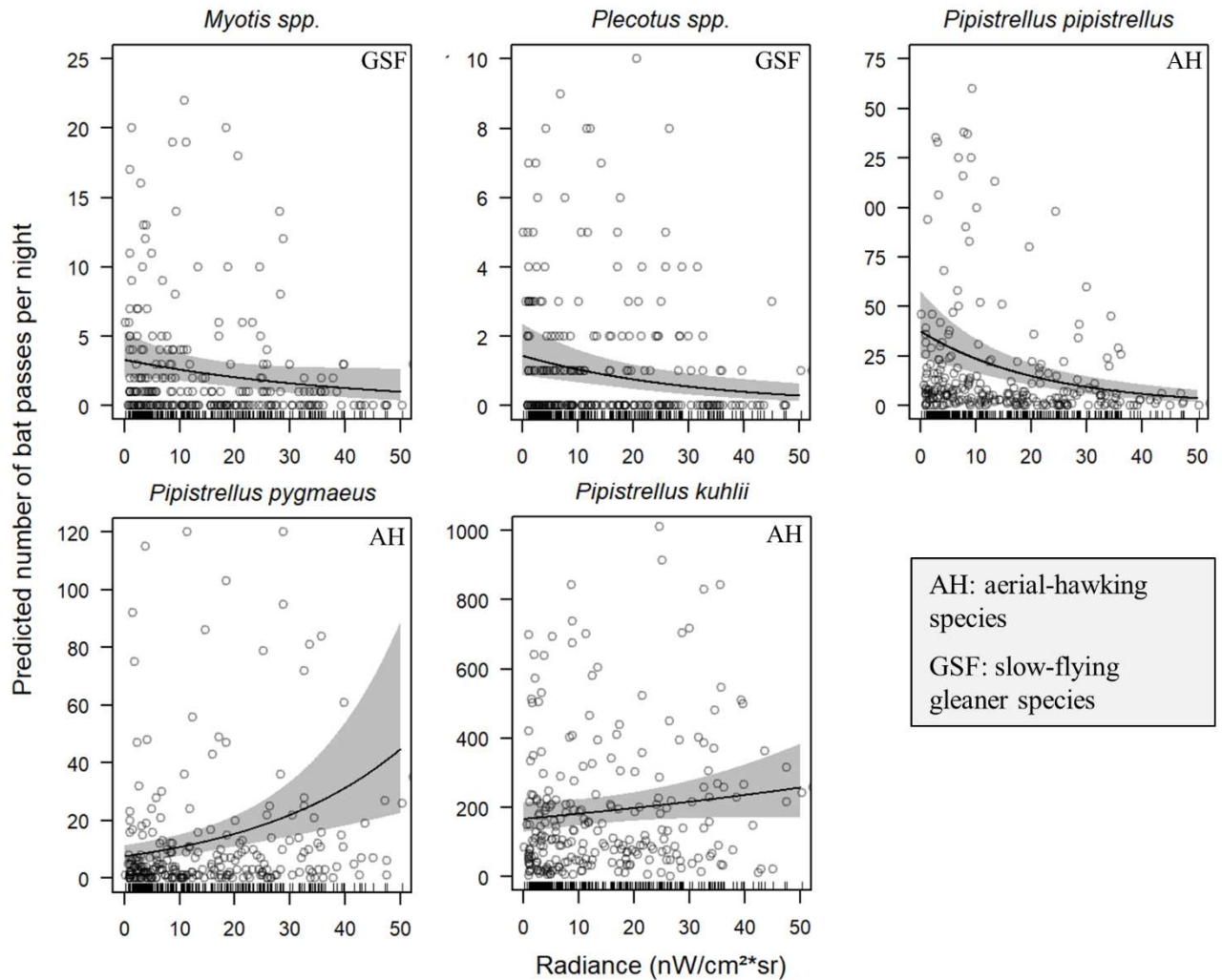
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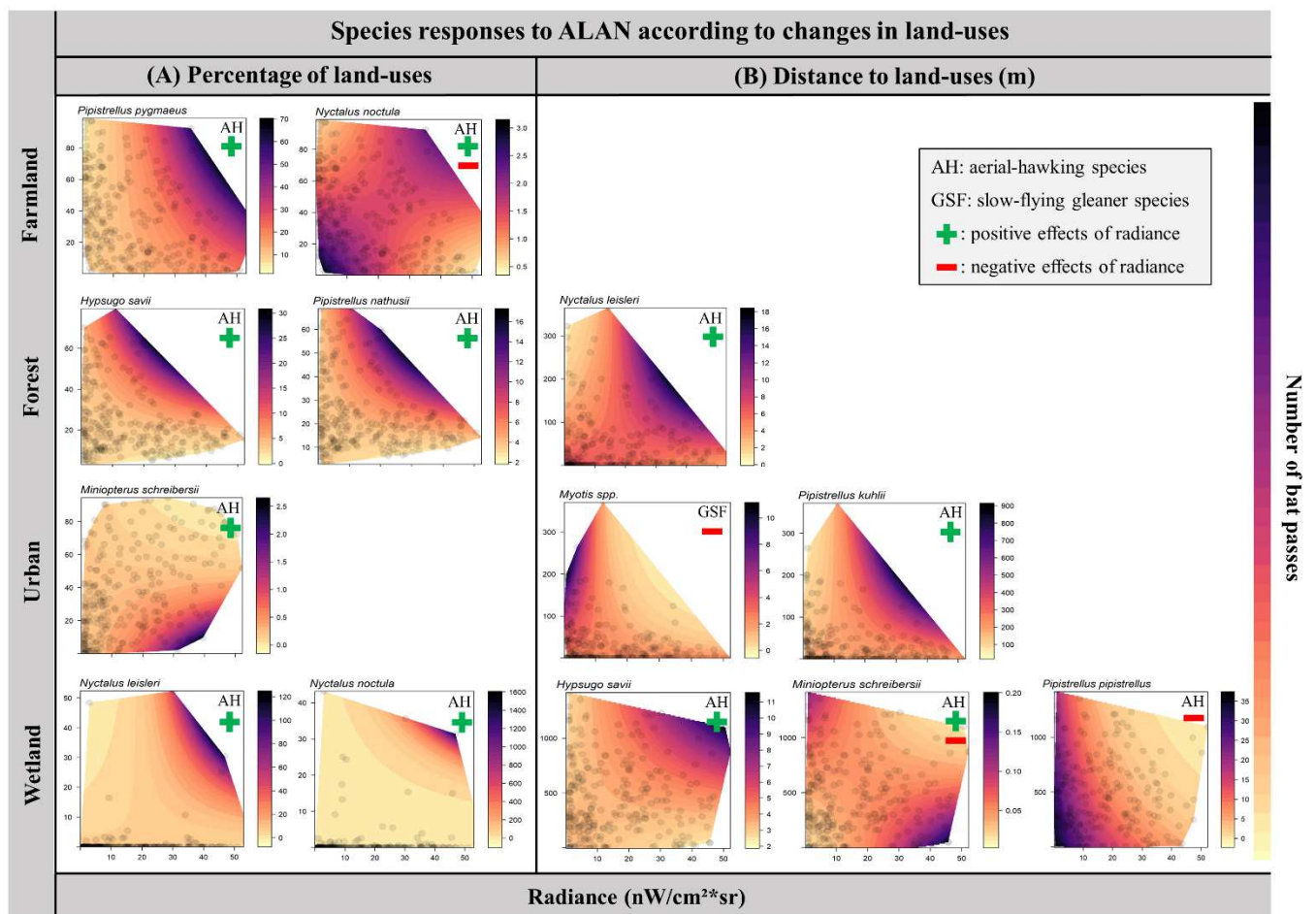
748 Figure 3. Relation between the predicted number of bat passes per night and radiance values
 749 predicted from best models for species or species groups significantly affected by the radiance
 750 variable alone (i.e. a global effect apart from its interactions with landscape variables), and
 751 associated 95% confidence intervals. Circles show each of the 253 recording sites.
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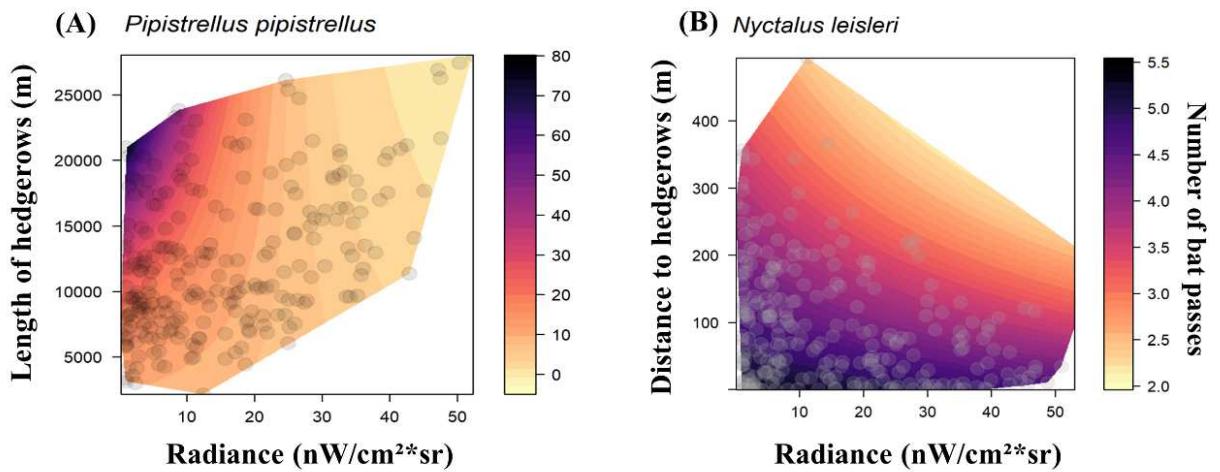
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755 Figure 4. Predicted number of bat passes from GLMMs according to the interaction between
 756 radiance and land-use variables computed as (A) proportions and (B) distances. The colour
 757 scale represents the predicted mean number of bat passes per night, darker colours show
 758 higher number of bat passes. Circles represent each of the 253 combinations between radiance
 759 and land-use values sampled in the study. Predictions were restricted to the maximum convex
 760 polygon of sampled radiance-landscape variables combinations, and white surfaces show
 761 uncovered gradients. For each plot, the bat guild (i.e. aerial-hawking or slow-flying gleaner
 762 species) and the direction of bat response to radiance are shown with acronyms and symbols.



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765 Figure 5. Predicted number of aerial-hawking species passes from GLMMs according to the
766 radiance in interaction with (A) the length of hedgerows in a 800m radius for *P. pipistrellus*
767 and (B) the distance to hedgerow for *N. leisleri*. The colour scale represents the predicted
768 mean number of bat passes per night, darker colours show higher number of bat passes.
769 Circles represent each of the 253 combinations between radiance and land-use values sampled
770 in the study. Predictions were restricted to the maximum convex polygon of sampled
771 radiance-landscape variables combinations, and white surfaces show uncovered gradients.
772 Both plots show a negative effect of light on bat taxa.

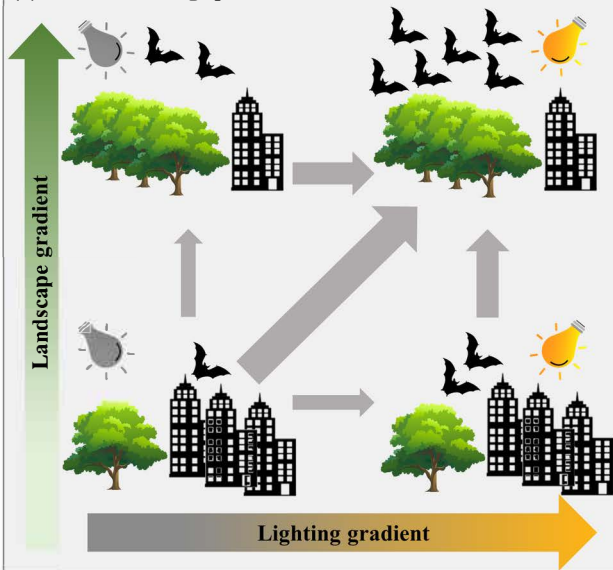


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775 Table 1. Averaged estimates, standard errors in parentheses and significance levels (*** P < 0.001, **
776 P < 0.01, * P < 0.05, . P < 0.1) from the set of best candidate models with an AICc delta < 2 for each
777 species (Barbar: *Barbastella barbastellus*; Eptser: *Eptesicus serotinus*; Hypsav: *Hypsugo savii*;
778 Minsch: *Miniopterus schreibersii*; Myosp: *Myotis* spp.; Nyclei: *Nyctalus leisleri*; Nycnoc: *Nyctalus*
779 *noctula*; Pipkuh: *Pipistrellus kuhlii*; Pipnat: *Pipistrellus nathusii*; Pippip: *Pipistrellus pipistrellus*;
780 Pippyg: *Pipistrellus pygmaeus*; Plesp: *Plecotus* spp.; Rhisp: *Rhinolophus* spp.). Estimates show the
781 effect of radiance and other environmental variables on bat activity. Significant results involving the
782 radiance variable are indicated in bold. Empty cells represent cases for which the variable was not
783 selected in the set of best candidate models.
784

Variables	Estimated parameters, standard errors and p-values of averaged candidate models with $\Delta AICc < 2$												
	<i>Barbar</i>	<i>Eptser</i>	<i>Hypsav</i>	<i>Minsch</i>	<i>Myosp</i>	<i>Nyclei</i>	<i>Nycnoc</i>	<i>Pipkuh</i>	<i>Pipnat</i>	<i>Pippip</i>	<i>Pippyg</i>	<i>Plesp</i>	<i>Rhisp</i>
Artificial light variable													
Radiance	-1.079 (2.120)	-0.837 (0.485).	0.015 (0.009).	0.094 (0.072)	-0.019 (0.010)*	-0.003 (0.003)	-0.001 (0.009)	0.69e-3 (0.30e-3)*	0.018 (0.011).	-0.005 (0.001)***	0.007 (0.002)***	-0.111 (0.035)**	-1.983 (1.291)
Proportion variables													
Farmland	/	/	/	/	/	0.002 (0.003)	-0.004 (0.010)	/	/	/	0.001 (0.002)	/	/
Forest	3.253 (1.436)*	/	0.043 (0.008)***	/	/	/	/	/	0.036 (0.012)**	/	/	/	/
Urban	/	/	/	-0.195 (0.074)**	/	/	/	/	/	/	/	/	/
Wetland	2.984 (1.105)**	0.287 (0.327)	0.013 (0.007).	0.029 (0.068)	-0.008 (0.014)	-0.002 (0.003)	0.024 (0.008)**	-0.21e-3 (0.20e-3)	0.018 (0.009).	-0.001 (0.001).	0.002 (0.002)	/	-1.115 (0.932)
Radiance: Farmland	/	/	/	/	/	/	0.022 (0.010)*	/	/	/	0.003 (0.002)*	/	/
Radiance: Forest	/	/	0.023 (0.008)**	/	/	/	/	/	0.026 (0.013)*	/	/	/	/
Radiance: Urban	/	/	/	-0.196 (0.071)**	/	/	/	/	/	/	/	/	/
Radiance: Wetland	/	0.468 (0.283).	0.008 (0.005).	/	-0.032 (0.023)	0.010 (0.003)***	0.026 (0.011)*	/	-0.008 (0.010)	-0.001 (0.001)	/	/	/
Distance to element variables													
Forest	/	-0.390 (0.411)	-0.010 (0.008)	-0.052 (0.067)	-0.027 (0.009)**	0.002 (0.004)	0.007 (0.008)	/	0.031 (0.010)**	-0.001 (0.001)	-0.002 (0.002)	-0.046 (0.04)	-3.223 (2.092)
Hedgerow	/	/	/	/	/	-0.005 (0.004)	/	/	/	-0.001 (0.001)	/	-0.064 (0.036).	0.835 (0.732)
Urban	/	-0.190 (0.406)	-0.026 (0.009)**	/	-0.011 (0.010)	-0.003 (0.003)	0.005 (0.008)	0.34e-3 (0.30e-3)	-0.028 (0.014).	-0.001 (0.001)	/	/	/
Wetland	/	-0.491 (0.425)	0.008 (0.006)	-0.048 (0.067)	/	/	0.004 (0.007)	0.39e-3 (0.20e-3).	/	-0.003 (0.001)**	0.003 (0.002).	0.058 (0.031).	-1.247 (0.783)
Radiance: Forest	/	/	/	/	-0.013 (0.009)	0.010 (0.004)**	/	/	0.021 (0.011).	-0.002 (0.001).	-0.003 (0.002)	/	-3.073 (1.807).
Radiance: Hedgerow	/	/	/	/	/	-0.007 (0.004)	/	/	/	0.002 (0.001)	/	/	/
Radiance: Urban	/	/	0.010 (0.007)	/	-0.025 (0.010)*	/	/	0.77e-3 (0.30e-3)*	0.029 (0.015).	/	/	/	/
Radiance: Wetland	/	-0.683 (0.492)	0.016 (0.006)**	-0.153 (0.083).	/	/	0.012 (0.007)	0.12e-3 (0.22e-3)	/	-0.001 (0.001)	-0.002 (0.002)	-0.011 (0.032)	/
Length variables													
Hedgerow	/	/	-0.020 (0.008)*	0.053 (0.068)	/	/	/	/	/	0.002 (0.001)	/	-0.051 (0.040)	/
Road	/	/	/	/	-0.031 (0.008)***	0.003 (0.003)	/	0.001 (0.30e-3)***	0.007 (0.010)	0.001 (0.001)	/	/	-2.865 (0.950)**
Road^2	/	/	/	/	/	/	/	-0.001 (0.30e-3)***	/	/	/	/	/
Wooded edges	/	0.101 (0.463)	/	0.084 (0.060)	0.023 (0.008)**	0.004 (0.003)	-0.007 (0.008)	0.001 (0.30e-3)***	/	/	0.006 (0.002)**	-0.049 (0.038)	/
Radiance: Hedgerow	/	/	0.012 (0.007).	/	/	/	/	/	/	-0.001 (0.001)	/	/	/
Radiance: Wooded edges	/	-0.917 (0.501).	/	/	/	-0.002 (0.003)	/	/	/	/	0.001 (0.002)	/	/

(a) Aerial-hawking species



(b) Gleaner-slow flying species

