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## Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program

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11 **Abstract**

12 **Context.** Light pollution is a global change affecting a major proportion of global land surface.  
13 Although the impacts of Artificial Light At Night (ALAN) have been documented locally for  
14 many taxa, the extent of effect of ALAN at a landscape scale on biodiversity is unknown.

15 **Objectives.** We characterized the landscape-scale impacts of ALAN on 4 insectivorous bat  
16 species *Pipistrellus pipistrellus*, *Pipistrellus kuhlii*, *Eptesicus serotinus*, *Nyctalus leisleri*, and  
17 compared the extent of their effects to other major land-use pressures.

18 **Methods.** We used a French national-scale monitoring program recording bat activity among 2-  
19 km car transect surveys, and extracted landscape characteristics around transects with satellite  
20 and land cover layers. For each species, we performed multi-model averaging at 4 landscape  
21 scales (from 200 to 1000 m buffers around transects) to compare the relative effects of the  
22 average radiance, the proportion of impervious surface and the proportion of intensive  
23 agriculture.

24 **Results.** For all species, ALAN had a stronger negative effect than impervious surface at the 4  
25 landscape scales tested. This effect was weaker than the effect of intensive agriculture. The  
26 negative effect of ALAN was significant for *P. pipistrellus*, *P. kuhlii* and *E. serotinus*, but not for  
27 *N. leisleri*. The effect of impervious surface varied among species while intensive agriculture had  
28 a significant negative effect on the 4 species.

29 **Conclusion.** Our results highlight the need to consider the impacts of ALAN on biodiversity in  
30 land-use planning and suggest that using only impervious surface as a proxy for urbanization may  
31 lead to underestimated impacts on biodiversity.

32 **Keywords:** outdoor lighting, urbanization, land-use planning, nightscape, bats, chiroptera

### 33 **Introduction**

34 Land-use changes, mostly agricultural intensification and urbanization, are considered as major  
35 drivers of global biodiversity loss (Foley et al. 2005). The habitat loss and fragmentation they  
36 induce have been associated globally to species decline (Donald et al. 2001; Tilman et al. 2001;  
37 Penone et al. 2012), large scale biotic homogenization (Devictor et al. 2007; Le Viol et al. 2012)  
38 and loss of ecosystem services (Kremen et al. 2002; Deguines et al. 2014). However, these land-  
39 use changes also generate different types of pollution such as chemical, noise and artificial light  
40 (Forman and Alexander 1998; Grimm et al. 2008; Kyba and Hölker 2013), whose extent of effect  
41 on biodiversity has not always been assessed (Grimm et al. 2008). In particular, Artificial Light  
42 At Night (ALAN) is an urban-induced pollution that affects a substantial part of world (Falchi et  
43 al. 2016) and that is increasing on average by 6 % per annum worldwide (Hölker et al. 2010).

44 The alteration of natural light cycles induced by the widespread use of ALAN has major impacts  
45 on the biological rhythms of both nocturnal and diurnal organisms (Gaston et al. 2014). The  
46 subsequent desynchronization of population rhythms of activity with their environment generates  
47 important costs for the fitness of individuals from a wide range of taxa such as birds, insects and  
48 bats (Boldogh et al. 2007; Nordt & Klenke 2013; Da Silva et al. 2015; Van Geffen et al. 2015;  
49 Robert et al. 2015). Furthermore, the response of species to ALAN are driven by  
50 attraction/repulsion behaviors, so the movements and distribution of species can be shifted at  
51 multiple spatial scales (Stone et al. 2009, 2012; Mathews et al. 2015). Taken together, the effects  
52 of ALAN on organisms likely disrupt the spatiotemporal dynamics of biological communities  
53 and ecosystems (Davies et al. 2015; Bennie et al. 2015; Sanders et al. 2015; Minaar et al. 2015).

54 So far, studies on the effects of ALAN on biodiversity have mostly been set up at local scales,  
55 focusing on physiological and behavioral responses of organisms to one or several streetlights

56 (Rich and Longcore 2006; Stone et al. 2012; Perkin et al. 2014; Jong et al. 2015). However, the  
57 landscape-scale impacts of ALAN on biodiversity are unknown (Kyba and Hölker 2013)  
58 although essential to infer its long-term consequences on population dynamics (Gaston and  
59 Bennie 2015). In fact, it is of major importance to characterize the relative contribution of ALAN  
60 to the habitat loss and fragmentation generated by land-use changes to address sustainable land-  
61 use planning strategies (Grimm et al. 2008; Gaston et al. 2014).

62 Particularly sensitive to habitat loss and fragmentation and increasingly threatened worldwide  
63 (Mickleburgh et al. 2002), bats are suitable model species to compare the effects of ALAN  
64 relative to other land-use pressures. As long-lived insectivorous species with a slow reproductive  
65 rate, microchiropteran bats are considered to be good indicators of the response of biodiversity to  
66 anthropogenic pressure (Jones et al. 2009). Furthermore, several studies have pointed to their  
67 value in providing ecosystem services such as pest control (Cleveland et al. 2006; Charbonnier et  
68 al. 2014).

69 Bat activity and occurrence are known to be negatively affected by increased urbanization (Hale  
70 et al. 2012; Jung and Threlfall 2016) as well as agricultural intensification (Wickramasinghe et al.  
71 2003; Jennings and Pocock 2009). However, the responses of bats to ALAN at a landscape scale  
72 are unclear. At a local scale, bat responses to ALAN vary among species according to their  
73 foraging strategy and flight abilities (Jones and Rydell 1994). Slow-flying species adapted to prey  
74 on insects in cluttered vegetation, such as *Rhinolophus spp.* and *Myotis spp.*, are more likely to be  
75 affected by illuminance (Rydell 1992; Stone et al. 2009, 2012; Kuijper et al. 2012; Azam et al.  
76 2015) due to higher risk of predation (Jones and Rydell 1994; Rydell et al. 1996). In contrast,  
77 fast-flying species adapted to hunt insects at dusk in the open air, such as *Pipistrellus spp.* and  
78 *Nyctalus spp.*, can benefit from new and predictable foraging opportunities provided by

79 streetlights (Rydell 1992; Blake et al. 1994; Lacoeyuilhe et al. 2014; Azam et al. 2015), which  
80 attract a large proportion of the surrounding flying insect biomass (Perkin et al. 2014). In this  
81 context, ALAN is likely to be a driver of habitat loss and fragmentation for slow-flying species  
82 while creating new and predictable foraging opportunities in the landscape for fast-flying species  
83 (Stone et al. 2012; Lacoeyuilhe et al. 2014; Azam et al. 2015).

84 However, movements and gap-crossing behaviors of fast-flying species can also be altered by  
85 ALAN in urban landscapes (Hale et al. 2015), suggesting that an increase in landscape-scale level  
86 of ALAN may reduce landscape connectivity for all species regardless of their foraging strategy.  
87 Such an increase may also reduce the availability of suitable dark roosting sites in the landscape  
88 although essential for the reproduction of all bat species (Boldogh et al. 2006). Overall,  
89 landscape-scale level of ALAN may significantly change the spatial dynamics of bat species at  
90 multiple spatial scales, although evidence is lacking as to whether its potential benefits for some  
91 species outweigh its costs.

92 In this study, using a French national-scale citizen-science database, we aimed to *i*) characterize  
93 the effects of ALAN on bat activity and probability of presence at 4 different landscape scales  
94 and *ii*) compare the relative effect of ALAN to other land-use effects with a particular emphasis  
95 on the effects of the proportion of impervious surfaces and of intensive agriculture. Our goal was  
96 to determine whether the extent of effect of ALAN is significant at a landscape-scale relative to  
97 land-use pressures that are considered as major threats for biodiversity (Foley et al. 2005).

98 **Material and methods**

99 *Car transect survey*

100 The data were provided by the French bat-monitoring program  
101 (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science program running since 2006 and  
102 coordinated by the French National Museum of Natural History (NMNH). Volunteer surveyors  
103 recorded bat activity while driving at a constant low-speed ( $25 \pm 5$  km/h) along a 30 km road  
104 circuit within a 10 km buffer around their home (Fig. 1). Surveyors were asked to design their  
105 road circuit so that it proportionally crossed the different land-cover types and it remained on  
106 low-traffic roads for security reasons. After final validation of the circuit outline, program  
107 coordinators randomly selected the starting point of the survey. Each circuit was then divided into  
108 10 x 2 km transects where bat were recorded, separated by 1 km road portions where recording  
109 was not carried out (Fig. 1b).

110 We used data from surveys carried out every year from the 15<sup>th</sup> of June to the 31<sup>st</sup> of July,  
111 corresponding to a seasonal peak in bat activity. Surveys started 30 minutes after sunset and  
112 lasted approximately 1.5 hour during the period of bat activity. They were only carried out when  
113 weather conditions were favorable (*i.e.* no rain, low wind speed of  $< 7$  m/s, temperature  $> 12^{\circ}\text{C}$ ).  
114 We obtained a total of 160 road circuits representing 1610 different transects (Fig. 1a) where  
115 coverage was largely representative of French land-cover (Table 1). As 56 % of transects were  
116 sampled for several years by surveyors (maximum = 6 years), we had 3996 transects replicates  
117 for the analyses.

118 #Fig. 1 approximately here#

119 #Table 1 approximately here#

120 *Biological data*

121 Along transects, volunteer surveyors recorded bat echolocation calls with ultrasound detectors  
122 connected to a Zoom H2 digital recorder (Samson technologies, USA) and reported the date of  
123 survey and temperature (°C). Sound was stored on Secured Card in Waveform Audio File  
124 Format, more commonly known as WAV format. The ultrasound detectors used by surveyors  
125 were either Tranquility Transect (Courtpan Design Ltd, UK) or D240X (Pettersson Elektronik,  
126 Sweden). As the 2 devices did not have the same record length, we applied a correction on the  
127 acoustic recordings of D240X to be able to compare the data obtained from both devices (See  
128 Table S1 and S2 for details). After a 2-day training course, surveyors classified all the  
129 echolocation calls to the most accurate taxonomic level using Syrinx 2.6 (Burt 2006) with setting  
130 provided by NMNH, and applied an identification confidence index to each of their recordings  
131 (0 when they were not sure, and 1 when they were sure of their identification). Data validation  
132 was then manually done by NMNH experts for recordings with a 0-confidence index (Table S1).  
133 We used data from 2006 to 2013 representing a total of 23610 bat passes. We conducted the  
134 analysis on *Pipistrellus pipistrellus* (n = 15355), *Eptesicus serotinus* (n = 2652),  
135 *Pipistrellus kuhlii* (n = 2319), which may include 8 % of *P. nathusius*; See Table S1) and  
136 *Nyctalus leisleri* (n = 2052). The first species represented 65 % of the dataset while the 3 others  
137 represented approximately 10 %.

138 *Landscape characteristics*

139 Around each of the 1610 transects, we generated a set of landscape variables calculated within  
140 4 different landscape buffers of 200 m, 500 m, 700 m and 1000 m using ArcGIS 10.2. We used  
141 radiance as a measure of ALAN as it is defined as the radiant flux (*i.e.* radiant power) reflected or  
142 emitted by a given surface. We used the VIIRS nighttime lights (2012) which is a 2-months



143 composite raster of radiance data (in  $nW/cm^2sr$ ) collected by the Suomi NPP-VIIRS Day/Night  
144 Band during 2 time-periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight  
145 (Baugh et al. 2013). We then computed the average radiance within each buffer with the tool  
146 “Zonal statistics as Table” from the package “Spatial Analyst” (See Fig. S1 for details).

147 We calculated the proportion (%) of impervious surface (Code 1.1 (consisting of 99 % of Code  
148 1.1.2); CORINE Land Cover/2006) and the proportion of intensive agriculture (Code 2.1;  
149 CORINE Land Cover/2006) within each buffer as they represented major land-use pressures. The  
150 proportion of impervious surface included buildings and pavement (roads, sidewalks, driveways  
151 and parking lots) that are covered by impenetrable materials such as asphalt, concrete, brick and  
152 stone. The proportion of intensive agriculture included irrigated and non-irrigated arable land  
153 such as cereals, leguminous and forage crops. The effect of road network which can also be  
154 considered as a land-use pressure (especially regarding landscape connectivity) could not be  
155 tested in our study because transects were mostly located in areas with secondary low-traffic  
156 roads. For this reason, we only took into account the total length of roads (IGN/2012) within each  
157 buffer as a potential confounding factor of the average luminance and the proportion of  
158 impervious surface. We also used as covariables: *i*) the proportion of extensive agriculture,  
159 defined as areas with a complex mosaic of annual and permanent cultures and semi-natural  
160 habitats (Code 2.4; CORINE Land Cover/2006); *ii*) the total length of streams and water sources  
161 (IGN/2012); and *iii*) the proportion of deciduous and mixed forests (Code 3.1; CORINE Land  
162 Cover/2006) as they were commonly represented in our buffers and were known to influence bat  
163 activity at a landscape scale (Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Fonderflick et al.  
164 2015). Only the proportion of impervious surface and the average radiance were highly correlated  
165 at the 4 landscape scales tested ( $r > 0.7$ , Table S3). We did not have multicollinearity problems in

166 models when we excluded one of these 2 highly correlated variables (Variance Inflation Factor  
167 (VIF) < 2; Fox and Monette 1992). At 1000 m landscape scale, there was 25 % overlap between  
168 nearby transects belonging to a same road circuit. However, this still allowed the measurement of  
169 variation in landscape characteristics within the same road circuit. However, we could not go into  
170 larger landscape scales as the overlapping rate between transect buffers would exceed 50 %.

### 171 *Statistical analyses*

172 We applied generalized linear mixed models using as a response variable the number of bat  
173 passes per transect with a Poisson error distribution for *P. pipistrellus*, and the presence/absence  
174 of species per transect with a Binomial distribution for *P. kuhlii*, *E. serotinus*, and *N. leisleri* (See  
175 Fig. S2 for details). The 7 landscape variables as well as the date of survey and the temperature  
176 were used as fixed effects whereas road circuit name and the year of survey were used as  
177 2 independent random effects. The 9 fixed effects were centered and standardized so that the  
178 regression coefficients were comparable in magnitude and their effects were biologically  
179 interpretable (Schielezeth 2010).

180 For each species and at each landscape scale, we generated a set of candidate models containing  
181 all possible combinations of the 9 fixed effects, except the simultaneous inclusion of the  
182 proportion of impervious surface and the average radiance in a same model as they were highly  
183 correlated at all landscape scales ( $r > 0.7$ , Table S2). All explanatory variables were included in  
184 24 models, except for the proportion of impervious surface and the average radiance. These 2  
185 variables were only included in 16 models as they could not be simultaneously included in a  
186 same model. For each set of candidate models, we did multi-model inference averaging to obtain  
187 a comparable averaged regression coefficient for each fixed effect (Smith et al. 2009; Grueber et  
188 al. 2011). The averaged regression coefficient is defined as the mean of all the partial regression

189 coefficients of the models tested, weighted by the Akaike's model weight (Burnham and  
190 Andersen 2002).

191 In addition, for each species and for each of the 4 landscape scales, we selected one single best  
192 model with the smallest AIC value to determine which of the 4 landscape scales tested was the  
193 most parsimonious (Nally 2000). For each species, models had the same structure at the  
194 4 landscape scales to allow for the comparison of AIC across scales. All the analyses were run  
195 under R 3.1.3 with the package "MuMIn"(Barton 2015) and "lme4" (Bates et al. 2015).

196 **Results**

197 For all species, multi-model averaging showed that average radiance had a stronger negative  
198 effect than the proportion of impervious surface at the 4 landscape scales considered (Fig. 2,  
199 Fig. 3). Selection of the best model led to similar results with models with smallest AIC always  
200 including average radiance instead of the proportion of impervious surface at the 4 landscape  
201 scales for all species except *N. leisleri* (Table 2, Fig. 3). The relative effect of average radiance  
202 was however weaker than the effect of the proportion of intensive agriculture (Fig. 2, Fig. 3)  
203 except for *E. serotinus* for which the effects of both landscape variables were of similar extent at  
204 500 m and 700 m landscape scales (Fig. 2d).

205 #Fig. 2 approximately here#

206 Average radiance had a significant negative effect on the probability of presence of *P. kuhlii* and  
207 *E. Serotinus* at the 4 landscape scales considered and on the activity of *P. pipistrellus* at 200 m  
208 landscape scale (Fig. 2; Fig. 4; Table S4). In particular, the activity of *P. kuhlii* appears to  
209 dramatically drop after a threshold of radiance value of 0.4 (Fig. 4b). It also had a negative effect  
210 on the probability of presence *N. leisleri* (Fig. 2c), although the effect was not significant  
211 (Fig. 4c; Table S4). The effect of the proportion of impervious surface varied among species,  
212 with a significant positive effect on the probability of presence of *N. leisleri* and on the activity of  
213 *P. pipistrellus* at 200 m landscape scale (Fig. 2a,c, Table S4), and a negative effect on the  
214 probability of presence of *P. kuhlii* and *E. serotinus* at the 4 landscape scales considered  
215 (Fig. 2b,d), although only significant at 1000 m landscape scale for *E. serotinus* and at  
216 700 and 1000 m landscape scales for *P. kuhlii* (Fig. 3, Table S3). The proportion of intensive  
217 agriculture had a significant negative effect for all species at the 4 landscape scales considered  
218 (Fig. 2; Fig. 3c, Table 2; Table S3).

219 #Fig. 3 approximately here#

220 Best model selection showed that the activity of *P. pipistrellus* and the probability of presence of  
221 *N. leisleri* were best predicted (smallest AIC) by models that included landscape variables  
222 measured at a 200 m landscape scale (Table 2). In contrast, the probability of presence of  
223 *E. serotinus* and *P. kuhlii* were best predicted at 500 m and 1000 m landscape scale respectively.

224 #Table 2 approximately here#

225 # Fig. 4 approximately here#

## 226 **Discussion**

227 Our results revealed that ALAN was more strongly associated with a decrease in bat activity and  
228 probability of presence than impervious surface for the 4 species studied (Fig. 2). Furthermore,  
229 although average radiance and impervious surface were highly correlated at the country-scale,  
230 ALAN was always a better predictor of bat activity and occurrence than impervious surface for  
231 all species except *N. leisleri* (Table 2). Given that the 4 species studied are the most common bat  
232 species in France (Arthur and Lemaire 2009), these results highlight the urgent necessity of  
233 taking into account such impacts on biodiversity in urban-planning (Grimm et al. 2008).

234 The effect of impervious surface was contrasted among the 4 species with a positive effect on  
235 *P. pipistrellus* and *N. leisleri*, and a negative effect on *P. kuhlii* and *E. serotinus*. It is however  
236 important to note that the positive correlations of impervious surface with species occurrence  
237 were significant at a 200 m landscape scale while negative correlations were observed at a  
238 1000 m landscape scale. It has been hypothesized that landscape variables affecting breeding and  
239 foraging success have a smaller scale of effect than variables influencing dispersal success  
240 (Jackson and Fahrig 2014; Miguet et al. 2015). In this context, the proportion of impervious  
241 surface may generate habitat loss and fragmentation at large landscape scale, while providing  
242 habitat heterogeneity and complementarity for foraging at a local scale (Jung and Kalko 2010;  
243 Jung and Threlfall 2016). Furthermore, most of the car transect surveys were located in rural and  
244 peri-urban areas along low-traffic roads (for safety reasons). This variation in species responses  
245 to an intermediate level of impervious surface has also been observed for a wide range of taxa  
246 such as invertebrates, reptiles, amphibians and non-flying mammals (McKinney 2008). It would  
247 be interesting to reproduce this analysis in areas with high level of urbanization to see if similar  
248 patterns of response remain.

249 Nevertheless, although dense urban cores were under-sampled in the program, the proportion of  
250 each land cover as well as the average radiance around transects were representative of land-use  
251 in mainland France (Table 1). In this context, our results suggest that only considering the  
252 proportion of impervious surface as a proxy for urbanization may lead to underestimated impacts  
253 on biodiversity because light pollution affects substantial parts of ecosystems surrounding urban  
254 areas (Kyba et al. 2011; Kyba & Hölker 2013; Gaston et al. 2015).

255 Unlike light-sensitive bats which are known to avoid illuminated areas (Stone et al. 2009, 2012),  
256 the 4 species in this study have often been recorded foraging under streetlights (Rydell 1992;  
257 Lacoëuilhe et al.2014; Azam et al.2015). At a local scale, they select illuminated areas rather than  
258 surrounding dark places, because streetlights offer new and predictable foraging opportunities by  
259 attracting a large portion of the surrounding insect biomass (Eisenbeis 2006; Perkin et al.2014).  
260 Surprisingly, our results showed that these so-called “light-attracted” species only presented  
261 negative or neutral response to ALAN at a landscape scale. This suggests that even if a streetlight  
262 can present foraging advantages for some species of bats locally, landscape-scale level of ALAN  
263 generates a landscape “filter” that negatively influences the occurrence and activity of bats in a  
264 given place.

265 This may be explained by the fact that ALAN does not only influence species foraging behavior,  
266 but also reproduction and commuting behaviors (Boldogh et al. 2006; Hale et al. 2015). First,  
267 artificial illumination of maternity roosts has major impacts on the fitness of juveniles and  
268 reproductive females by desynchronizing the timing of bat nightly emergence with insects’ peak  
269 of abundance (Jones & Rydell, 1994; Boldogh et al. 2006; Downs et al. 2003). Landscape scale  
270 level of ALAN may hence exert an important pressure on the reproductive success of maternity  
271 colonies and decrease the availability of suitable roosts. Second, ALAN has been shown to

272 decrease landscape connectivity by altering movements and gap-crossing behaviors of  
273 *P. pipistrellus* individuals in an urban matrix (Hale et al. 2015). Although bats are highly mobile  
274 and may be able to take alternative dark routes in the landscape, such effects may generate  
275 increased costs in flight time and in stress with important implications for individual fitness  
276 especially during reproduction (Stone et al. 2009). So, it appears that, regardless of species  
277 foraging behavior, landscape-scale level of ALAN may significantly impact local population  
278 dynamics (Gaston and Bennie 2015). This hypothesis, consistent with Mathews et al. 2015, has  
279 important conservation implications as we can expect an even stronger impact of landscape-scale  
280 level of ALAN on light-sensitive species which are particularly negatively affected by habitat  
281 loss and fragmentation (Safi and Kerth 2004; Frey-Ehrenbold et al. 2013).

282 The massive insect mortality caused by ALAN (Eisenbeis 2006) is likely to have a negative  
283 effect on bats (Van Langevelde et al. 2011). Common macromoths have experienced major  
284 declines in the UK in recent decades (Conrad et al. 2006), and it has been hypothesized that urban  
285 areas and their associated sky glow may act as long-term ecological sinks, depleting the  
286 surrounding landscapes of moth species (Bates et al. 2014). Crashes in insect populations in and  
287 around illuminated areas could explain landscape-scale negative effects of ALAN on bats.

288 Nevertheless, the effect of ALAN was weaker than the effect of intensive agriculture which was  
289 significantly negative for the 4 species at the 4 landscapes scales considered. Agricultural  
290 intensification has been associated to dramatic declines in biodiversity because of the habitat loss;  
291 the clearance in structural connectivity elements like hedgerows and the massive use of  
292 agrochemicals it generates (Donald et al. 2001; Wickramasinghe et al. 2004; Jennings and  
293 Pocock 2009). Bats are highly dependent on structural linear elements for commuting between  
294 roosting and foraging sites in agricultural landscapes (Downs and Racey 2006; Frey-Ehrenbold



295 2013; Vandeveld et al. 2014). Furthermore, for a given microhabitat bat activity was  
296 significantly lower in conventional farms compared to organic farms, suggesting the important  
297 adverse effect of agrochemicals on prey density (Wickramasinghe et al. 2003). As nocturnal  
298 insectivorous species, bats' response to land-use is likely to reflect the productivity of the  
299 impacted insect community (Jones et al. 2009). Therefore, the concomitant landscape-scale  
300 negative effects of intensive agriculture and ALAN may reflect a large scale depletion of prey  
301 resource in human-altered landscapes.

302 For the last century, worldwide human population has experienced a major increase in the  
303 number of urban dwellers (Grimm et al. 2008; United Nations 2014). This has led to a massive  
304 expansion of cities and human infrastructures with important consequences on biodiversity and  
305 ecosystems functions within urban areas but also in peripheral natural and semi-natural habitats  
306 (McKinney 2008; MacDonald et al. 2008). In this context, our results show the importance of  
307 integrating light pollution issues in sustainable urban-planning schemes to allow the persistence  
308 of biodiversity in anthropogenic landscapes (Kyba et al.2011; Gaston et al. 2015). Such schemes  
309 should be scheduled in urban and peri-urban areas to illuminate only where and when it is needed  
310 with a particular emphasis on the enhancement of dark shelters in human-dominated landscapes  
311 (Gaston et al. 2012). These recommendations are of particular relevance considering that we are  
312 currently at an important crossroad in lighting management, as lighting equipment reaches its  
313 end-of-life in developed countries and is expanding in developing countries. Both trends occur  
314 concomitantly with the emergence of energy-efficient lamps such as Light Emitting Diode  
315 (Hölker et al. 2010). Such technologies offer many opportunities to limit light pollution by  
316 controlling streetlamp parameters (light spectrum, intensity and directionality) at a local scale  
317 (Kyba et al. 2014). However, the enhancement of the luminous efficiency of LED technologies

318 and subsequent energy saving may come with a “rebound effect” because their cost-effectiveness  
319 may lead to an increased use of outdoor lighting in previously unlit areas (Kyba et al.2014). In  
320 this context, our results highlight that careful outdoor lighting planning at large spatial scales is  
321 crucial to conciliate biodiversity and urban development, and avoid increasing light pollution  
322 phenomena.

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534

535 **Table 1** The land-cover variables surrounding each transect at a range of spatial scales (200-  
536 1000 m), as well as their representativeness in mainland France. The variables are the average  
537 radiance, the proportions of impervious surface, intensive agriculture, extensive agriculture,  
538 forests, and mean length per hectare of roads and streams. The range represents the minimum and  
539 the maximum values encountered for each variable around transects at 1000 m landscape-scale  
540 (similar range were observed for the 3 other landscape scales tested).

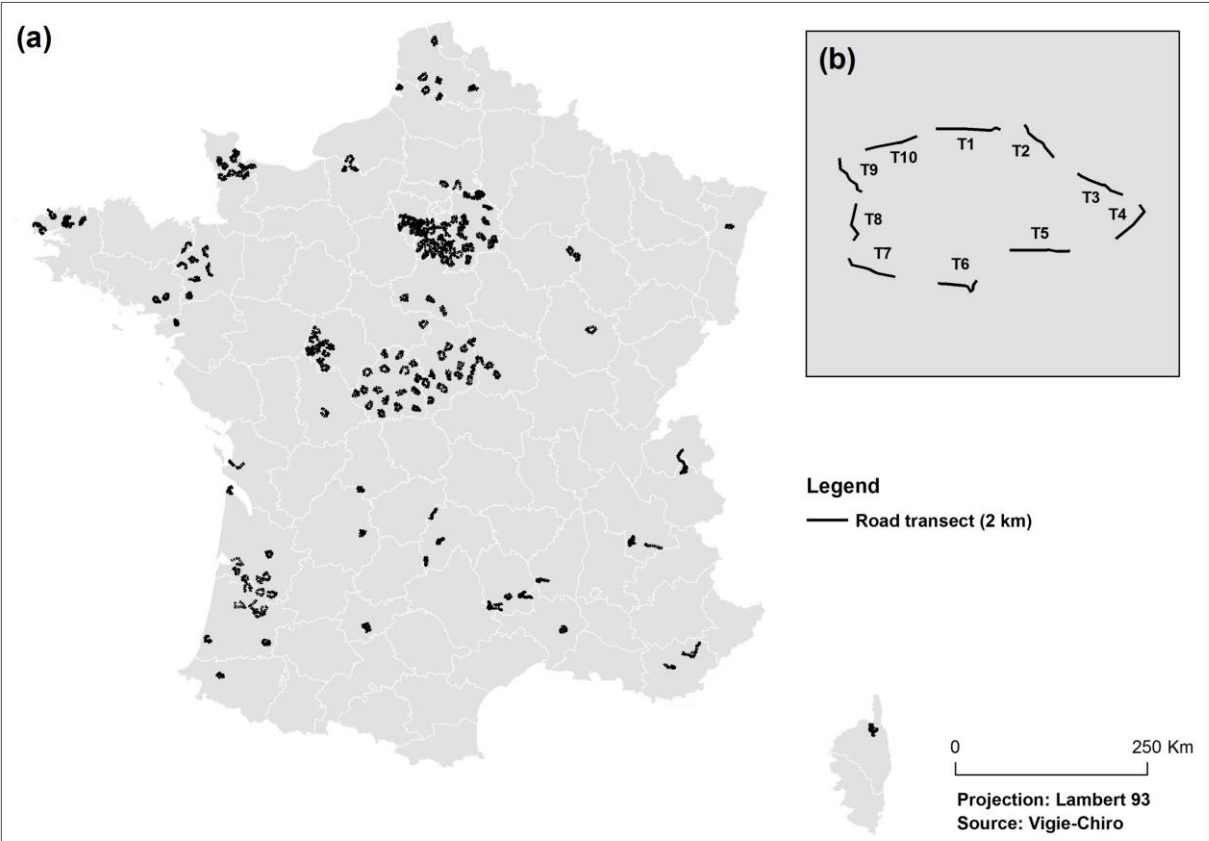
<b>Landscape Variables</b>	<b>Mainland France</b>	<b>Transects (200 m)</b>	<b>Transects (500 m)</b>	<b>Transects (700 m)</b>	<b>Transects (1000 m)</b>	<b>Range (min-max)</b>
Av. radiance (nW/cm <sup>2</sup> sr)	3.2	2.21	2.15	2.08	2.07	0.1-55.5
Imper. surf. (%)	5.2	11.3	8.74	7.3	6.5	0-92
Inten. agri. (%)	28.1	32.5	34.0	34.3	34.9	0-100
Exten. agri. (%)	11.0	12.9	11.5	11.8	11.4	0-92
Forests (%)	19.9	18.6	24.7	20.7	21.2	0-100
Roads (m/ha)	1.92	12.8	6.8	5.4	4.3	0-9391
Streams (m/ha)	6.67	12.9	10.5	9.8	9.1	0-22262

**Table 2** Estimated standardized regression coefficients and standard errors (\*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05, . P = +/- 0.05) from AIC best model selection for the average luminance or the proportion of impervious surface, and the proportion of intensive agriculture for each species and at each of the 4 landscape scales considered. The explanatory variables kept in the final model were significant in at least one of the 4 landscape scales considered.

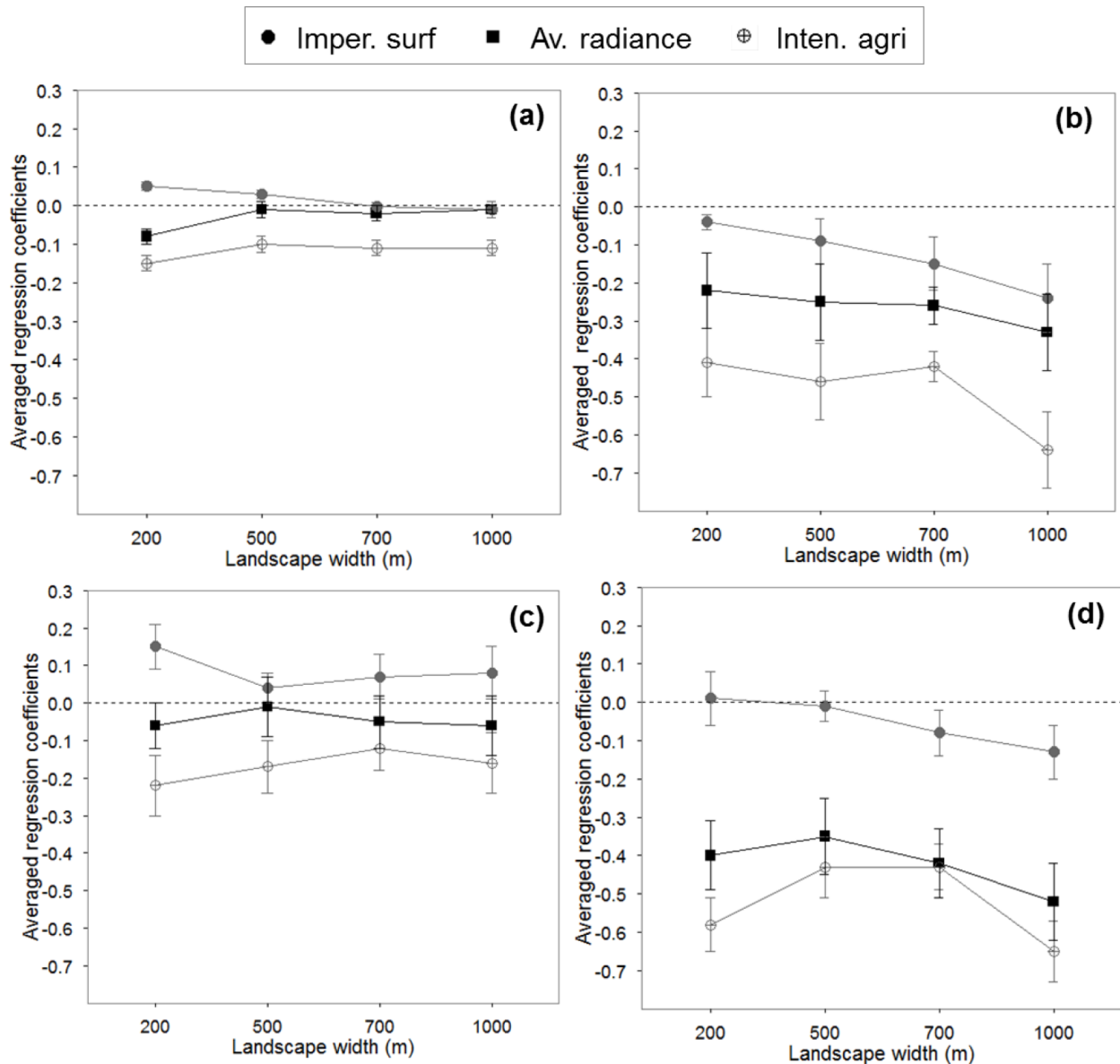
Species	Scale	Av. luminance	Imper. surf.	Inten. agri.	AIC	Final model formula
<i>P. pipistrellus</i>	NULL	/	/	/	26989	/
	200	-0.08 (0.01)***	/	-0.14 (0.01)***	<b>25252</b>	Av. lum. + Inten. agri. + Forests + Streams + Roads + Date + Temp.
	500	-0.05 (0.01)***	/	-0.13 (0.02)***	25308	
	700	-0.03 (0.01)*	/	-0.12 (0.02)***	25378	
	1000	-0.02 (0.01).	/	-0.11 (0.02)***	25414	
<i>P. kuhlii</i>	NULL	/	/	/	3757	/
	200	-0.22 (0.09)*	/	-0.42 (0.08)***	3308	Av. lum. + Inten. agri. + Exten. agri. + Forests+ Streams + Temp.
	500	-0.27 (0.10)**	/	-0.49 (0.09)***	3305	
	700	-0.29 (0.10)**	/	-0.55 (0.09)***	3300	
	1000	-0.32 (0.10)***	/	-0.61 (0.09)***	<b>3289</b>	
<i>N. leisleri</i>	NULL	/	/	/	3431	/
	200	/	0.14 (0.06)*	-0.20 (0.07)**	<b>3204</b>	Imper. surf.+ Inten. agri. + Exten. agri. + Streams + Temp.
	500	/	0.03 (0.04)	-0.18 (0.07)**	3215	
	700	/	0.11 (0.06)	-0.14 (0.07)*	3212	
	1000	/	0.07 (0.07)	-0.12 (0.07).	3217	
<i>E. serotinus</i>	NULL	/	/	/	3961	/
	200	-0.38 (0.09)***	/	-0.53 (0.07)***	3579	Av. lum.+ Inten. agri. + Exten. agri. + Forests + Roads + Temp.
	500	-0.37 (0.09)***	/	-0.44 (0.08)***	<b>3573</b>	
	700	-0.50 (0.10)***	/	-0.59 (0.08)***	3577	
	1000	-0.52 (0.10)***	/	-0.63 (0.08)***	3579	



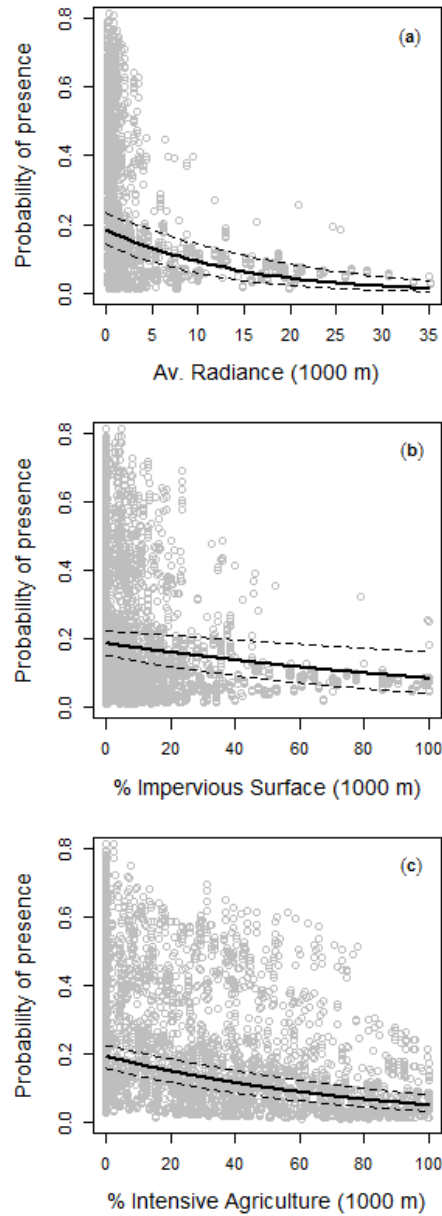
**Figure captions**



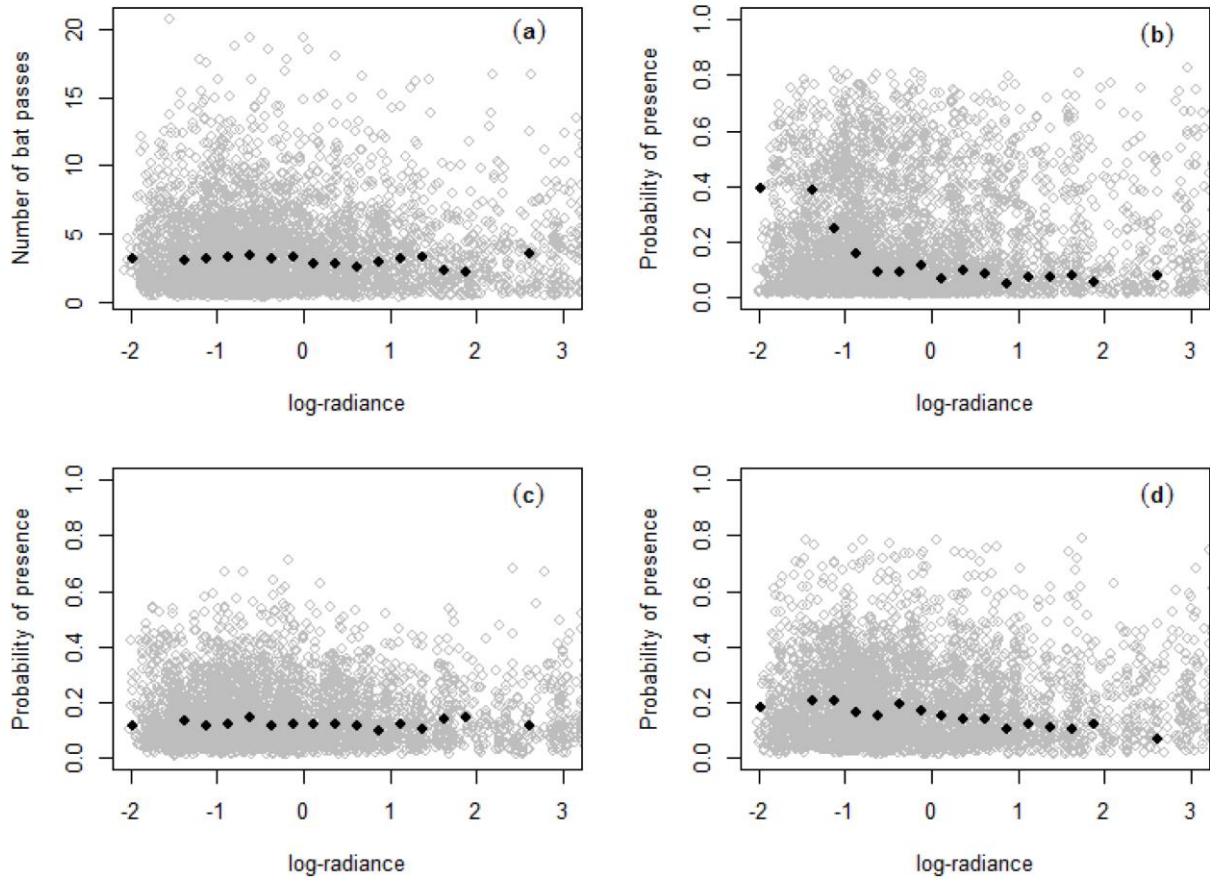
**Fig. 1** (a) Map of the distribution in France of the 160 road circuits from the French Bat Monitoring Program and (b) example of one road circuit composed of 10 transects (T1-T10).



**Fig. 2** Averaged standardized partial regression coefficients and associated standard errors from GLMMs model averaging for the average radiance (black squares), the proportion of impervious surfaces (filled grey dots) and the proportion of intensive agriculture (grey empty circles) for **(a)** *P. pipistrellus*, **(b)** *P. kuhlii*, **(c)** *N. leisleri*, **(d)** *E. serotinus* at 200, 500, 700 and 1000 m landscape scales. The 3 landscape variables have a significant effect on species abundance for **(a)**, and probability of presence for **(b)**, **(c)**, and **(d)**, when the error bars of coefficients do not overlap with the 0-horizontal dashed line.



**Fig. 3** Relation between *P. kuhlii* predicted probability of presence and **(a)** the average radiance, **(b)** the proportion of impervious surface and **(c)** the proportion of intensive agriculture at a 1000 m landscape scale. The solid lines represent the predicted responses obtained with GLMMs and the dashed lines represent the standard errors. Average luminance and impervious surface were tested in 2 separate models which both had the exact same structure and covariables (i.e. Table 2).



**Fig. 4** Mean number of bat pass of **(a)** *P. pipistrellus*, and mean probability of presence of **(b)** *P. kuhlii*; **(c)** *N. leisleri*, and **(d)** *E. serotinus* per bin of 0.25 log-radiance, within 200 m landscape scale for **(a)** and **(c)**, 500 m landscape scale for **(d)** and 1000 m landscape scale for **(d)**. The models ran at these landscape scales best predicted species activity and probability of presence w (i.e. Table 4).

## Online Appendices

**Table S1** Detailed information on the French national bat-monitoring program (<http://vigienature.mnhn.fr/>), coordinated by the National Museum of Natural History (MNHN).

<b>Aim of the program</b>	Monitoring the temporal trends of bat populations at a national scale	
<b>Sampling protocol</b>		
<i>Scope</i>	10 km around surveyors' home.	
<i>Circuit length</i>	30 km	
<i>Number of transect per circuit</i>	10	
<i>Transect length</i>	2 km separated of at least 1 km	
<i>Period of sampling</i>	from the 15 <sup>th</sup> of June to the 31 <sup>th</sup> of July	
<i>Weather conditions</i>	no rain, low wind speed (< 7 m/s), temperature > 12°C	
<i>Survey start</i>	30 minutes after sunset	
<b>Bat recording characteristics</b>		
<i>Acoustic detectors</i>	Tranquility Transect Bat detector&D240x	
<i>Intercalibration of detectors</i>	At the MNHN	
<b>Acoustic settings</b>	<b><i>Tranquility Transect</i></b>	<b><i>D240x</i></b>
<i>Suppliers</i>	Courtpan Design Ltd, UK	Pettersson Elektronik
<i>High pass filter</i>	5 kHz	18 kHz
<i>Frequency</i>	96 000 sample/sec	96 000 sample/sec
<i>Record length (sec)</i>	0.32	0.1
<i>Post-recording treatment</i>	/	Elimination of acoustic sequences spaced of less than 3.2 sec.
<i>Time expansion</i>	X10	X10
<i>Recording device</i>	Zoom H2 digital recorder (Samson technologies, USA)	
<i>File storage format</i>	WAV	
<b>Bat identification</b>		
<i>Software</i>	Syrinx 2.6	
<i>Procedure</i>	<ul style="list-style-type: none"> <li>- <b>Training:</b> 2-day training course+ online self-training courses</li> <li>- <b>Bat first identification:</b> by volunteers</li> <li>- <b>Bat identification validation:</b> by MNHN</li> </ul>	
<i>Taxon identification level</i>	Species level for all species except for <i>Myotis sp.</i> + Analysis of <i>P. kuhlii</i> number of bat pass on 270 transects showed that <i>Pipistrellus kuhlii</i> response variable may include less than 8 % <i>Pipistrellus nathusius</i> , as these two species overlap in their acoustic signatures.	

**Table S2** Effects of the bat detector (either D240X of Tranquility Transect) and the age of microphones (Age) on the duration of bat pass detected of a sample of direct acoustic recordings of the FBMP. The table shows the averaged partial regression coefficient and p-value from GLMMs. Bold police indicates P-value < 0.05.

	<i>P. pipistrellus</i> N=5070	<i>P. kuhli</i> N=549	<i>E. serotinus</i> N=487	<i>N. Leisleri</i> N=256
Bat detector	<b><i>P=0.03 ; D240x&gt;TT</i></b>	<i>P=0.74</i>	<i>P=0.16</i>	<i>P=0.95</i>
Age	<i>P=0.11</i>	<i>P=0.06</i>	<i>P=0.95</i>	<i>P=0.43</i>
Bat detector : Age	<i>P=0.26</i>	<i>P=0.76</i>	<i>P=0.84</i>	<i>P=0.27</i>

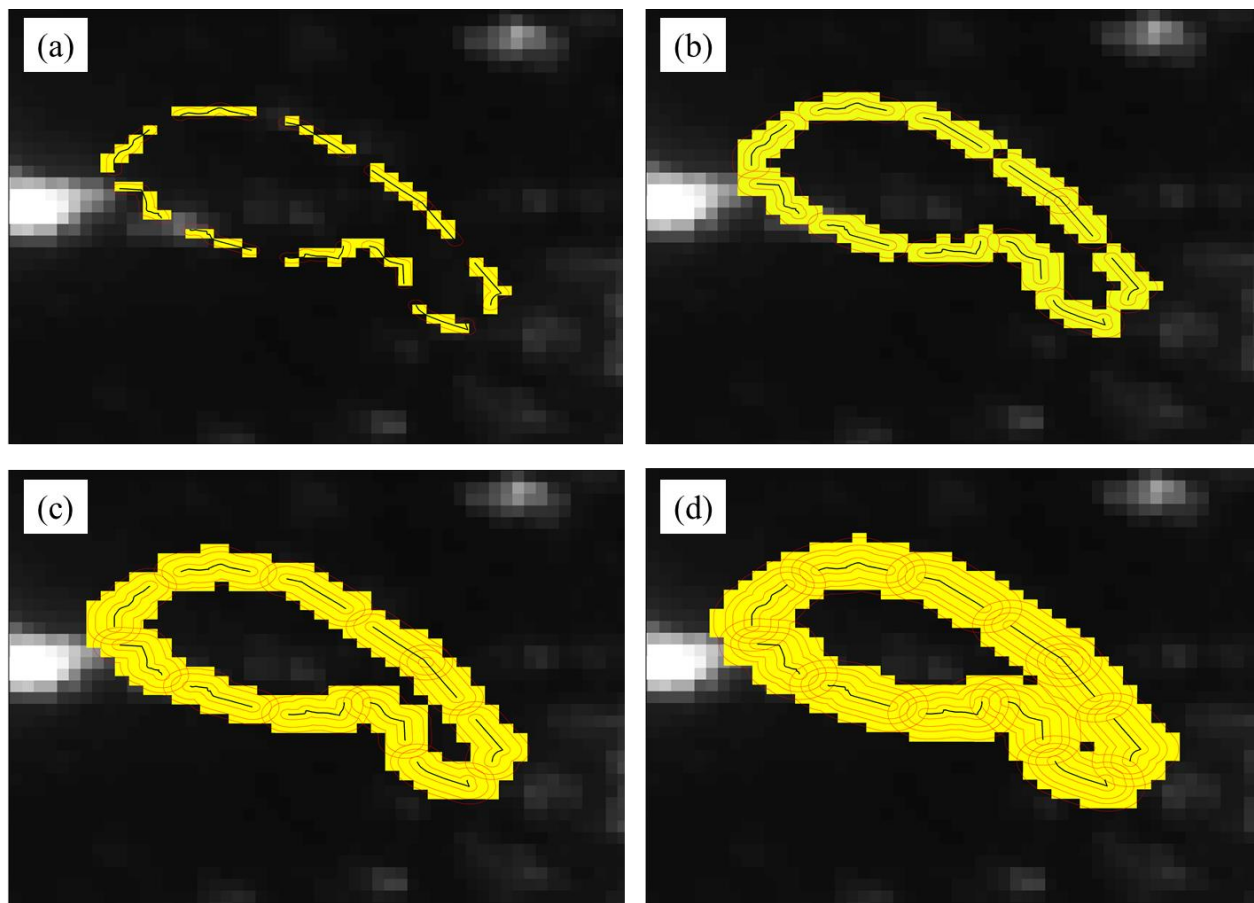
**Table S3** Correlation coefficients of the 7 landscape variables included in the analysis (i.e. the average luminance, the proportions of impervious surface, intensive agriculture, extensive agriculture, forests, the total length of primary roads and streams (m)), at the 1000 m landscape-scale which showed the strongest the correlation coefficients between landscape variables.

<b>Landscape Variables</b>	<b>Correlation coefficients</b>					
	<i>Imper. surf.</i>	<i>Inten. agri.</i>	<i>Exten. agri.</i>	<i>Forests</i>	<i>Roads</i>	<i>Streams</i>
<i>Av. luminance</i>	<b>0.85</b>	-0.10	-0.14	-0.07	0.13	0.02
<i>Imper.surf.</i>	/	-0.12	-0.16	-0.06	0.14	0.04
<i>Inten. agri.</i>	/	/	-0.32	-0.46	0.04	-0.30
<i>Exten. agri.</i>	/	/	/	-0.25	-0.007	0.09
<i>Forest</i>	/	/	/	/	-0.02	-0.007
<i>Roads</i>	/	/	/	/	/	-0.009

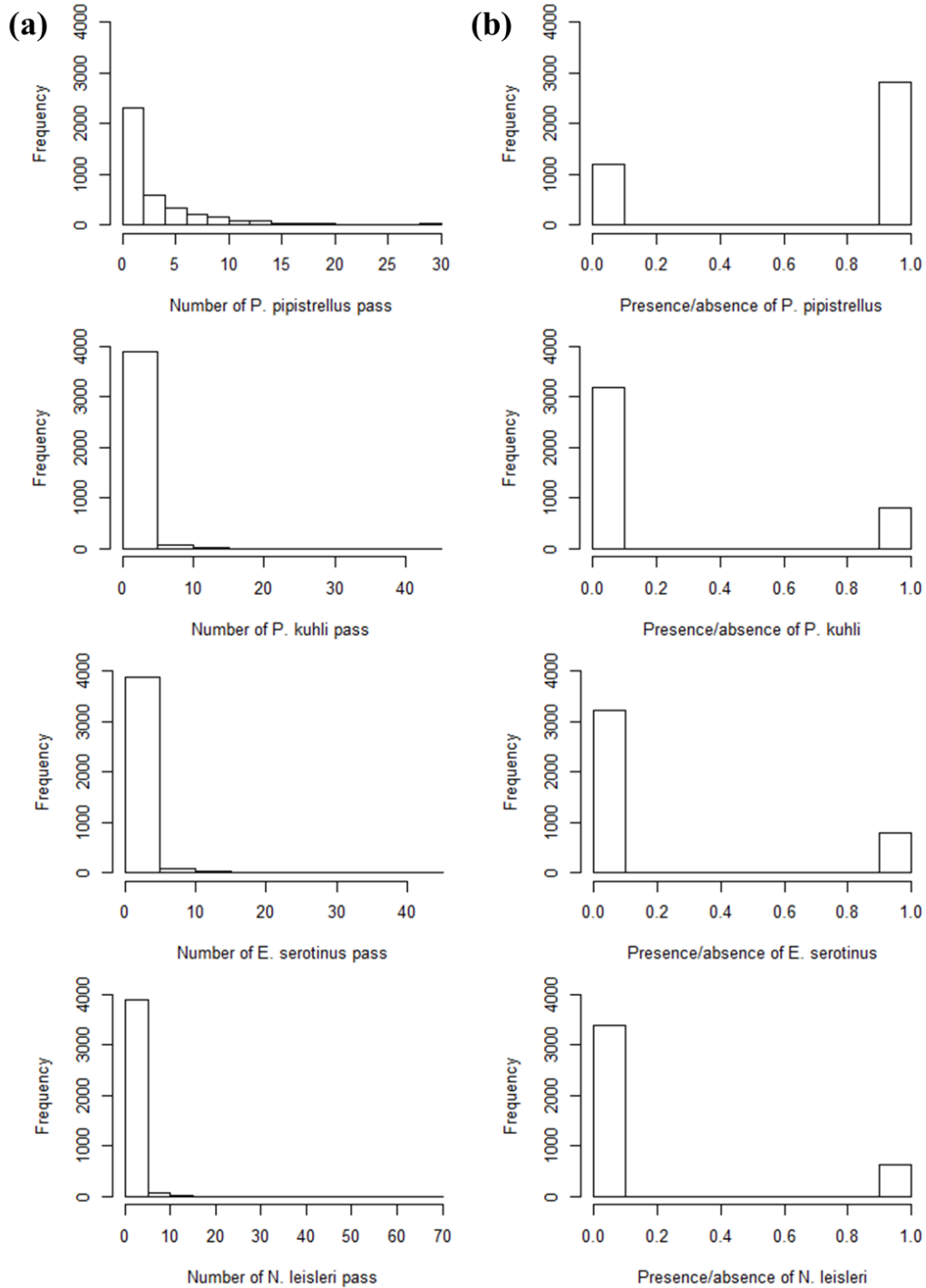
**Table S4** Averaged partial regression coefficient and associated standard errors from multi-model averaging of the 9 fixed effects included in the analysis (i.e. the average luminance, the proportions of impervious surface, intensive agriculture, extensive agriculture, forests, the total length of primary roads and streams (m), and the date and temperature) for the 4 species and at 4 landscape scales considered. Bold police indicates that the estimates were significantly different from 0 (P-value < 0.05).

Species	Scale	Av. luminance	Imper. surf.	Inten. agri.	Exten. agri.	Forests	Roads	Streams	Date	T°C
<i>P. pipistrellus</i>	200	<b>-0.08 (0.02)</b>	<b>0.05 (0.01)</b>	<b>-0.15 (0.02)</b>	-0.02 (0.01)	<b>0.09 (0.01)</b>	-0.01 (0.01)	<b>0.03 (0.00)</b>	<b>0.10 (0.01)</b>	<b>0.06 (0.01)</b>
	500	-0.01 (0.02)	0.03 (0.01)	<b>-0.10 (0.02)</b>	0.01 (0.01)	<b>0.12 (0.02)</b>	<b>-0.03 (0.01)</b>	<b>0.05 (0.00)</b>	<b>0.10 (0.01)</b>	<b>0.06 (0.01)</b>
	700	-0.02 (0.02)	-0.001 (0.01)	<b>-0.11(0.02)</b>	0.01 (0.01)	<b>0.11 (0.01)</b>	-0.01 (0.01)	<b>0.05 (0.01)</b>	<b>0.10 (0.01)</b>	<b>0.06 (0.01)</b>
	1000	-0.01 (0.01)	-0.01 (0.02)	<b>-0.11 (0.02)</b>	0.02 (0.02)	<b>0.11 (0.01)</b>	-0.009 (0.01)	<b>0.06 (0.01)</b>	<b>0.10 (0.01)</b>	<b>0.06 (0.01)</b>
<i>P. kuhlii</i>	200	<b>-0.22 (0.10)</b>	-0.04 (0.02)	<b>-0.41 (0.09)</b>	0.10 (0.06)	<b>-0.16 (0.06)</b>	0.06 (0.04)	-0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	500	<b>-0.25 (0.10)</b>	-0.09 (0.06)	<b>-0.46 (0.10)</b>	<b>0.14 (0.06)</b>	-0.14 (0.07)	0.07 (0.05)	0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	700	<b>-0.26 (0.05)</b>	<b>-0.15 (0.07)</b>	<b>-0.42 (0.04)</b>	<b>0.06 (0.02)</b>	<b>-0.14 (0.02)</b>	0.02 (0.02)	<b>0.04 (0.02)</b>	0.02 (0.02)	<b>0.07 (0.02)</b>
	1000	<b>-0.33 (0.10)</b>	<b>-0.24 (0.09)</b>	<b>-0.64 (0.10)</b>	0.12 (0.07)	<b>-0.25 (0.07)</b>	0.01 (0.05)	0.08 (0.06)	0.04 (0.06)	<b>0.13 (0.06)</b>
<i>E. serotinus</i>	200	<b>-0.40 (0.09)</b>	0.01 (0.07)	<b>-0.58 (0.07)</b>	<b>-0.19 (0.06)</b>	0.08 (0.05)	0.07 (0.04)	-0.08 (0.04)	0.01 (0.06)	<b>0.19 (0.06)</b>
	500	<b>-0.35 (0.10)</b>	-0.01 (0.04)	<b>-0.43 (0.08)</b>	-0.07 (0.08)	<b>0.23 (0.06)</b>	<b>0.10 (0.05)</b>	-0.02 (0.05)	0.01 (0.05)	<b>0.18 (0.06)</b>
	700	<b>-0.42 (0.09)</b>	-0.08 (0.06)	<b>-0.43 (0.06)</b>	<b>-0.13 (0.05)</b>	0.04 (0.04)	0.01 (0.03)	-0.02 (0.03)	0.02 (0.04)	<b>0.13 (0.05)</b>
	1000	<b>-0.52 (0.10)</b>	<b>-0.13 (0.07)</b>	<b>-0.65 (0.08)</b>	<b>-0.21 (0.07)</b>	0.05 (0.07)	0.03 (0.05)	-0.02 (0.05)	0.02 (0.05)	<b>0.19 (0.07)</b>
<i>N. leisleri</i>	200	-0.06 (0.06)	<b>0.15 (0.06)</b>	<b>-0.22 (0.08)</b>	-0.11 (0.07)	-0.03 (0.08)	-0.03 (0.05)	<b>0.20 (0.05)</b>	0.06 (0.06)	<b>0.28 (0.06)</b>
	500	-0.01 (0.08)	0.04 (0.04)	<b>-0.17 (0.07)</b>	<b>-0.15 (0.07)</b>	0.07 (0.07)	-0.01 (0.04)	<b>0.23 (0.05)</b>	0.06 (0.06)	<b>0.28 (0.06)</b>
	700	-0.05 (0.07)	0.07 (0.06)	-0.12 (0.06)	<b>-0.19 (0.07)</b>	-0.02 (0.06)	0.01 (0.05)	<b>0.17 (0.03)</b>	0.05 (0.05)	<b>0.21 (0.05)</b>
	1000	-0.06 (0.08)	0.08 (0.07)	-0.16 (0.08)	<b>-0.25 (0.08)</b>	-0.05 (0.08)	0.05 (0.05)	<b>0.23 (0.06)</b>	0.05 (0.06)	<b>0.27 (0.06)</b>





1  
 2 **Fig. S1** Demonstration of the procedure done to calculate average radiance within the buffers of  
 3 (a) 200 m, (b) 500 m, (c) 700 m and (d) 1000 m width from the VIIRS Nighttime Light raster  
 4 used to. The average radiance was computed by the tool “zonal statistics as Table” from the  
 5 package “Spatial Analyst” of ArcGIS 10.2 which proceed by creating a raster (yellow) from the  
 6 polygon shapefile input (red) before applying an internal resampling so that input raster  
 7 resolution match with the resolution of the VIIRS Nighttime Light raster.



8  
9 **Fig. S2** Distribution of the response variable of *P. pipistrellus*, *P. kuhli*, *E. serotinus* and  
10 *N. leisleri* in number of bat pass per transect at the left hand side of the figure (a), and in  
11 presence/absence at the right hand side of the figure (b). We chose to follow a poisson  
12 distribution for *P. pipistrellus*, and a binomial distribution for *P. kuhli*, *E. serotinus* and  
13 *N. leisleri* for statistical analyses.