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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Abstract

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

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

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

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

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

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

Introduction

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

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

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

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

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

Bat activity and occurrence are known to be negatively affected by increased urbanization (Hale et al. 2012; Jung and Threlfall 2016) as well as agricultural intensification (Wickramasinghe et al. 2003; Jennings and Pocock 2009). However, the responses of bats to ALAN at a landscape scale are unclear. At a local scale, bat responses to ALAN vary among species according to their foraging strategy and flight abilities (Jones and Rydell 1994). Slow-flying species adapted to prey on insects in cluttered vegetation, such as *Rhinolophus spp*. and *Myotis spp.*, are more likely to be affected by illuminance (Rydell 1992; Stone et al. 2009, 2012; Kuijper et al. 2012; Azam et al. 2015) due to higher risk of predation (Jones and Rydell 1994; Rydell et al. 1996). In contrast, fast-flying species adapted to hunt insects at dusk in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.*, can benefit from new and predictable foraging opportunities provided by streetlights (Rydell 1992; Blake et al. 1994; Lacoeuilhe et al. 2014; Azam et al. 2015), which attract a large proportion of the surrounding flying insect biomass (Perkin et al. 2014). In this context, ALAN is likely to be a driver of habitat loss and fragmentation for slow-flying species while creating new and predictable foraging opportunities in the landscape for fast-flying species (Stone et al. 2012; Lacoeuilhe et al. 2014; Azam et al. 2015).

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

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

Material and methods

Car transect survey

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

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

#Fig. 1 approximately here#

#Table 1 approximately here#

Biological data

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

Landscape characteristics

Around each of the 1610 transects, we generated a set of landscape variables calculated within 4 different landscape buffers of 200 m, 500 m, 700 m and 1000 m using ArcGIS 10.2. We used radiance as a measure of ALAN as it is defined as the radiant flux (*i.e.* radiant power) reflected or emitted by a given surface. We used the VIIRS nighttime lights (2012) which is a 2-months composite raster of radiance data (in nW/cm^2sr) collected by the Suomi NPP-VIIRS Day/Night Band during 2 time-periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh et al. 2013). We then computed the average radiance within each buffer with the tool “Zonal statistics as Table” from the package “Spatial Analyst” (See Fig. S1 for details).

We calculated the proportion (%) of impervious surface (Code 1.1 (consisting of 99 % of Code 1.1.2); CORINE Land Cover/2006) and the proportion of intensive agriculture (Code 2.1; CORINE Land Cover/2006) within each buffer as they represented major land-use pressures. The proportion of impervious surface included buildings and pavement (roads, sidewalks, driveways and parking lots) that are covered by impenetrable materials such as asphalt, concrete, brick and stone. The proportion of intensive agriculture included irrigated and non-irrigated arable land such as cereals, leguminous and forage crops. The effect of road network which can also be considered as a land-use pressure (especially regarding landscape connectivity) could not be tested in our study because transects were mostly located in areas with secondary low-traffic roads. For this reason, we only took into account the total length of roads (IGN/2012) within each buffer as a potential confounding factor of the average luminance and the proportion of impervious surface. We also used as covariables: *i)* the proportion of extensive agriculture, defined as areas with a complex mosaic of annual and permanent cultures and semi-natural habitats (Code 2.4; CORINE Land Cover/2006); *ii)* the total length of streams and water sources (IGN/2012); and *iii)* the proportion of deciduous and mixed forests (Code 3.1; CORINE Land Cover/2006) as they were commonly represented in our buffers and were known to influence bat activity at a landscape scale (Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Fonderflick et al. 2015). Only the proportion of impervious surface and the average radiance were highly correlated at the 4 landscape scales tested (r > 0.7, Table S3). We did not have multicollinearity problems in models when we excluded one of these 2 highly correlated variables (Variance Inflation Factor (VIF) < 2; Fox and Monette 1992). At 1000 m landscape scale, there was 25 % overlap between nearby transects belonging to a same road circuit. However, this still allowed the measurement of variation in landscape characteristics within the same road circuit. However, we could not go into larger landscape scales as the overlapping rate between transect buffers would exceed 50 %.

Statistical analyses

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

For each species and at each landscape scale, we generated a set of candidate models containing all possible combinations of the 9 fixed effects, except the simultaneous inclusion of the proportion of impervious surface and the average radiance in a same model as they were highly correlated at all landscape scales (r > 0.7, Table S2). All explanatory variables were included in 24 models, except for the proportion of impervious surface and the average radiance. These 2 variables were only included in 16 models as they could not be simultaneously included in a same model. For each set of candidate models, we did multi-model inference averaging to obtain a comparable averaged regression coefficient for each fixed effect (Smith et al. 2009; Grueber et al. 2011). The averaged regression coefficient is defined as the mean of all the partial regression coefficients of the models tested, weighted by the Akaike's model weight (Burnham and Andersen 2002).

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

Results

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

#Fig. 2 approximately here#

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

#Fig. 3 approximately here#

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

#Table 2 approximately here#

Fig. 4 approximately here#

Discussion

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

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

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

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

This may be explained by the fact that ALAN does not only influence species foraging behavior, but also reproduction and commuting behaviors (Boldogh et al. 2006; Hale et al. 2015). First, artificial illumination of maternity roosts has major impacts on the fitness of juveniles and reproductive females by desynchronizing the timing of bat nightly emergence with insects’ peak of abundance (Jones & Rydell, 1994; Boldogh et al. 2006; Downs et al. 2003). Landscape scale level of ALAN may hence exert an important pressure on the reproductive success of maternity colonies and decrease the availability of suitable roosts. Second, ALAN has been shown to decrease landscape connectivity by altering movements and gap-crossing behaviors of *P. pipistrellus* individuals in an urban matrix (Hale et al. 2015). Although bats are highly mobile and may be able to take alternative dark routes in the landscape, such effects may generate increased costs in flight time and in stress with important implications for individual fitness especially during reproduction (Stone et al. 2009). So, it appears that, regardless of species foraging behavior, landscape-scale level of ALAN may significantly impact local population dynamics (Gaston and Bennie 2015). This hypothesis, consistent with Mathews et al. 2015, has important conservation implications as we can expect an even stronger impact of landscape-scale level of ALAN on light-sensitive species which are particularly negatively affected by habitat loss and fragmentation (Safi and Kerth 2004; Frey-Ehrenbold et al. 2013).

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

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

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

For the last century, worldwide human population has experienced a major increase in the number of urban dwellers (Grimm et al. 2008; United Nations 2014). This has led to a massive expansion of cities and human infrastructures with important consequences on biodiversity and ecosystems functions within urban areas but also in peripheral natural and semi-natural habitats (McKinney 2008; MacDonald et al. 2008). In this context, our results show the importance of integrating light pollution issues in sustainable urban-planning schemes to allow the persistence of biodiversity in anthropogenic landscapes (Kyba et al.2011; Gaston et al. 2015). Such schemes should be scheduled in urban and peri-urban areas to illuminate only where and when it is needed with a particular emphasis on the enhancement of dark shelters in human-dominated landscapes (Gaston et al. 2012). These recommendations are of particular relevance considering that we are currently at an important crossroad in lighting management, as lighting equipment reaches its end-of-life in developed countries and is expanding in developing countries. Both trends occur concomitantly with the emergence of energy-efficient lamps such as Light Emitting Diode (Hölker et al. 2010). Such technologies offer many opportunities to limit light pollution by controlling streetlamp parameters (light spectrum, intensity and directionality) at a local scale (Kyba et al. 2014). However, the enhancement of the luminous efficiency of LED technologies and subsequent energy saving may come with a “rebound effect” because their cost-effectiveness may lead to an increased use of outdoor lighting in previously unlit areas (Kyba et al.2014). In this context, our results highlight that careful outdoor lighting planning at large spatial scales is crucial to conciliate biodiversity and urban development, and avoid increasing light pollution phenomena.

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

Landscape Variables	**Mainland France**	**Transects (200 m)**	**Transects (500 m)**	**Transects (700 m)**	**Transects (1000 m)**	**Range (min-max)**
Av. radiance (nW/cm^2sr)	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**
	NULL	/	/	/	26989	/
	200	-0.08 (0.01)***	/	-0.14 (0.01)***	**25252**	Av. lum. + Inten. agri. + Forests + Streams + Roads + Date + Temp.
P. pipistrellus	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	
	NULL	/	/	/	3757	/
	200	-0.22 (0.09)*	/	-0.42 (0.08)***	3308	Av. lum. + Inten. agri. + Exten. agri. + Forests+ Streams + Temp.
P. kuhlii	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)***	**3289**	
	NULL	/	/	/	3431	/
	200	/	0.14 (0.06)*	-0.20 (0.07)**	**3204**	Imper. surf.+ Inten. agri. + Exten. agri. + Streams + Temp.
N. leisleri	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	
	NULL	/	/	/	3961	/
	200	-0.38 (0.09)***	/	-0.53 (0.07)***	3579	Av. lum.+ Inten. agri. + Exten. agri. + Forests + Roads + Temp.
E. serotinus	500	-0.37 (0.09)***		-0.44 (0.08)***	**3573**	
	700	-0.50 (0.10)***	/	-0.59 (0.08)***	3577	
	1000	-0.52 (0.10)***	/	-0.63 (0.08)***	3579	

Figure captions

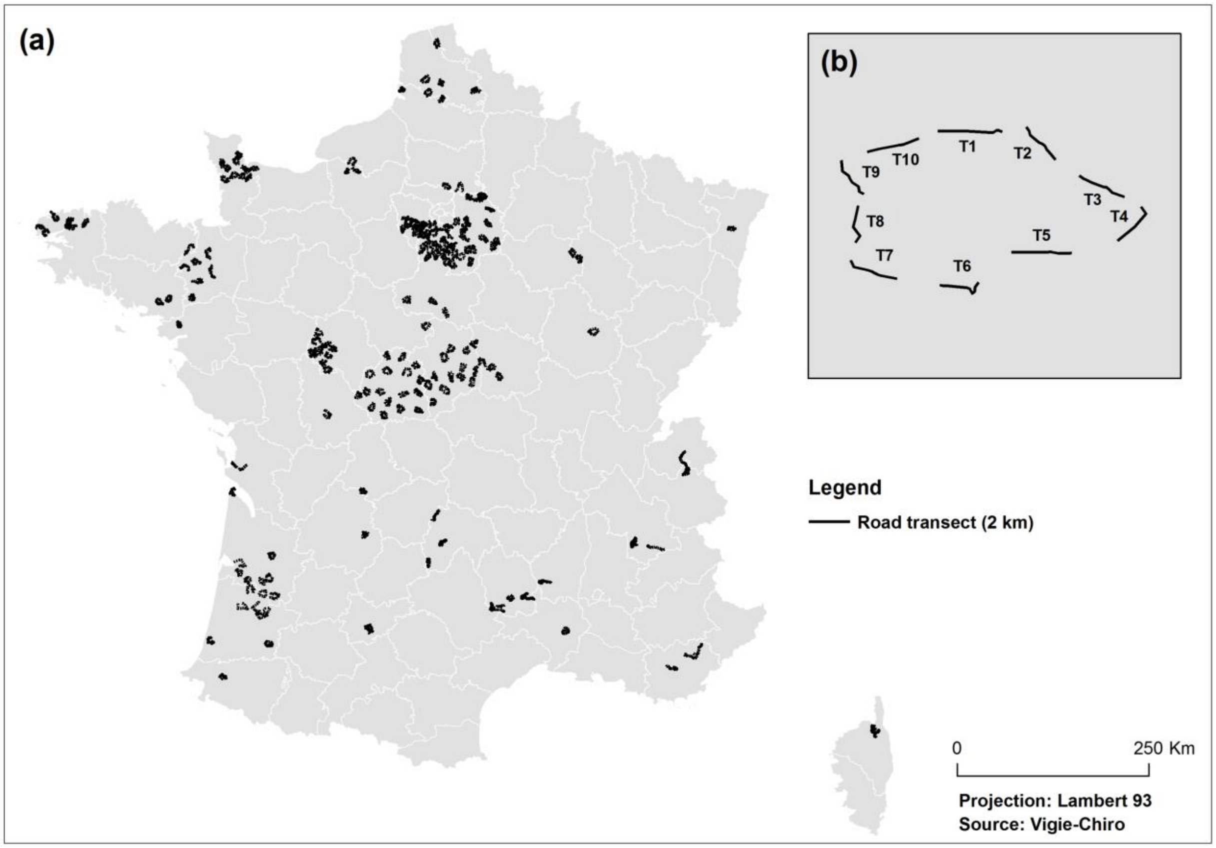

Fig. 1 **(a)** Map of the distribution in France of the 160 road circuits from the French Bat Monitoring Program and **(b)** example of one road circuit composed of 10 transects (T1-T10).

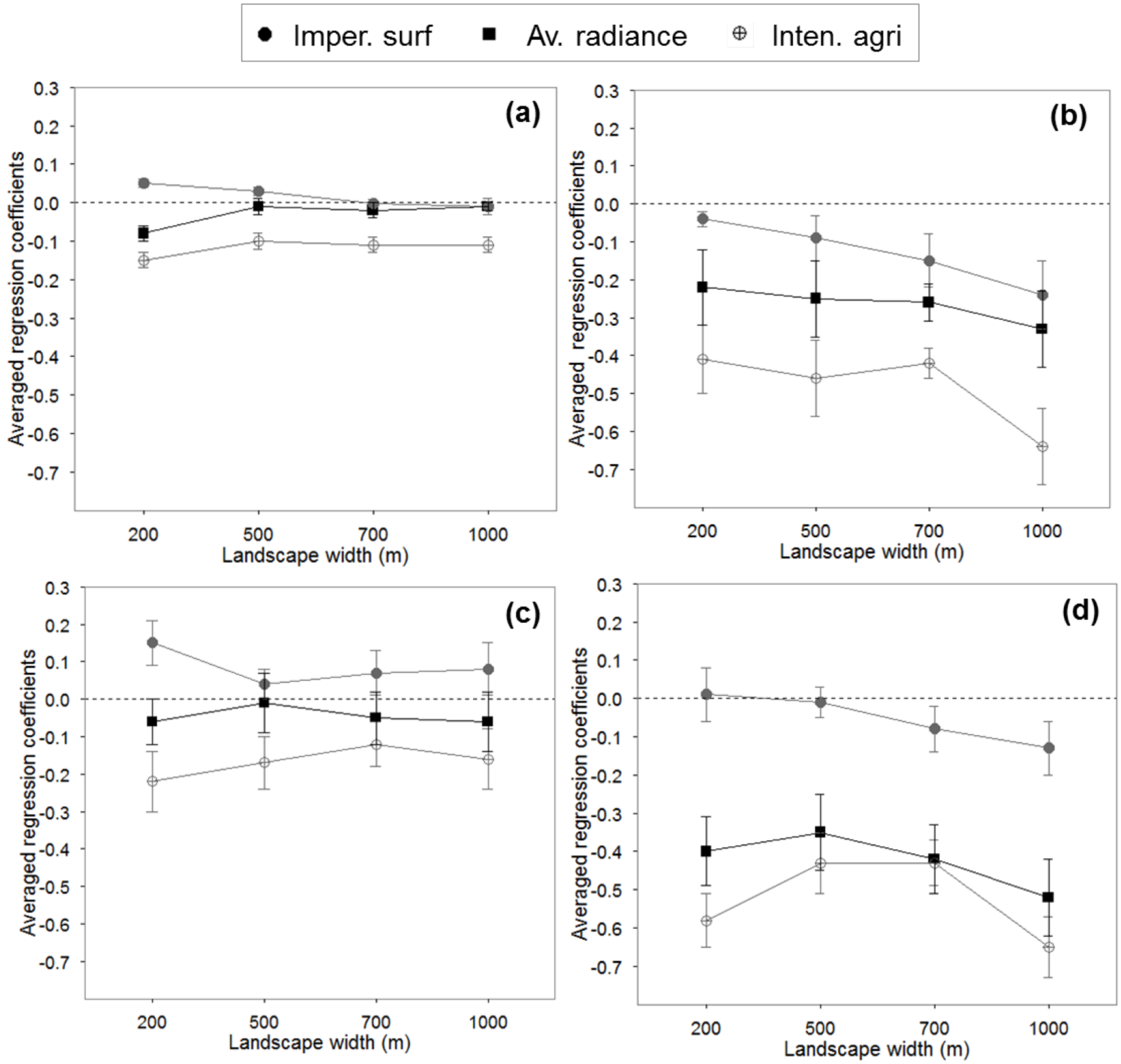

Fig. 2 Averaged standardized partial regression coefficients and associated standard errors from GLMMs model averaging for the average radiance (black squares), the proportion of impervious surfaces (filled grey dots) and the proportion of intensive agriculture (grey empty circles) for **(a)** *P. pipistrellus*, **(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.

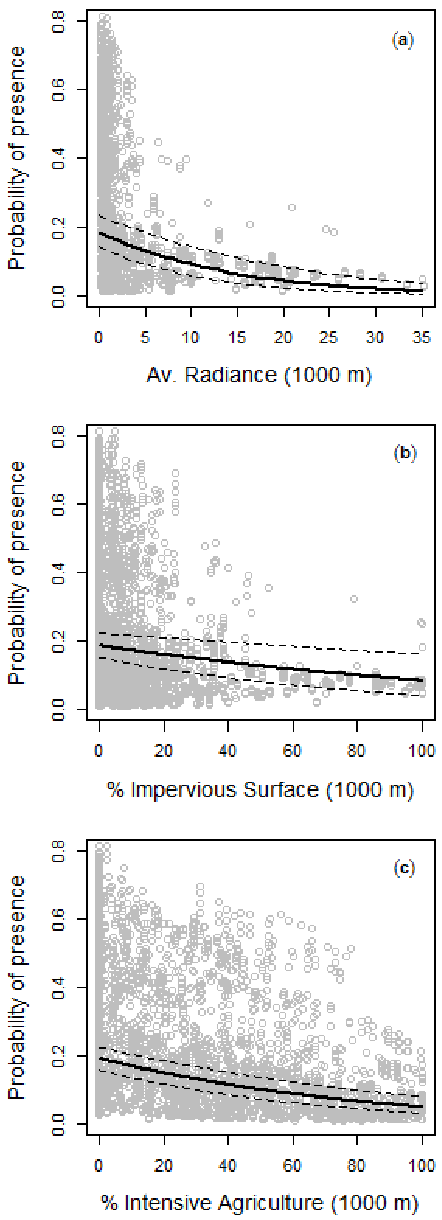

Fig. 3 Relation between *P. kuhlii* predicted probability of presence and **(a)** the average radiance, **(b)** the proportion of impervious surface and **(c)** the proportion of intensive agriculture at a 1000 m landscape scale. The solid lines represent the predicted responses obtained with GLMMs and 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).

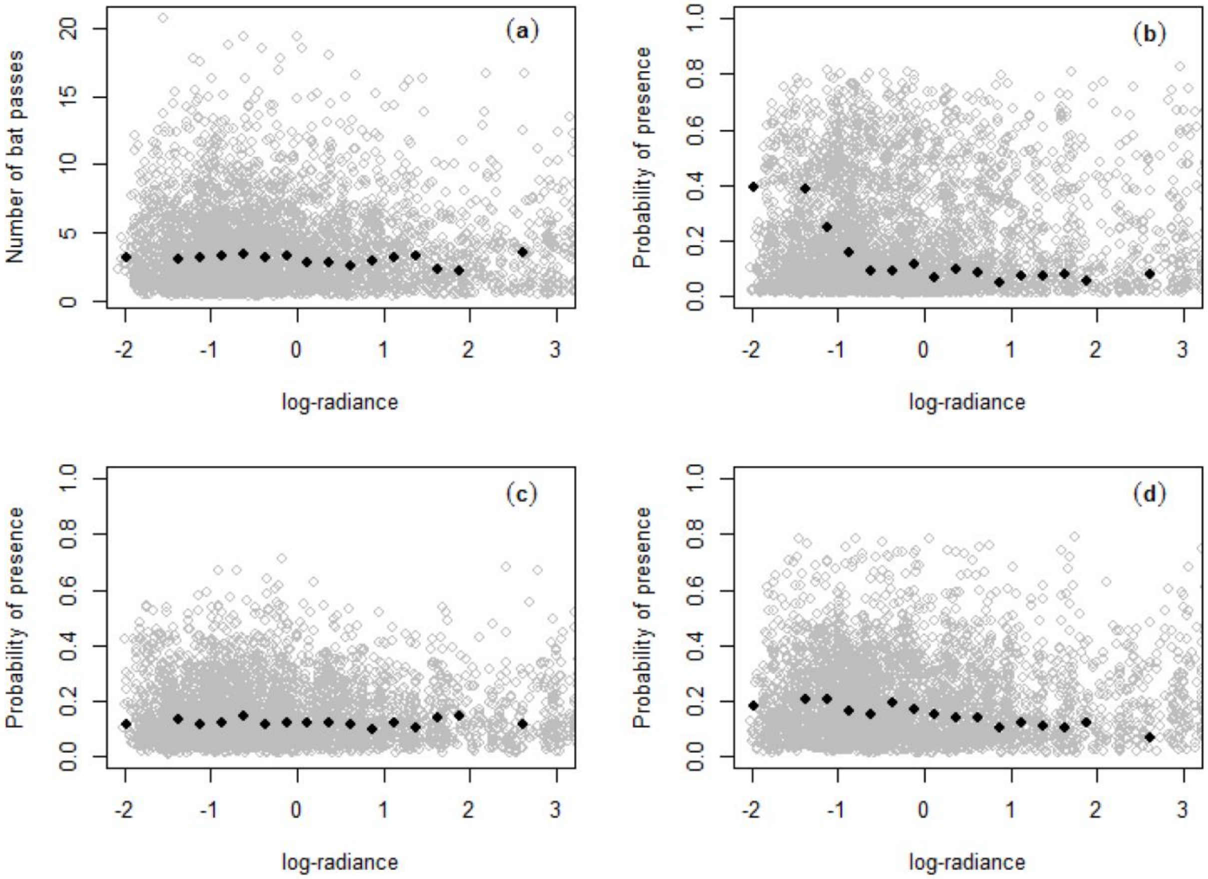

Fig. 4 Mean number of bat pass of **(a)** *P. pipistrellus*, and mean probability of presence of **(b)** *P. kuhlii;* **(c)** *N. leisleri*, and **(d)** *E. serotinus* per bin of 0.25 log-radiance, within 200 m landscape scale for **(a)** and **(c)**, 500 m landscape scale for **(d)** and 1000 m landscape 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).

Aim of the program	Monitoring the temporal trends of bat populations at a national scale	
Sampling protocol		
Scope	10 km around surveyors' home.	
Circuit length	30 km	
Number of transect per circuit	10	
Transect length	2 km separated of at least 1 km	
Period of sampling	from the 15th of June to the 31th of July	
Weather conditions	no rain, low wind speed (< 7 m/s), temperature > 12°C	
Survey start	30 minutes after sunset	
Bat recording characteristics		
Acoustic detectors	Tranquility Transect Bat detector&D240x	
Intercalibration of detectors	At the MNHN	
Acoustic settings	***Tranquility Transect***	***D240x***
Suppliers	Courtpan Design Ltd, UK	Pettersson Elektronik
High pass filter	5 kHz	18 kHz
Frequency	96 000 sample/sec	96 000 sample/sec
Record length (sec)	0.32	0.1
Post-recording treatment	/	Elimination of acoustic sequences spaced of less than 3.2 sec.
Time expansion	X10	X10
Recording device	Zoom H2 digital recorder (Samson technologies, USA)	
File storage format	WAV	
Bat identification		
Software	Syrinx 2.6	
Procedure	- **Training**: 2-day training course+ online self-training courses - **Bat first identification**: by volunteers - **Bat identification validation**: by MNHN	
Taxon identification level	Species level for all species except for *Myotis sp.* + Analysis of P. kuhlii number of bat pass on 270 transects showed that *Pipistrellus kuhlii* response variable may include less than 8 % *Pipistrellus nathusius*, 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.

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

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.

Landscape Variables	**Correlation coefficients**					
	Imper. surf.	*Inten. agri.*	*Exten. agri.*	*Forests*	*Roads*	*Streams*
Av. luminance	**0.85**	-0.10	-0.14	-0.07	0.13	0.02
Imper.surf.	/	-0.12	-0.16	-0.06	0.14	0.04
Inten. agri.	/	/	-0.32	-0.46	0.04	-0.30
Exten. agri.	/	/	/	-0.25	-0.007	0.09
Forest	/	/	/	/	-0.02	-0.007
Roads	/	/	/	/	/	-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**
P. pipistrellus	200	**-0.08 (0.02)**	**0.05 (0.01)**	**-0.15 (0.02)**	-0.02 (0.01)	**0.09 (0.01)**	-0.01 (0.01)	**0.03 (0.00)**	**0.10 (0.01)**	**0.06 (0.01)**
	500	-0.01 (0.02)	0.03 (0.01)	**-0.10 (0.02)**	0.01 (0.01)	**0.12 (0.02)**	**-0.03 (0.01)**	**0.05 (0.00)**	**0.10 (0.01)**	**0.06 (0.01)**
	700	-0.02 (0.02)	-0.001 (0.01)	**-0.11(0.02)**	0.01 (0.01)	**0.11 (0.01)**	-0.01 (0.01)	**0.05 (0.01)**	**0.10 (0.01)**	**0.06 (0.01)**
	1000	-0.01 (0.01)	-0.01 (0.02)	**-0.11 (0.02)**	0.02 (0.02)	**0.11 (0.01)**	-0.009 (0.01)	**0.06 (0.01)**	**0.10 (0.01)**	**0.06 (0.01)**
P. kuhlii	200	**-0.22 (0.10)**	-0.04 (0.02)	**-0.41 (0.09)**	0.10 (0.06)	**-0.16 (0.06)**	0.06 (0.04)	-0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	500	**-0.25 (0.10)**	-0.09 (0.06)	**-0.46 (0.10)**	**0.14 (0.06)**	-0.14 (0.07)	0.07 (0.05)	0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	700	**-0.26 (0.05)**	**-0.15 (0.07)**	**-0.42 (0.04)**	**0.06 (0.02)**	**-0.14 (0.02)**	0.02 (0.02)	**0.04 (0.02)**	0.02 (0.02)	**0.07 (0.02)**
	1000	**-0.33 (0.10)**	**-0.24 (0.09)**	**-0.64 (0.10)**	0.12 (0.07)	**-0.25 (0.07)**	0.01 (0.05)	0.08 (0.06)	0.04 (0.06)	**0.13 (0.06)**
E. serotinus	200	**-0.40 (0.09)**	0.01 (0.07)	**-0.58 (0.07)**	**-0.19 (0.06)**	0.08 (0.05)	0.07 (0.04)	-0.08 (0.04)	0.01 (0.06)	**0.19 (0.06)**
	500	**-0.35 (0.10)**	-0.01 (0.04)	**-0.43 (0.08)**	-0.07 (0.08)	**0.23 (0.06)**	**0.10 (0.05)**	-0.02 (0.05)	0.01 (0.05)	**0.18 (0.06)**
	700	**-0.42 (0.09)**	-0.08 (0.06)	**-0.43 (0.06)**	**-0.13 (0.05)**	0.04 (0.04)	0.01 (0.03)	-0.02 (0.03)	0.02 (0.04)	**0.13 (0.05)**
	1000	**-0.52 (0.10)**	**-0.13 (0.07)**	**-0.65 (0.08)**	**-0.21 (0.07)**	0.05 (0.07)	0.03 (0.05)	-0.02 (0.05)	0.02 (0.05)	**0.19 (0.07)**
N. leisleri	200	-0.06 (0.06)	**0.15 (0.06)**	**-0.22 (0.08)**	-0.11 (0.07)	-0.03 (0.08)	-0.03 (0.05)	**0.20 (0.05)**	0.06 (0.06)	**0.28 (0.06)**
	500	-0.01 (0.08)	0.04 (0.04)	**-0.17 (0.07)**	**-0.15 (0.07)**	0.07 (0.07)	-0.01 (0.04)	**0.23 (0.05)**	0.06 (0.06)	**0.28 (0.06)**
	700	-0.05 (0.07)	0.07 (0.06)	-0.12 (0.06)	**-0.19 (0.07)**	-0.02 (0.06)	0.01 (0.05)	**0.17 (0.03)**	0.05 (0.05)	**0.21 (0.05)**
	1000	-0.06 (0.08)	0.08 (0.07)	-0.16 (0.08)	**-0.25 (0.08)**	-0.05 (0.08)	0.05 (0.05)	**0.23 (0.06)**	0.05 (0.06)	**0.27 (0.06)**

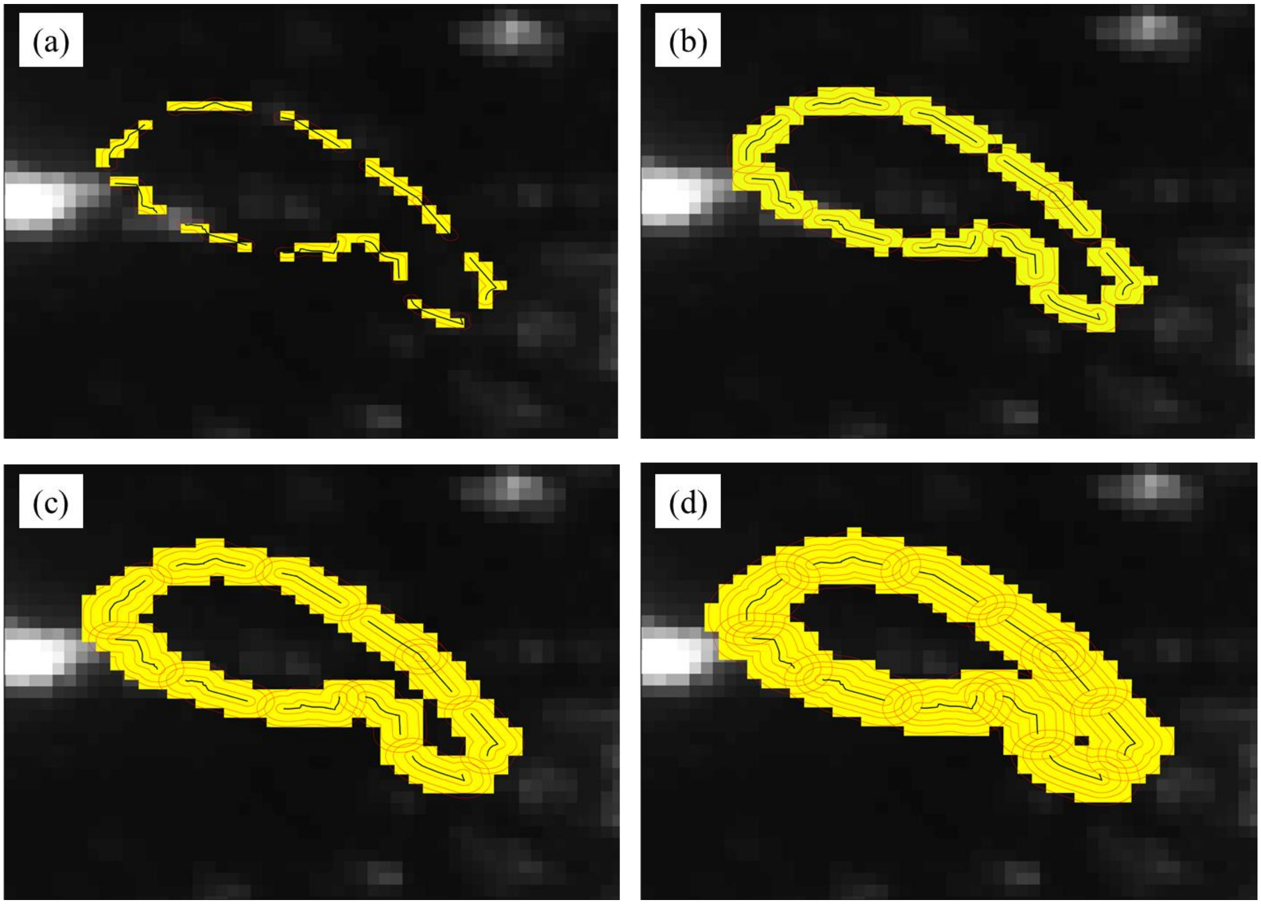

Fig. S1 Demonstration of the procedure done to calculate average radiance within the buffers of **(a)** 200 m, **(b)** 500 m, **(c)** 700 m and **(d)** 1000 m width from the VIIRS Nighttime Light raster used to. The average radiance was computed by the tool “zonal statistics as Table” from the package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

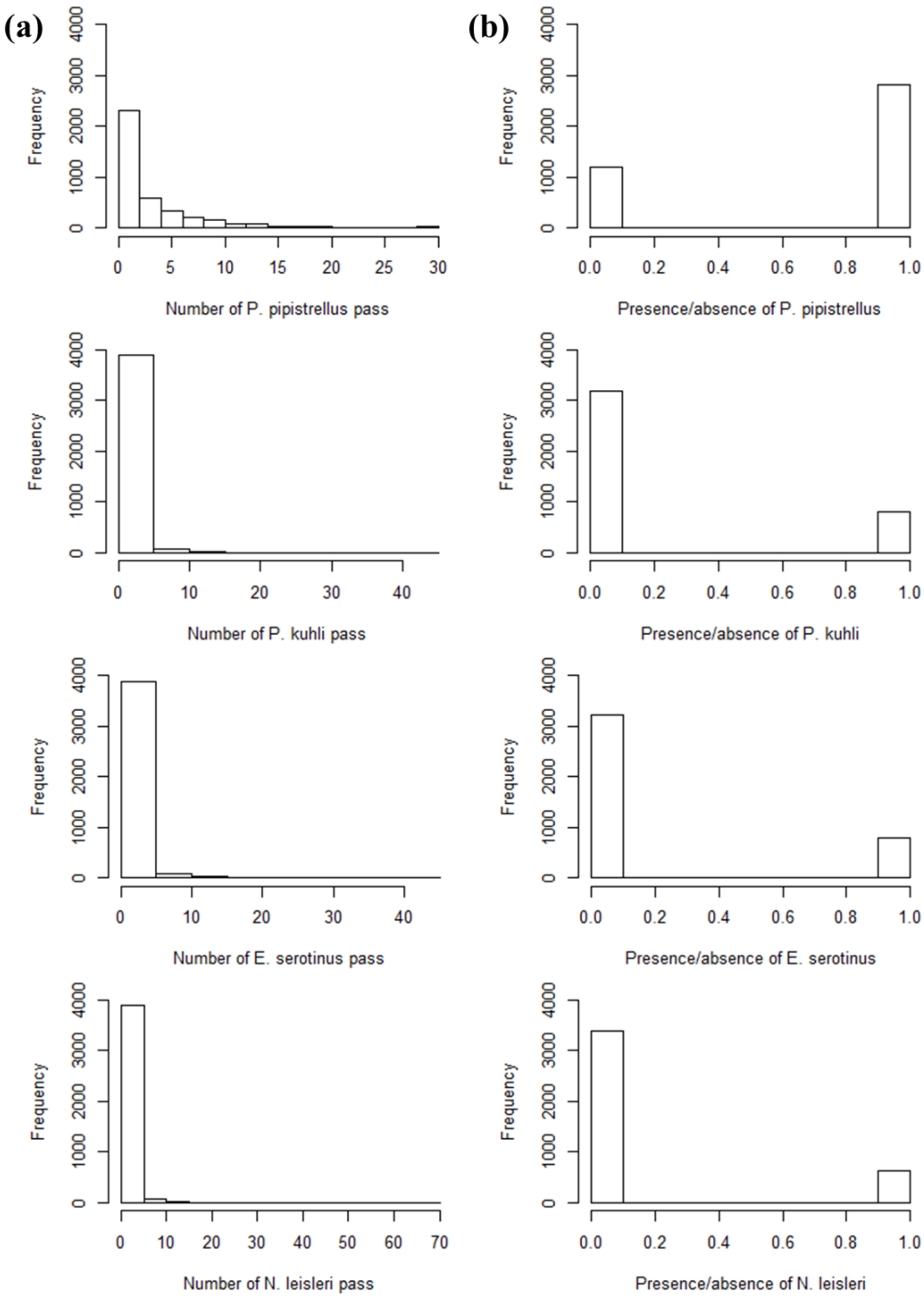

Fig. S2 Distribution of the response variable of *P. pipistrellus*, *P. kuhli*, *E. serotinus* and *N. leislerii* in number of bat pass per transect at the left hand side of the figure **(a)**, and in presence/absence at the right hand side of the figure **(b)**. We chose to follow a poisson distribution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