Landscape Ecol (2019) 34:793–809
https://doi.org/10.1007/s10980-019-00803-0

RESEARCH ARTICLE

Reducing light pollution improves connectivity for bats in urban landscapes

Alexis Laforge · Julie Pauwels · Baptiste Faure · Yves Bas · Christian Kerbiriou · Jocelyn Fonderflick · Aurélien Besnard

Received: 9 September 2018 / Accepted: 11 March 2019 / Published online: 30 March 2019

Abstract
Context Light pollution can alter animal movements and landscape connectivity. This is particularly true in urban landscapes where a need to incorporate conservation issues in urban planning is urgent.
Objectives We investigated how potential light-reduction scenarios at conurbation scale change landscape connectivity for bats.
Methods Through random stratified sampling and species distribution modelling, we assessed the relative importance of light pollution on bat presence probability and activity. We recorded bats during one entire night on each 305 sampling points in 2015. In 2016, we surveyed 94 supplementary points to evaluate models performance. We used our spatial predictions to characterize landscape resistance to bat movements. Then we applied a least-cost modelling approach to identify nocturnal corridors and estimated the impact of five light-reduction scenarios on landscape connectivity for two light non-tolerant bat species.
Results We found that light pollution detected from satellite images was a good predictor of bat presence and activity up to 700 m radius. Our results exhibited contrasting responses to average radiance: *M. daubentonii* responded negatively, *P. nathusii* had a positive response for low values then a negative response after a threshold radiance value of 20 $W.m^{-2}.sr^{-1}$ and *E. serotinus* responded positively. Five and four light-reduction scenarios significantly improved landscape

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-019-00803-0) contains supplementary material, which is available to authorized users.

A. Laforge · Y. Bas · J. Fonderflick · A. Besnard
CNRS, PSL Research University, EPHE, UM, SupAgro, IRD, INRA, UMR 5175 CEFE, 34293 Montpellier, France

A. Laforge
Conservatoire d'Espaces Naturels Midi-Pyrénées, 75 voie du TOEC, BP 57611, 31076 Toulouse, France

A. Laforge (✉)
INRA, UMR Dynafor, 1201 - Université de Toulouse - INPT - ENSAT, INPT - EI PURPAN, INRA, 24 Chemin de Borde Rouge- Auzeville, 31326 Castanet Tolosan, France
e-mail: Alexis.Laforge@inra.fr

J. Pauwels · Y. Bas · C. Kerbiriou
Museum National d'Histoire Naturelle, Centre d'Ecologie et des Sciences de la Conservation, UMR 7204 MNHN-CNRS-UPMC, 55 rue Buffon, 75005 Paris, France

B. Faure
Biotope, Agence Nord-Littoral ZA de la Maie, Avenue de l'Europe, 62720 Rinxent, France

C. Kerbiriou
Museum National d'Histoire Naturelle Ringgold standard institution, Station de Biologie Marine de Concarneau, Place de la Croix, 29900 Concarneau, France

connectivity for *M. daubentonii* and *P. nathusii* respectively.

Conclusions Light-reduction measures should be included in urban planning to provide sustainable conditions for bats in cities. We advocate for the use of our methodological approach to further studies to find the best trade-off between conservation needs and social acceptability.

Keywords Artificial light at night (ALAN) · Chiroptera · Land-use planning · Species distribution modelling (SDM) · Least-cost path analysis

Introduction

The ability of animals to move between habitats or between (sub)populations is crucial for population viability, and thus for biodiversity conservation (Zeller et al. 2012). Such movements require the landscape matrix to be pervious (Tischendorf and Fahrig 2000), a permeability usually referred to as landscape connectivity: i.e. the degree to which a landscape facilitates or impedes the movement of individuals (Tischendorf and Fahrig 2000). Identifying and restoring the conditions, structures and processes that facilitate animal movement within a landscape have thus become a global conservation priority. The goal is to mitigate widespread anthropogenic landscape modifications and their impacts on biodiversity (LaPoint et al. 2015). The first attempts to identify (with the aim of maintaining) ecological corridors in landscapes were based on structural connectivity and used landscape configuration metrics such as habitat patch size or length of linear landscape elements (such as hedges) thought to act as conduits or barriers to movement (Taylor et al. 2006). However, this approach often ignored non-structural landscape factors that might influence landscape connectivity (LaPoint et al. 2015) such as artificial light at night (ALAN).

Light pollution is known to have certain negative impacts on ecosystems (Gaston et al. 2015), but knowledge of the extent of its effect on landscape connectivity is sparse (Hölker et al. 2010; Hale et al. 2015; Azam et al. 2016). Worldwide, ALAN increased both in extent (2.2% per year) and in radiance (1.8% per year) between 2012 and 2016 (Kyba et al. 2017), potentially threatening a substantial proportion of global biodiversity, as 30% of all vertebrates and more than 60% of all invertebrates are nocturnal (Hölker et al. 2010). The widespread occurrence of ALAN has major impacts on animal movements and species distribution at multiple spatial scales; this is the case for a range of species and taxa, such as birds, butterflies, eels, turtles, zooplankton and bats (Hölker et al. 2010; Gaston et al. 2014). This makes it critical to characterize the relative contribution of ALAN to landscape fragmentation and then to use this information to propose sustainable land-use planning strategies (Grimm et al. 2008; Gaston et al. 2014; Azam et al. 2016). As ALAN is most prevalent in urban areas with an annual growth rate of 6% per year (Hölker et al. 2010) and public lighting renewal policies (Tsao et al. 2010), species in urban environments are particularly affected. Many bat species, for example, have adapted to live in built-up areas (Dietz et al. 2009) and can thus be directly confronted by light pollution. They are also one of the rare examples of species in urban environments that are protected at the European level (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora).

To investigate the effect of ALAN on landscape connectivity, insectivorous bats are a good study case, as they are both nocturnal and very sensitive to habitat loss and fragmentation (Mickleburgh et al. 2002; Frey-Ehrenbold et al. 2013). Studies have found that bat occurrence and activity can be negatively or positively affected by ALAN depending on their foraging strategy, their flight ability, and on the landscape scale considered (Hale et al. 2012; Azam et al. 2016). For example, at a local scale, the illumination of hedges or riverbanks near colonies of slow-flying gleaner species such as *Rhinolophus* spp. and *Myotis* spp. was observed to have a negative impact on bat activity, altering individuals' movement behaviour as they sought to avoid the newly illuminated areas (Kuijper et al. 2008; Stone et al. 2009). In contrast, fast-flying species that hunt insects at dusk in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.,* can benefit at a local spatial scale from new foraging areas provided by ALAN (Lacoeuilhe et al. 2014; Azam et al. 2015). However, ALAN has been shown to decrease landscape connectivity by altering movement and gap-crossing behaviour of *Pipistrellus pipistrellus* (Schreber 1774) individuals in an urban

matrix (Hale et al. 2015). These findings suggest that ALAN can act as a barrier for bats and thus further increase landscape fragmentation. This highlights the importance of integrating light pollution measures in sustainable urban-planning strategies in order to maintain biodiversity in urban landscapes through darker environments (Gaston et al. 2015). Yet knowledge concerning how bat communities respond to urbanization and ALAN is currently insufficient to ensure the conservation or development of effective nocturnal corridors (McDonnell and Hahs 2008; Hale et al. 2012; Mathews et al. 2015). This is notably due to the fact that highly urbanized areas are often undersampled, as sampling bats in cities is challenging, leading to a lack of data for this type of landscape (LaPoint et al. 2015).

To begin to address this, this study aimed to: (i) assess to what degree ALAN contributes to landscape fragmentation for bats, (ii) provide a methodological basis for identifying nocturnal corridors, and (iii) evaluate the effect of different light-reduction scenarios on landscape connectivity for bats in order to improve ALAN planning. To achieve these goals, we used species distribution modelling based on standardized empirical data from random stratified sampling to model bat species' use of urban landscapes, to characterize landscape resistance to bat movement (Stevenson-Holt et al. 2014) and to identify the most suitable habitat patches to connect. We then used least-cost path modelling to identify nocturnal corridors and assess the effects of different light-reduction scenarios on landscape connectivity. A summary of the methodological procedure is shown in Fig. 1.

Materials and methods

Study area

The study was carried out in 2015 and 2016 in the metropolitan area of Lille in northern France (50.6294 N, 3.0571 E; Fig. 2). It is the second-largest conurbation in France, with more than 1.1 million inhabitants. The study area covered 27,307 hectares and 41 municipalities. The climate is predominantly temperate and oceanic with mild average daily temperatures (1–10 °C in winter, 11–23 °C in summer) and a constant level of rainfall throughout the year (743 mm per year^{-1} on average). The area is dominated by dense urbanization and intensive agricultural landscapes (respectively 65% and 23% of the total study area). Woodland and natural areas are restricted to relatively small patches, which are mainly urban parks on riverbanks or around ponds (Fig. 2).

Sampling design

When using species distribution models (SDMs), a crucial assumption in defining landscape-resistance values is that all the habitats in the studied landscape have been randomly sampled with the same effort (Beier et al. 2008). Thus we defined a random stratified sampling method to record bat passes in every landscape context in the study area in terms of three covariates: proportion of impervious surfaces (including buildings and paved areas such as roads, sidewalks, driveways and parking lots), proportion of tree cover, and ALAN (Fig. 2). These variables were selected because they are known to influence bat presence and activity (Fonderflick et al. 2015; Hale et al. 2015; Azam et al. 2016) and because their variations in the study area are large enough to yield significant gradients. The data concerning ALAN in the study area was obtained from VIIRS Nighttime Imagery (2012), consisting of a 2-month composite raster of radiance data (in nW/cm^{-2}.sr) collected by the Suomi NPP-VIIRS Day/Night Band during two time periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh et al. 2013). This data was produced by the Earth Observation Group, NOAA National Geophysical Data Centre (http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html). The VIIRS Nighttime Imagery that we downloaded in 2014 had a resolution of 300 × 463 m. The pixel was oblong and in WGS84 coordinates system. We needed to convert this raster in another coordinates system (lambert 93) to use it with land uses data from the French National Institute for Geographic and Forestry Information (http://www.ign.fr/). The value of average radiance of each new pixel in LB93 was set to the value of the nearest initial pixel. By doing the interpolation, the pixels became square with a resolution of 250 × 250 m (Fig. 2). We carefully checked that the change in pixel shape did not alter pattern of the data. Then, all the other landscape variables were built using a grid at a resolution of 250 m × 250 m with the software QGIS 2.14 (QGIS development

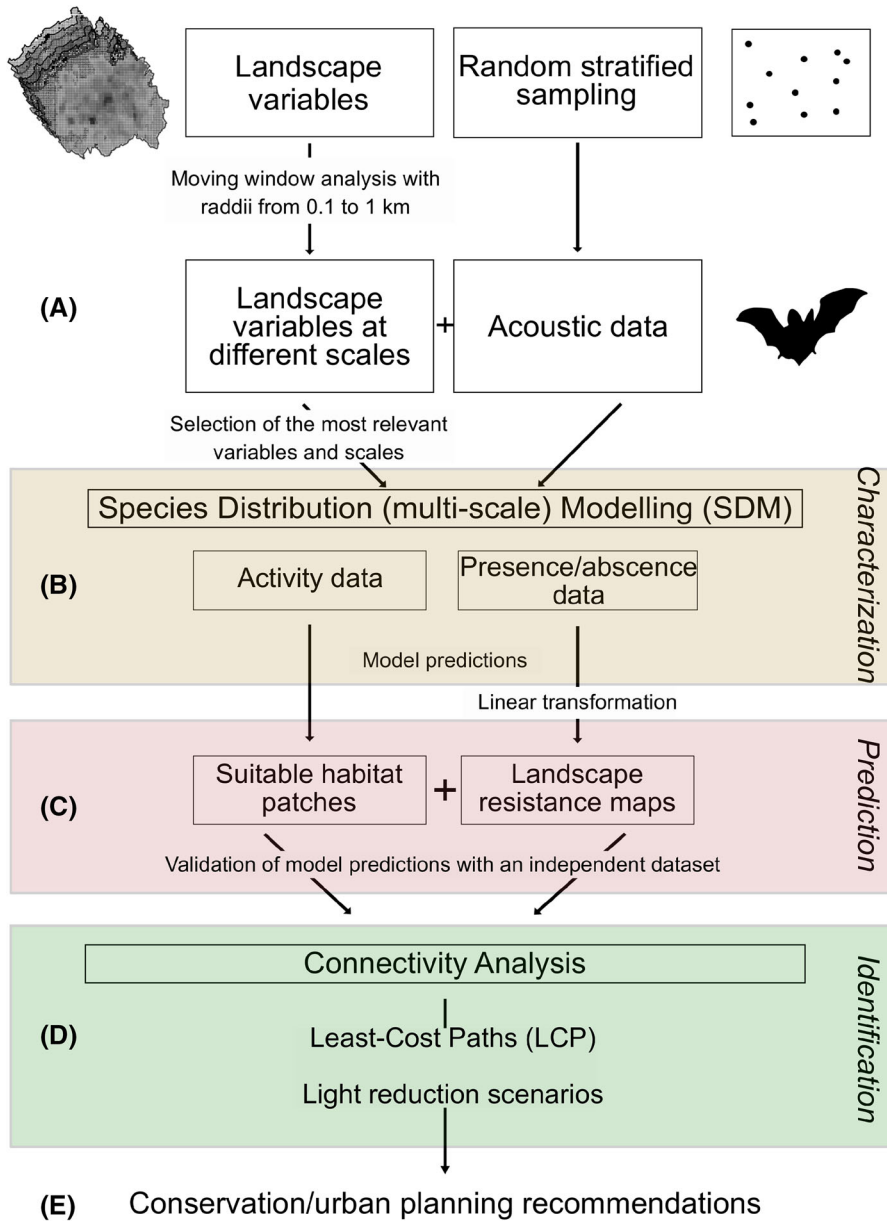


Fig. 1 Summary of methodological procedure followed to assess the effects of light-reduction scenarios on landscape connectivity for bats

team 2016). For each cell, we calculated the values of the three variables and grouped them into five categories of equal size (0–20%, 20–40%, 40–60%, 60–80%, 80–100% for the proportion of impervious surfaces and tree cover and 2.6–17, 17–31.4, 31.4–45.8, 45.8–60.2, 60.2–74.6 nW/cm^{-2}.sr for ALAN).

In order to obtain the most representative sampling of the three landscape gradients, we developed an algorithm to randomly select at most two cells in all combinations of these three covariates. We carried out this sampling procedure twice: once for exclusively non-aquatic cells and once for cells with any water coverage (watercourses and ponds). It is known that wetlands are important habitats for bats in urban contexts and hence are a strong predictor for both bat occurrence and activity (Straka et al. 2016). This procedure allowed us to randomly select 305 cells in 2015 and 94 cells in 2016 (Fig. 2).

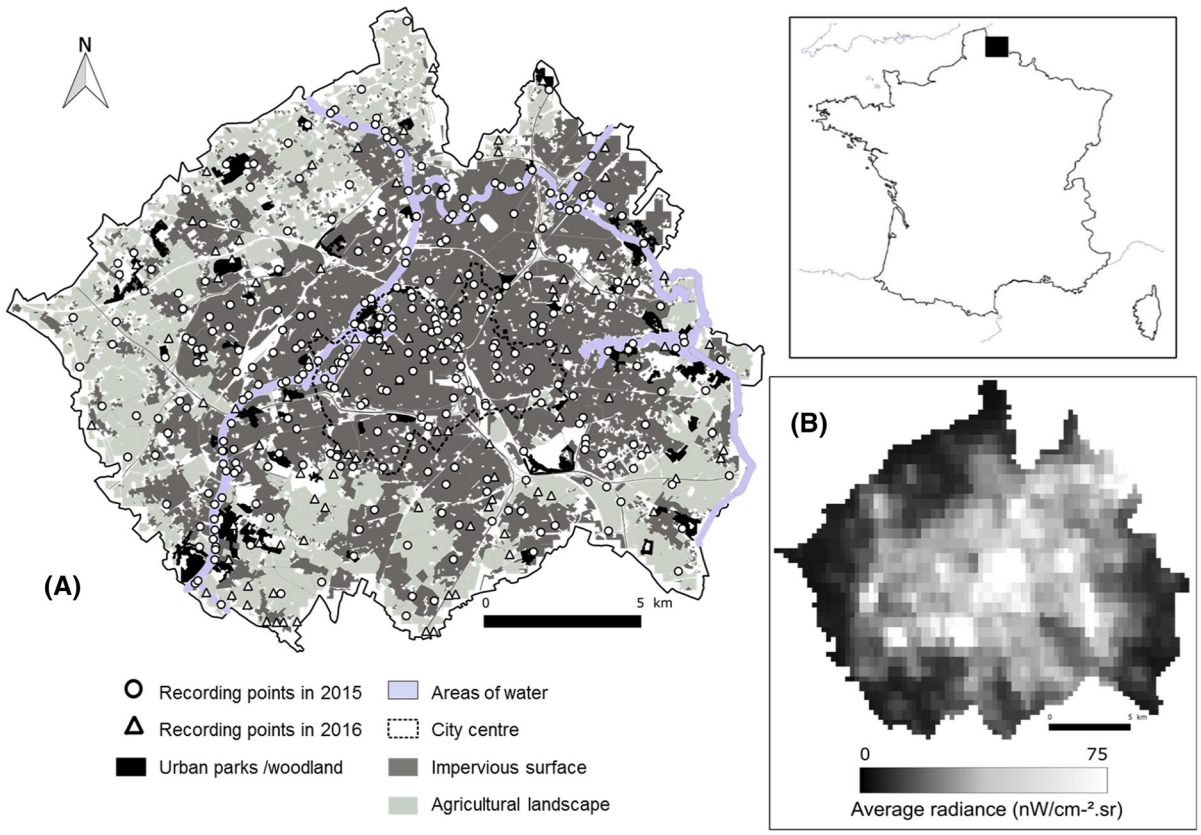


Fig. 2 **a** Map of the study area (the conurbation of Lille, France) showing the locations where acoustic sampling was carried out (recording points) in the summers of 2015 and 2016, as well as the main landscape elements. **b** Spatial gradient of average radiance in the study area obtained from the Earth Observation Group, NOAA National Geophysical Data Centre (http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html)

Bat surveys

We used acoustic surveys to gather bat presence–absence and activity data to define an activity index (AI), which is the number of minutes in which at least one bat call was recorded (Miller 2001; Haquart 2013). We recorded all bat passes during one full night (30 min before dusk to 30 min after dawn) for each cell using stationary automated ultrasound detectors (Song Meter SM2BAT, Wildlife Acoustics, USA) fitted with multidirectional microphones (SMX-US weatherproof ultrasonic microphone, Wildlife Acoustics, USA). The position of the detectors in the cells was not identical because of the constraints of hiding these in an urban landscape. The sampling was carried out between 1 June and 31 August in 2015, corresponding to the seasonal peak of activity of bat species in this region, as recommended by the French national bat-monitoring program 'Vigie-Chiro' (http://www.vigienature.mnhn.fr/). Since bats echolocate continuously (several calls per seconds) while commuting or foraging, we assumed detection probability was perfect. Recordings were only made when there was no rain, the wind was below 30 km/h and the ambient temperature above 12 °C. We used the software SonoChiro© (Bas et al. 2013) to automatically classify the echolocation passes to the most accurate taxonomic level possible. We then checked this classification by screening all ambiguous passes with Syrinx software version 2.6 (Burt 2006) and using existing identification keys (Barataud et al. 2015). Identification was possible to species level for most of our acoustic data, as there is low bat-species diversity in the study area. This avoided problematic acoustic overlaps between certain species pairs such as *Pipistrellus nathusii/Pipistrellus kuhlii, Myotis daubentonii/Myotis mystacinus/Myotis bechsteinii* and

Eptesicus serotinus/Nyctalus leisleri. In fact, *P. kuhlii, M. mystacinus, M. bechsteinii* and *N. leisleri* are very rare in the study area according to regional atlas data (Dutilleul 2009). Nevertheless, to reduce false absences, the recording points where we were only able to identify a group of species that includes the studied species (but in which the studied species itself was not identified with 100% certainty) were excluded from the analysis of that species (Boughey et al. 2011).

Species distribution modelling (SDM)

When SDM is used to calculate landscape resistance, the underlying assumption is often made that habitats selected by a species for foraging also facilitate their movements (LaRue and Nielsen 2008). However, to date this assumption has rarely been tested, and Roever et al. (2012) have pointed out that it is unlikely that the same landscape variables determine both habitat selection and movement behaviour. As a result, we used presence–absence data to define landscape resistance, reasoning that resistance is not directly linked with the level of activity but more to the probability that a bat would move through the landscape. To define habitat patches, we used bat activity data, since a high level of activity can denote a foraging area or a roosting site. Often, researchers select suitable habitat patches on the basis of expert opinion and assign each landscape feature a constant resistance value (FitzGibbon et al. 2007). In contrast, our methodological procedure provided predictions at each location rather than constant resistance values for a particular land cover type, which we believe is likely to result in more accurate models to describe ecological patterns (Beier et al. 2008).

We modelled the presence probability and the activity of bat species using Generalized Additive Models (GAM; Hastie and Tibshirani 1990). These provide useful flexibility for modelling ecologically realistic relationships in SDMs and fitting complex nonlinear relationships between predictors and the response variable (Elith et al. 2006; Elith and Leathwick 2009). Species' presence probability was modelled with presence–absence data using a binomial error distribution and a logit link function. The activity index was modelled using a negative binomial error distribution and a log link function to take into account the overdispersion of our data (Zuur et al. 2009). The models were trained with the data collected in 2015; the performance evaluations were based on data from independent field sampling collected in 2016 (for details on the methods used to evaluate model performance, see Online Appendix 1).

For details on the multiscale and multivariate model selection methods, the multicollinearity and spatial autocorrelation evaluations see Online Appendix 2. The statistical analysis was carried out in R 3.2.5 (package "Raster", "ROCR", "GAM").

Connectivity analysis

To identify nocturnal corridors for bats, we used the least-cost network process outlined by Watts et al. (2010). All the steps of this process (Fig. 1) were performed in ArcView 10 with the Spatial Analyst extension (ESRI, Redlands, CA).

Selection and localization of suitable habitat patches

In a first step, we identified the most suitable habitat patches (these were later used as nodes to connect through-corridors, using predictive bat activity maps). Patches were defined as areas where activity values were in the 'High' category of the French bat activity framework (Haquart 2013) i.e. AI $>$ 12 min per night for *M. daubentonii*; $>$ 50 for *E. serotinus*; $>$ 33 for *P. nathusii*. We then arbitrarily kept only the suitable habitat patches with a surface area of up to 25,000 m^2 (i.e. 10 aggregated cells).

Landscape resistance maps

Presence probability maps obtained with SDM can be interpreted as the landscape resistance level to movement between habitat patches: the lower the presence probability, the more resistant that landscape is to the movement of the species (Guisan and Thuiller 2005). To transform previously obtained SDM maps into resistance areas, we inverted them by calculating the landscape resistance value for each cell in the following way: $R_i = P_{max} - P_i$.

where R_i is the landscape resistance value of a given cell, P_{max} is the value of the maximum presence probability obtained on the predictive map and P_i is the value of the prediction of the given cell (Zeller et al. 2012).

Least-cost paths

We modelled the corridor network using the least-cost path (LCP) modelling technique (Watts et al. 2010), a graph-theory derived method (Urban and Keitt 2010). The LCP modelling was performed with Linkage Mapper toolbox (for more information on the technique, see McRae and Kavanagh 2011) using ArcGis 10 (ESRI, Redlands, CA). All pairs of suitable habitat patches were connected using LCP.

Light-reduction scenarios

The main objective of our study was to provide realistic conservation recommendations for policymakers and urban landscape planners. Light management in a conservation goal is very challenging because of the conflict of interest with social and political issues (aesthetics, tourism, safety, outdoor night-time activities, etc.). Thus, rather than demonstrating the absolute effect of light reduction on landscape connectivity (i.e. random light-reduction scenarios) we compared five light-reduction scenarios, considered more realistic and useful to help policymakers and urban planners to make the best trade-off between conservation and social/political issues. We tested five light-reduction scenarios for: (1) urban municipalities of more than 10,000 inhabitants, (2) urban municipalities of less than 10,000 inhabitants, (3) urban parks, (4) main roads, and (5) wetlands (the spatial distribution of these areas is shown in Online Appendix S3.1; the means and standard deviations of initial radiance values before light reduction with the total unlit area for each scenario is shown in Online Appendix S3.2). For light-reduction scenarios 1 and 2, we chose not to change the light intensity in predominantly privately lit areas (see Online Appendix 3). This choice was made in order to provide realistic recommendations for policymakers and city authorities whose remit is managing ALAN from public sources. To apply this, for each pixel in the NOAA satellite picture we reduced the initial radiance value proportionally to the surface area within the pixel corresponding to areas where light would be turned off in the scenario considered. We then re-used our selected models to predict the resistance maps with modified ALAN pictures as inputs and thus redone the whole process (Fig. 1 from step B) for each light reductions scenarios. We used a paired Student's *t* test to test whether the LCP's least-cost distances were significantly lower with the scenarios than with predictions using unmodified light radiance data. In using presence probability to define landscape resistance due to ALAN, our hypothesis was that presence would be negatively impacted by ALAN. Hence, we applied the scenarios only to light-intolerant bat species, as it is unlikely that reducing ALAN would deteriorate landscape connectivity for light-tolerant species.

Results

In 2015, we recorded 235 793 bat passes at 305 locations during 164 700 recording hours. In 2016, we recorded 40 553 bat passes at 94 locations over 50 760 recording hours. Of all the bat passes recorded, 264 667 (95.7%) were identified as *P. pipistrellus*. Because *P. pipistrellus* was present at all sampling locations, its presence probability could not be modelled based on the covariates, so we did not include this species for further analysis. We registered 6 971 bat passes (2.5%) identified as *Pipistrellus nathusii*, 2 161 bat passes (0.8%) identified as *Myotis daubentonii*, and 1 250 bat passes (0.4%) identified as *Eptesicus serotinus*. Using the procedure designed to avoid false absences (see 'Methods'), we based our analysis on 297 locations for *E. serotinus*, 282 locations for *M. daubentonii* and 291 locations for *P. nathusii*.

Most relevant variables

While the percentage of impervious surfaces was not identified as a variable having a significant effect on the presence probability or activity of bats (except on the activity of *M. daubentonii*), average radiance had significant effects on both the presence probability and the activity of the three species (except on the activity of *P. nathusii*). In all models, the average radiance was the second or third most important variable. Our results showed contrasting trends: the effect of average radiance was positive for *E. serotinus*, whereas it was negative for *M. daubentonii* (Figs. 3, 4). In the case of *P. nathusii,* average radiance had a positive effect at low values, then a negative effect after a threshold radiance of 20 $W.m^{-2}.sr^{-1}$ (Figs. 3c, 4c). For the three studied species, the response curves of activity and presence probability to average radiance

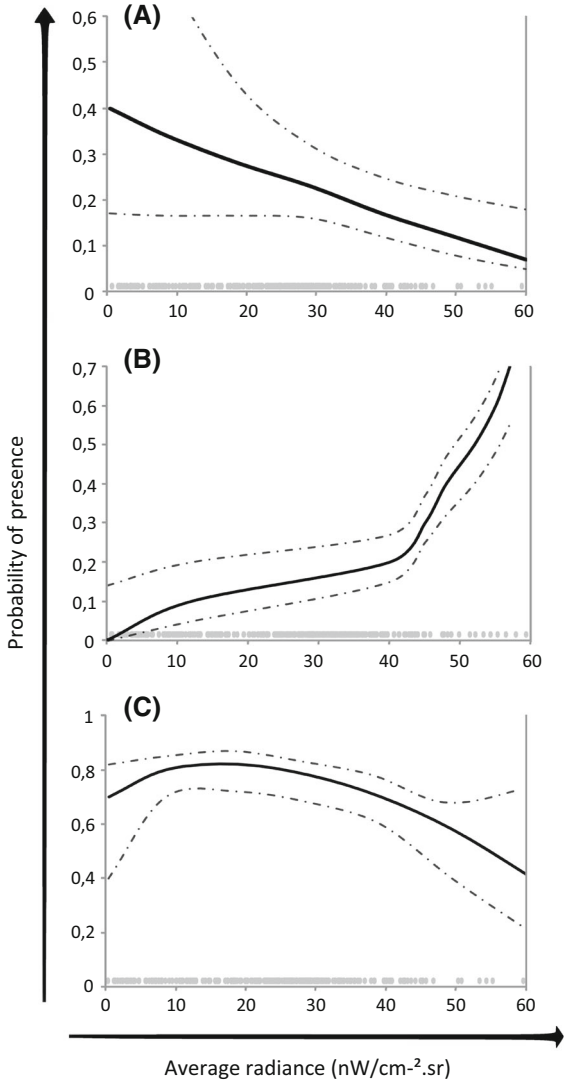


Fig. 3 Representative GAM response curves showing species presence probability at a location along the average radiance gradient. **a** is the response of *M. daubentonii* at a scale of 300 m, **b** is the response of *E. serotinus* at a scale of 700 m, and **c** is the response of *P. nathusii* at a scale of 100 m

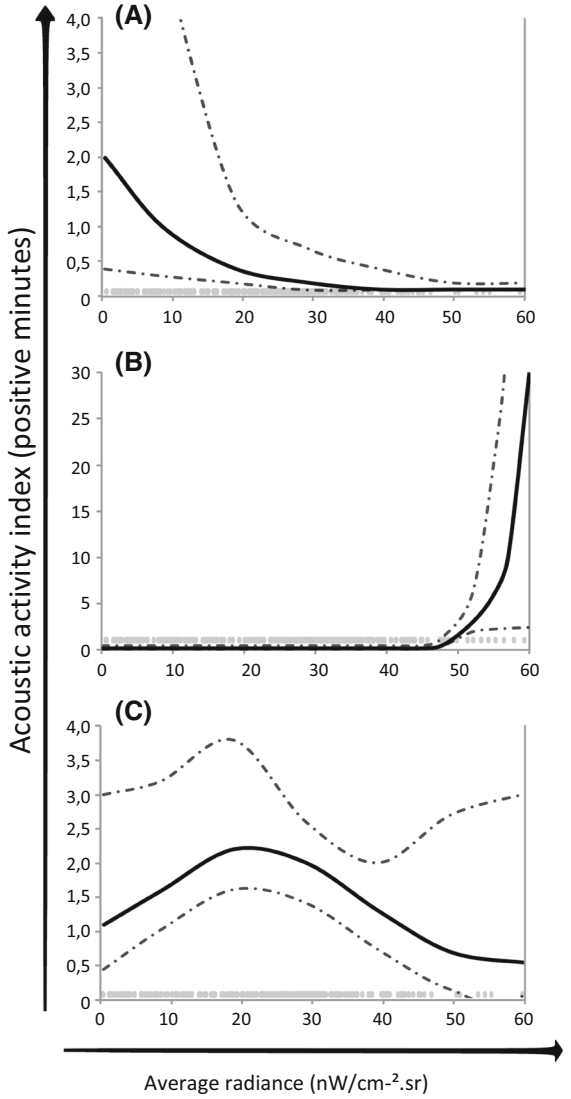


Fig. 4 Representative GAM response curves showing species activity at a location along the average radiance gradient. **a** is the response of *M. daubentonii* at a scale of 100 m, **b** is the response of *E. serotinus* at a scale of 500 m, and **c** is the response of *P. nathusii* at a scale of 800 m

were similar (Figs. 3, 4). Average radiance showed significant effects at scales from 100 to 700 m (Table 1). Distance to water represented the best predictor and the most important landscape factor (it was always significant) explaining the distribution of the three species in terms of both presence probability and activity (Table 1). We never found the same groups of selected variables between activity models and presence probability models (Table 1). The number of patches with tree cover and the distance to vegetation had significant effects only on bat activity but not on presence probability. In contrast, the percentage of surface area covered by water only had a significant effect on presence probability but not on activity (Table 1).

Model evaluation

The AUC values showed that the predictive performance of the presence probability model was at the

Table 1 Summary of the multiscale models that best predicted bat presence probability and activity and their evaluation scores

Species	Landscape variables and spatial scales (m)						Deviance explained	AIC	AUC	COR	Sensitivity	Specificity	NRMSE
	100	200	300	500	700	800							
Presence probability													
Pipnat	$Light_3$* $road_4$*					$Water_2$** $distwater_1$**	24.4%	319.5	0.73***	0.87***	77.78	48.98	
Eptser					$Light_3$** $distwater_1$*	$Water_2$*	13.9%	251.1	0.72*	0.65	20.00	96.43	
Myodau		$Water_4$ $road_5$ $distwater_1$**	$Light_3$*			$Veget_2$*	27.3%	214.5	0.75***	0.68*	25.00	96.15	
Activity													
Pipnat	$urban_3$					$Light_4$ nTP_2*** $distwater_1$***	39.3%	1348.2		0.3**			0.22
Eptser				$Light_2$***	$Distwater_1$***	$Distveget_3$*	35.2%	506.8		− 0.03			0.17
Myodau	$Light_3$** $road_2$*** $urban_5$** $distveget_4$*					$Distwater_1$*** $veget_6$	62%	554.7		0.5***			0.15

The subscript numbers indicate the rank of importance of the landscape variable (e.g. $distwater_2$ = distwater is the second most important variable in the model). Species: Pipnat, *Pipistrellus nathusii*; Eptser, *Eptesicus serotinus*; Myodau, *Myotis daubentonii*. The landscape variables include *light* ALAN, *road* total length of roads, *water* proportion of surface area covered in water, *distwater* mean distance to water, *veget* proportion of tree cover, *urban* proportion of impervious surfaces, *nTP* mean number of tree patches, *distveget* mean distance to tree patches. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

same quality level for the three studied species (Table 1). For *E. serotinus* and *M. daubentonii*, specificity values showed that absence was better predicted than presence, with 96% of absences in 2016 correctly predicted by the 2015 model (i.e. these were confirmed as real absences by the 2016 model). In contrast, the presence of *P. nathusii* was better predicted than its absence (see Table 1). In terms of correlation coefficients (COR), the model for *P. nathusii* had the best predictive performance for presence probability (COR = 0.87). In comparison, the predictive performance of the activity models was poorer, with COR values ranging from − 0.03 to 0.5 (Table 1).

Predicted distribution

The presence probability of *E. serotinus* and *M. daubentonii* was concentrated on areas with water. In contrast, *P. nathusii* had a more homogeneous spatial distribution (Fig. 5-1). The most urbanized and illuminated section of the conurbation's major canal was the least suitable section for *M. daubentonii* and *P. nathusii*, whereas it was the most conducive for *E. serotinus* (Fig. 5-1). Our results also showed that the city centre is on the whole a barrier to bat movement, although *E. serotinus* was predicted to have two suitable patches in urban parks of the centre (Fig. 5-1).

The activity-based models demonstrated the importance of parks for bat foraging in urban areas (Fig. 5-2). Indeed, the only habitat patches in the city centre predicted to be very suitable for all species were the largest urban parks of the city, which are located along the banks of the canal in the middle of the most illuminated section of the watercourse. The activity of *M. daubentonii* was much higher along the canals outside the city (in the northern and southern sections) than in the centre of Lille, except in urban parks. *E. serotinus* was very active in urban parks and forest patches of the study area. The activity of *P. nathusii*, which had a wider distribution in the study area but was not very abundant, was most concentrated in urban parks near canals and at suburban boundary zones between agricultural landscapes, suburban areas and forests (Fig. 5-2). Based on these predictive activity maps and a French bat activity framework (Haquart 2013), we identified 14 suitable habitat patches for *E. serotinus*, 47 for *M. daubentonii* and 22 for *P. nathusii* (Fig. 5-3).

Fig. 5 Modelled distribution of presence probability (*1*) and activity (*2*) of the three studied species. (*3*) represents the least-cost paths identified in the study area. The activity gradient (defined by minutes in which at least one bat call of the species was recorded) has values bounded between 0 and 114 min for *E. serotinus*, 0 and 326 for *P. nathusii*, 0 and 540 for *M. daubentonii*

Least-cost paths and light-reduction scenarios

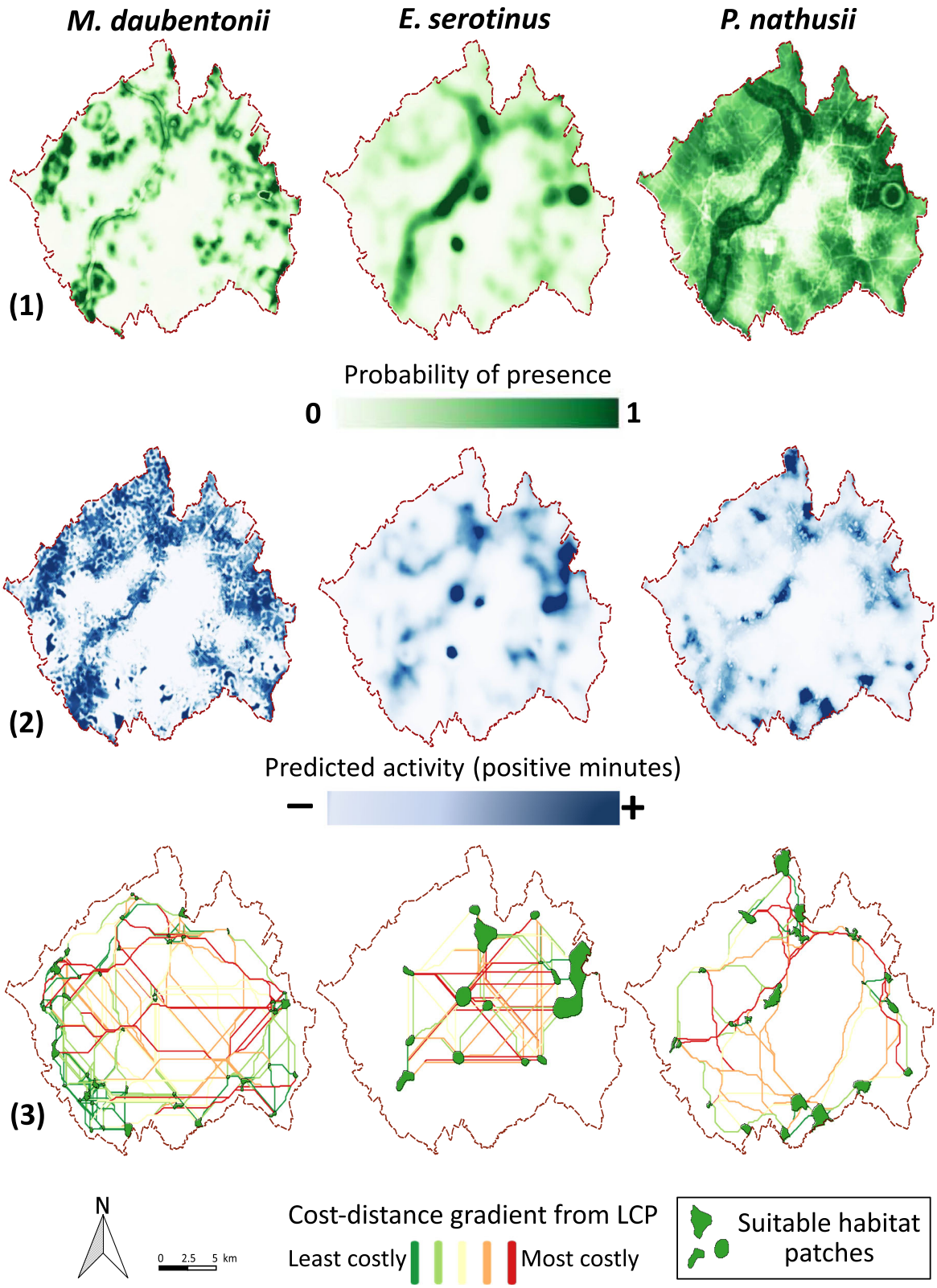
We assessed all the least-cost paths (LCPs) connecting each pair of suitable habitat patches (91 for *E. serotinus*, 1081 for *M. daubentonii* and 231 for *P. nathusii*) (Fig. 5-3) and then tested them for the five light-reduction scenarios (We did not apply these scenarios to the LCPs of *E. serotinus* because of its positive response to light). For *M. daubentonii*, all scenarios improved connectivity by significantly reducing the LCP cost-distance values (Fig. 6). For *P. nathusii* as well, all scenarios improved connectivity in the study area, except for scenario 2, which significantly increased the LCP cost-distance values. The scenarios ranged from more to less effective in the following order: (4) > (5) > (3) > (1) > (2) for *M. daubentonii*, and (1) > (3) > (4) > (5) for *P. nathusii* (Fig. 6).

Discussion

Our results show that average radiance is an important predictor of the occurrence and activity of bats even in a highly urbanized context. They also demonstrate that light reduction is effective in improving connectivity for bats in an urban landscape. This emphasizes the importance of taking light pollution into account in addition to structural landscape criteria when defining biodiversity conservation strategies such as the restoration of ecological networks in urban planning (Grimm et al. 2008; Azam et al. 2016).

Model evaluation

While the presence probability models resulted in relatively accurate predictions, this was less the case with the activity models (Table 1). We expect this lack of accuracy is due to the fact that we measured activity very locally, while it is very sensitive to spatial and


M. daubentonii
E. serotinus
P. nathusii
(1)
Probability of presence
0
1
(2)
Predicted activity (positive minutes)
−
+
(3)
N
0 2.5 5 km
Cost-distance gradient from LCP
Least costly
Most costly
Suitable habitat patches

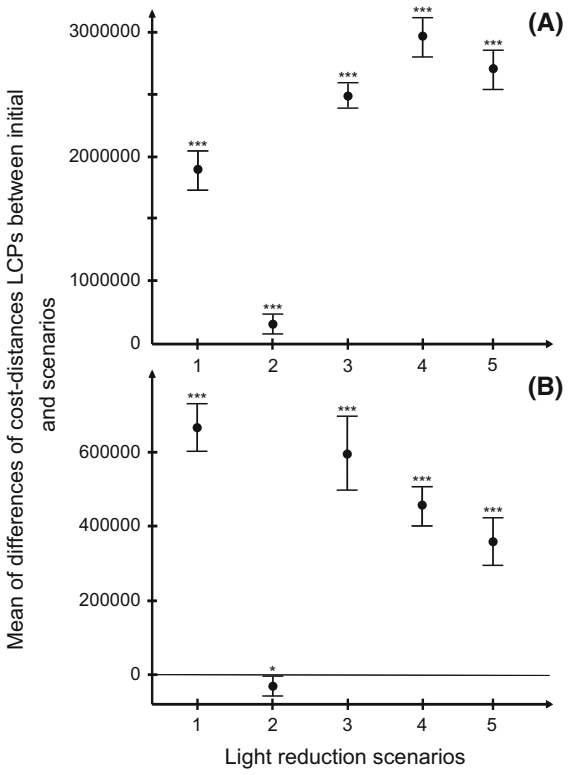


Fig. 6 Means of differences (with 95% confidence intervals) of paired cost-distances between the LCP with initial radiance intensity and the LCP after each light-reduction scenario using Student's *t*-test on the two studied species sensitive to light. **a** *M. daubentonii*; **b** *P. nathusii*. Light-reduction scenarios tested the effect of light reduction in: (1) urban municipalities of more than 10,000 inhabitants; (2) urban municipalities of less than 10,000 inhabitants; (3) urban parks; (4) main roads; (5) wetlands. $*P < 0.05$; $***P < 0.001$

temporal variations in prey resources. Furthermore, predicting activity levels using only landscape variables is very difficult since spatial variation in species abundance can be driven by other factors, such as the complex interaction between stochastic temporal variations in abundance and dispersal of species in space (Ives and Klopper 1997). For example, we observed a non-negligible difference in precipitation levels between 2015 (mean rainfall/day = 1.6 mm ± 3.1) and 2016 (mean rainfall/day = 7.4 mm ± 11.2) during the same period (June–July, when sampling was carried out). As Erickson and West (2002) found that average summer precipitation can explain the largest proportion of variance in bat activity levels, this difference in rainfall could be a factor that limited the model's prediction performance. In any case, the weak prediction performance was not a problem because we used activity levels only to identify the most suitable habitat patches. We kept the same patches to test the different light-reduction scenarios, so their comparison is relevant irrespective of the quality of the predictions.

By the evaluation of spatial autocorrelation, we found virtually no autocorrelation for presence probability but some significant but low values of Moran's I for activity (see Online Appendix 2). This spatial autocorrelation is potentially linked to very high local abundances unexplained by the models because of the very high variance somewhat inherent to this kind of species, the activity variable, and unavailable missing variables (proximity of roosts, spatial and temporal peak of food resources abundances). The presence of this autocorrelation suggests that caution must be taken in interpreting the statistical tests associated to these models on activity. Moreover autocorrelation is supposed to inflate type I error but not to bias the estimates of the models (the response curves). The patterns we obtained could thus be discussed. This conclusion is reinforced by the fact that the results of activity modeling, related to light average radiance, are highly consistent with those of the probabilities of presence (Figs. 3, 4). Furthermore we only used presence probability to assess landscape connectivity and efficiency of light-reduction scenarios. The modelling of bat activity was only used to locate the nodes that we linked with the least-cost paths, a selection that would not be impacted by spatial autocorrelation.

Alan: a major impact of urbanization on bats

Our findings show that average radiance is a more important landscape parameter for modelling bat distribution than the proportion of impervious surfaces in a highly urbanized area (Table 1). This supports the findings of Azam et al. (2016) at a country scale and confirms the predictions of other studies that have predicted that the effect of ALAN on the movement of bats is expected to be much more pronounced in urban contexts (Hale et al. 2012, 2015; Russo and Ancillotto 2015). This suggests to us the urgency that ALAN, as a consequence of urbanization, be taken into account in ecological corridor modelling in order to maintain functional connectivity of bat populations in urban areas.

Our study is the first to precisely describe the effect of ALAN on the presence probability and activity of *P. nathusii* and *M. daubentonii* (Figs. 3, 4). The negative response of *M. daubentonii* to average radiance is consistent with previous studies of *Myotis spp*. as a group (Stone et al. 2012). Indeed, *Myotis* species are light-sensitive: these slow fliers systematically seek to avoid the potentially increased predation risk in illuminated zones (Rydell 1991). *P. nathusii* had an intermediate response to ALAN, with a light-tolerance threshold of $\approx$ 20 W m^2 sr^{-1} (Figs. 3c, 4c). We believe that this response pattern is driven by a trade-off between the benefits of the concentration of insects at low-intensity light and the cost of increased predation risk from high-intensity light. *E. serotinus* had a positive response to average radiance due to its ecological plasticity and fast flight capacity, allowing these bats to exploit illuminated foraging areas rich in insects (Figs. 3b, 4b). This positive response at scales of 500 m (for activity) and 700 m (for presence probability) (Table 1) is not consistent with the results of Azam et al. (2016), who found that average radiance had a negative effect on the presence probability of this species at all considered landscape scales (200, 500, 700 or 1000 m). We hypothesize that in highly urbanized landscapes, *E. serotinus* is more light-tolerant than in more natural landscapes, with streetlights becoming sub-optimal foraging areas as there are few optimal foraging areas for the species in the study area (Stone et al. 2015). Such contradictory results highlight that the relationship between bat activity/presence and ALAN is complex and may be dependent on species, context and scale (Hale et al. 2012; Mathews et al. 2015; Azam et al. 2016).

Key landscape variables for bats in urban contexts

Distance to water represented the best predictor of the presence probability and activity of bats in our study area (Table 1). Bat distribution was mainly concentrated around wetlands (Fig. 5). Aquatic habitats such as canals and ponds are known to be a key factor in bat activity and distribution in urban areas (Straka et al. 2016). This is particularly true for *M. daubentonii* and *P. nathusii*, species that are adapted to aquatic habitats and forage on aquatic insects such as Diptera, Trichoptera and Ephemeroptera (Dietz et al. 2006; Krüger et al. 2014). While *E. serotinus* has a more generalist diet and foraging habits, the close relationship between areas of water and its distribution/activity found in our study may result from the fact that aquatic insects are more available than terrestrial insects in urban areas (Akasaka et al. 2009).

Variables associated with wooded vegetation also had positive significant effects on the activity of the three studied species (Table 1). In the literature, it is widely documented that wooded vegetation such as riparian vegetation, forest patches or hedges are key habitats for bats and have essential ecological and functional importance, providing commuting routes between roosts and foraging habitats, landmarks for orientation, protection against predators and wind, and roosting sites, as well as supporting higher insect densities in wetland areas (Boughey et al. 2011; Fonderflick et al. 2015).

The city centre of our study area was on the whole avoided by the studied species, which is consistent with previous studies (Gaisler et al. 1998; Russo and Ancillotto 2015). Dense urbanization inevitably reduces favourable habitats and wooded vegetation, impacting the richness and abundance of the bat community (Hale et al. 2012). The findings show that *P. nathusii* activity was higher in suburban areas than in the city centre, which is in line with several previous studies (Coleman and Barclay 2012; Luck et al. 2013). This might be explained by the intermediate disturbance hypothesis (Connell 2013), in which suburban conditions, halfway along a gradient from natural to urban habitat, produce 'optimal' intermediate levels of disturbance – in intensity and frequency – for a large number of species such as *P. nathusii* (Russo and Ancillotto 2015). *E. serotinus* is considered to be one of the most urban-tolerant species in Europe (Arthur and Lemaire 2009), which is consistent with the fact that it was the only species in our study with two suitable habitat patches in the city centre (apart from the banks of watercourses) (Fig. 5).

We found that landscape variables with significant effects on bats differ between presence probability and activity (Table 1). This suggests different functional and ecological relationships between the landscape and the movement and foraging behaviour of bats and confirms the relevance of our methodology.

Light reduction improves urban landscape connectivity

The effectiveness of the different light-reduction scenarios in improving landscape connectivity for

the studied species depended on (1) the spatial distribution of unlit areas (i.e. where light reduction is applied, see Online Appendix S3.1), (2) the initial radiance values in those areas before light reduction (Online Appendix S3.2), (3) the response curves of species presence probability to average radiance (Fig. 3), and (4) the predicted spatial distribution of bat species depending on their response to landscape variables (Fig. 5).

In comparison with *M. daubentonii*, *P. nathusii* had the widest spatial distribution (Fig. 5). Thus the effect of light-reduction scenarios was less dependent on the spatial distribution of unlit areas than on the initial radiance values and the species' response curves to average radiance (Fig. 3). For this species, the higher the initial radiance value of a given part of the landscape, the stronger the effect of light reduction in improving landscape connectivity for this species (Fig. 6 and Online Appendix S3.2). The four scenarios significantly improving landscape connectivity for *P. nathusii* have high initial radiance in the range of values where the species response is negative (Fig. 3), so reducing ALAN in those areas should improve landscape connectivity. However, reducing ALAN in municipalities of less than 10,000 inhabitants would decrease landscape connectivity because the initial mean radiance values in those areas is 10.2 $W.m^{-2}.sr^{-1}$, a value in a range where *P. nathusii* responds positively to radiance (Fig. 3, Online Appendix S3.2).

For *M. daubentonii*, every light-reduction scenario significantly improved landscape connectivity because of this species' general negative response to radiance (Fig. 6). *M. daubentonii* is a specialist gleaner bat species that is mostly present in wetlands, flies at low altitudes and depends on vegetation to commute. So the light-reduction scenarios for urban areas (1 and 2) were the least effective in improving connectivity for *M. daubentonii* simply because those areas are not used by this species. The next most effective scenarios to improve connectivity for this species were reducing ALAN in urban parks (third most effective) and wetlands (second most effective). Surprisingly, the most effective scenario to increase landscape connectivity for *M. daubentonii* was light reduction on main roads. We believe this is mostly due to the spatial distribution of the main roads in our study area (see Online Appendix S3.1), where these cross or are close to wetlands (ponds and canals) and urban parks. Reducing ALAN on main roads potentially improved the quality of wetlands and urban park habitats to a greater extent than light reduction solely on wetlands or solely on urban parks. But this result seems very context dependent and should be tested in other cities.

Our results indicate that modelling light-reduction scenarios can be a powerful tool to assess the potential effectiveness of future urban landscape planning and to guide policymaking. Planning that takes into account light pollution must of course be driven by a trade-off between biodiversity conservation priorities and social/political acceptability (aesthetics, safety, outdoor night-time activities, etc.). For instance, light-reduction measures are likely to be better accepted by inhabitants in small zones around watercourses than in large areas in city centres. Moreover, our findings show that light-reduction scenarios over large areas are not necessarily the most effective in improving connectivity for bats; in any case, the part of the landscape to best apply light reduction is not always the same for each species. For a given context, it is important to clarify the best combination of factors between light reduction/extinction scenarios, the total surface area, the spatial distribution of the species (a few large areas or many small areas), the priority habitats and the intensity of light reduction in order to optimize the conservation measure, as well as considering the social/political acceptability in urban landscapes.

Methodological approaches

To our knowledge, this is the first study based on this specific methodology: using a random stratified design with 399 full-night recording points in a highly urbanized context. We advocate the use of this methodology for future studies aiming to identify landscape corridors. While our data is not movement data per se, as the individuals were recorded in movement we have assumed that an LCP modelling approach remained relevant for our case. We only used presence probability to define landscape resistance despite the fact that this last necessarily impacts both occurrence and activity. The activity is a measure with a very high variability, the highest values being the foraging and roosting areas. A high activity value therefore means a low resistance but a low activity value does not necessarily mean a low resistance

because a bat commuting area may have low activity values relative to foraging areas. So it is conservative to only take the occurrence that means at least one bat can fly through. This is still quite coarse, but we argue that is the best we can do with this kind of data in regard to the study's objectives. The results, though, would benefit from comparison with movement data obtained by radio-telemetry or miniaturized GPS tags (Stevenson-Holt et al. 2014; LaPoint et al. 2015), which have recently been adapted for microchiropteran species (Weller et al. 2016).

We used light data from satellite pictures that are not very accurate which could question their ecological relevance for point recordings of bat. Despite this low accuracy, we found strong relations between light and bat presence/activity which make our results very conservative. Furthermore, a very bright pixel because of the presence of just one light source will have an effect far beyond the light source, namely the light halo phenomena. This is likely why light generates a ''filter'' at landscape scale that alters the movement behaviors and activity of bats (Hale et al. 2015; Azam et al. 2016). Indeed some bats are able to forage around streetlights (positive effect at local scale) such as *P. pipistrellus,* considered as a very light-tolerant species, although at landscape scales light influence negatively the activity and the landscape connectivity of this same species (Hale et al. 2015; Azam et al. 2016). Previous studies suggest that light negatively influence the commuting and dispersal movements at larger scales (i.e. landscape scale) than variables affecting foraging success (Jackson and Fahrig 2014; Azam et al. 2016; Miguet et al. 2016). Thus, we argue that the light data used in the present study were relevant for our objectives.

This study modelled the functional connectivity between the most important foraging sites (in regard to bat activity levels). Functional connectivity between foraging sites is relevant for conservation as it is well known that bats use several foraging sites per night (Arthur and Lemaire 2009; Dietz et al. 2009). Nonetheless, we strongly recommend, in cities where there is sufficient knowledge of roost locations, using this methodology to model the connectivity between roosts and foraging areas, as this is critical to ensuring the survival of populations (Fischer and Lindenmayer 2007).

Conclusion

Our results found that ALAN has a preponderant impact on some bat species in an urban landscape, and that light reduction improves landscape connectivity from semi-natural habitats such as urban parks or wetlands to city centres. The findings provide important details that could be used to inform future urban conservation strategies: the effectiveness of each light-reduction scenario varied and seems to depend on the ecological plasticity and requirements of each species. Furthermore, light reduction would not be totally effective without the presence of landscapes that are vital for bats such as wetlands and wooded vegetation, whatever the surface area or the initial intensity of light pollution. As the studied species responded significantly to ALAN at different scales, it is critically important to build large nocturnal corridors in order to optimize the efficacy of light-reduction measures.

Acknowledgements We thank Yohan Tison from "La Ville de Lille", Sophie Wrobel and Claire Poitout from "Espaces Naturels Lille Métropole", Matthieu Lageard from « Biotope » , Jean-François Julien and Alexandre Haquart for their field assistance, equipment lending and with acoustic identification. The project "TRAME NOIRE" was funded by the "conseil regional Nord-Pas-de-Calais" and by "Fondation pour la recherche sur la biodiversité".

References

Akaike H (1974) A new look at the statistical model identification. Autom Control IEEE Trans 19:716–723

Akasaka T, Nakano D, Nakamura F (2009) Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (Myotis daubentonii) in the Shibetsu River, a large lowland river in Japan. Biol Conserv 142:1302–1310.

Arthur L, Lemaire M (2009) Les chauves-souris de France. Belgique, Luxemb Suisse

Azam C, Kerbiriou C, Vernet A, Julien JF, Bas Y, Plichard L, Maratrat J, Le Viol I (2015) Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? Glob Chang Biol 21:4333–4341

Azam C, Le Viol I, Julien JF, Bas Y, Kerbiriou C (2016) Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. Landscape Ecol 53:1694–1703

Barataud M, Tupinier Y, Limpens H, Cockle-Betian A (2015) Acoustic ecology of European bats: species identification, study of their habitats and foraging behaviour. 352

Bas Y, Escallon A, Ferre M, Haquart A, Rufray V, Disca T, Julien JF (2013) Automatic echolocation call identification in Europe vs. the Neotropics: more species does not mean more difficult. XVI Int Bat Res Conf San Jose, Costa Rica

Baugh K, Hsu FC, Elvidge C, Zhizhin M (2013) Nighttime lights compositing using the VIIRS day-night band: preliminary results. Proc Asia-Pacific Adv Netw 35:70–86

Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. Conserv Biol 22:836–851.

Boughey KL, Lake IR, Haysom KA, Dolman PM (2011) Improving the biodiversity benefits of hedgerows: how physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. Biol Conserv 144:1790–1798.

Brad H. McRae and D. M. Kavanagh. (2011) Linkage Mapper Connectivity Analysis Software. 1–22. https://doi.org/10.1002/ejoc.201200111

Burt J (2006) Syrinx, Version 2.6h. University of Washington, Seattle, USA

Coleman JL, Barclay RMR (2012) Urbanization and the abundance and diversity of Prairie bats. Urban Ecosyst 15:87–102.

Connell JH (2013) Diversity in Tropical Rain Forests and Coral Reefs. Science 199:1302–1310

Dietz M, Encarnação JA, Kalko EKV (2006) Small scale distribution patterns of female and male Daubenton' s bats (Myotis daubentonii) Small scale distribution patterns of female and male Daubenton' s bats (Myotis daubentonii). Acta Chiropterologica 8:403–415.

Dietz C, von Helversen O, Nill D (2009) L'encyclopédie des chauves-souris d'Europe et d'Afrique du Nord: biologie, caractéristiques, protection. Delachaux et Niestlé

Dutilleul S (2009) Plan Régional de Restauration des Chiroptères du Nord-Pas-de-Calais: Période 2009-2013. Coord Mammal du Nord la Fr 95

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Townsend AP, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Sobero´n J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography (Cop) 29:129–151

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697.

Erickson JL, West SD (2002) The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17–24.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Glob Ecol Biogeogr 16:265–280.

FitzGibbon S, Putland D, Goldizen A (2007) The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. Landscape Ecol 22:1513–1525.

Fonderflick J, Azam C, Brochier C, Cosson E, Quékenborn D (2015) Testing the relevance of using spatial modeling to predict foraging habitat suitability around bat maternity: a case study in Mediterranean landscape. Biol Conserv 192:120–129

Frey-Ehrenbold A, Bontadina F, Arlettaz R, Obrist MK (2013) Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. J Appl Ecol 50:252–261.

Gaisler J, Zukal J, Rehak Z, Homolka M (1998) Habitat preference and fight activity of bats in a city. J Zool 244:439–445

Gaston KJ, Duffy, JP, Gaston S, Bennie J, Davies TW (2014) Human alteration of natural light cycles: causes and ecological consequences. Oecologia 176:917–931

Gaston KJ, Visser ME, Hölker F (2015) The biological impacts of artificial light at night: the research challenge. Philos Trans R Soc Lond B 370:20140133.

Grimm NB, Foster D, Groffman P, Grove JM, Hopkinson CS, Nadelhoffer KJ, Pataki DE, Peters DPC (2008) The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. Front Ecol Environ 6:264–272

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009.

Hale JD, Fairbrass AJ, Matthews TJ, Sadler JP (2012) Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large uk conurbation. PLoS ONE 7:e33300.

Hale JD, Fairbrass AJ, Matthews TJ, Davies G, Sadler JP (2015) The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. Glob Chang Biol 21:2467–2478

Haquart A (2013) Référentiel d'activité des chiroptères—Eléments pour l'interprétation des dénombrements de chiroptères avec les méthodes acoustiques en zone méditerranéenne française. Biotope, Ec Prat des Hautes Etudes, p 99

Hastie TJ, Tibshirani RJ (1990) Generalized additive models, volume 43 of Monographs on Statistics and Applied Probability. CRC Press, Boca Raton

Hölker F, Wolter C, Perkin EK, Tockner K (2010) Light pollution as a biodiversity threat. Trends Ecol Evol 25:681–682.

Ives AR, Klopper ED (1997) Spatial variation in abundance created by stochastic temporal variation. Ecology 78:1907–1913.

Jackson ND, Fahrig L (2014) Landscape context affects genetic diversity at a much larger spatial extent than population abundance. Ecology 95:871–881.

Krüger F, Clare EL, Symondson WO, Keišs O, Pētersons G (2014) Diet of the insectivorous bat Pipistrellus nathusii during autumn migration and summer residence. Mol Ecol 23:3672–3683

Kuijper DP, Schut J, van Dullemen D, Toorman H, Goossens N, Ouwehand J, Limpens HJGA (2008) Experimental evidence of light disturbance along the commuting routes of pond bats (Myotis dasycneme). Lutra 51:37–49

Kyba CCM, Kuester T, Sánchez de Miguel A, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge CD, Gaston KJ, Guanter L (2017) Artificially lit surface of Earth at night increasing in radiance and extent. Sci Adv 3:e1701528

Lacoeuilhe A, Machon N, Le Bocq A, Kerbiriou C (2014) The influence of low intensities of light pollution on bat communities in a semi-natural context. Plos ONE 9:103042.

LaPoint S, Balkenhol N, Hale J, Sadler J, Ree R (2015) Ecological connectivity research in urban areas. Funct Ecol 29:868–878

LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in midwestern North America using least-cost path methods. Ecol Modell 212:372–381.

Luck GW, Smallbone L, Threlfall C, Law B (2013) Patterns in bat functional guilds across multiple urban centres in south-eastern Australia. Landscape Ecol 28:455–469.

Mathews F, Roche N, Aughney T, Jones N, Day J, Baker J, Langton S (2015) Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. Philos Trans R Soc B 370:20140124–20140124

McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecol 23:1143–1155.

Mickleburgh SP, Hutson AM, Racey PA (2002) A review of the global conservation status of bats Major threats. Oryx 36:18–34.

Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? Landscape Ecol 31:1177–1194

Miller BW (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. Acta Chiropterol 3:93–105

Roever CL, Van Aarde RJ, Leggett K (2012) Functional responses in the habitat selection of a generalist mega-herbivore, the African savannah elephant. Ecography (Cop) 35:972–982

Russo D, Ancillotto L (2015) Sensitivity of bats to urbanization: a review. Mamm Biol 80:205–212.

Rydell J (1991) Seasonal use of illuminated areas by foraging northern bats Eptesicus nilssoni. Holarct Ecol 14:203–207

Stevenson-Holt CD, Watts K, Bellamy CC, Nevin OT, Ramsey AD (2014) Defining landscape resistance values in least-cost connectivity models for the invasive grey squirrel: A comparison of approaches using expert-opinion and habitat suitability modelling. PLoS ONE 9:e112119

Stone EL, Harris S, Jones G (2015) Impacts of artificial lighting on bats: a review of challenges and solutions. Mamm Biol 80:213–219.

Stone EL, Jones G, Harris S (2009) Street lighting disturbs commuting bats. Curr Biol 19:1123–1127.

Stone EL, Jones G, Harris S (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. Glob Chang Biol 18:2458–2465.

Straka TM, Lentini PE, Lumsden LF, Wintle BA, van der Ree R (2016) Urban bat communities are affected by wetland size, quality, and pollution levels. Ecol Evol 6:4761–4774

Taylor PD, Fahrig L, With KA (2006) Landscape connectivity: a return to the basics. Conserv Biol Ser 14:29

Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Tsao JY, Saunders HD, Creighton JR, Coltrin ME, Simmons JA (2010) Solid-state lighting: an energy-economics perspective. J Phys D Appl Phys 43:354001

Urban D, Keitt T (2010) Landscape connectivity: a Graph-theoretic perspective. Ecology 82:1205–1218

Watts K, Eycott AE, Handley P, Ray D, Humphrey JW, Quine CP (2010) Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecol 25:1305–1318

Weller TJ, Castle KT, Liechti F, Hein CD, Schirmacher MR, Cryan PM (2016) First direct evidence of long-distance seasonal movements and hibernation in a migratory bat. Sci Rep 6:34585

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) In Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W (eds) Mixed effects models and extensions in ecology with R. Springer, New York