

12. Annexes et valorisations scientifiques

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Landscape-dependent effects of artificial light on bat activity

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Level of knowledge about artificial light effects on bats



Large scale

Global responses



Intermediate scale

Connectivity
Global responses

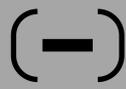


Local scale

Disorientation
Attraction/revulsion
Light characteristics
Barrier effects



Known effects

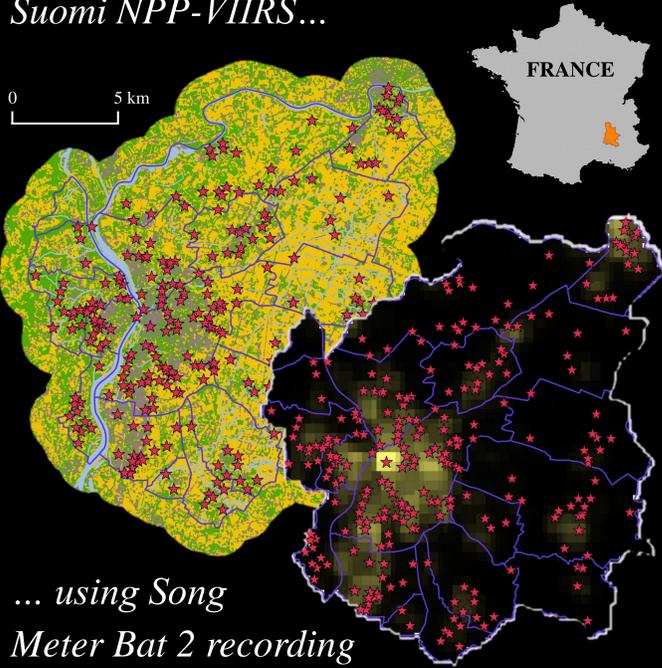


1) Poorly studied scale in term of global responses to artificial light

2) What about the spatial variation of effects in relation with landscape composition?

Sampling design

254 sampling sites stratified considering 3 land-use types (% of forests, % of impervious surfaces and distance to wetlands) and the radiance from the Suomi NPP-VIIRS...



... using Song Meter Bat 2 recording simultaneously 10 sites per night with various landscape compositions in June 2017

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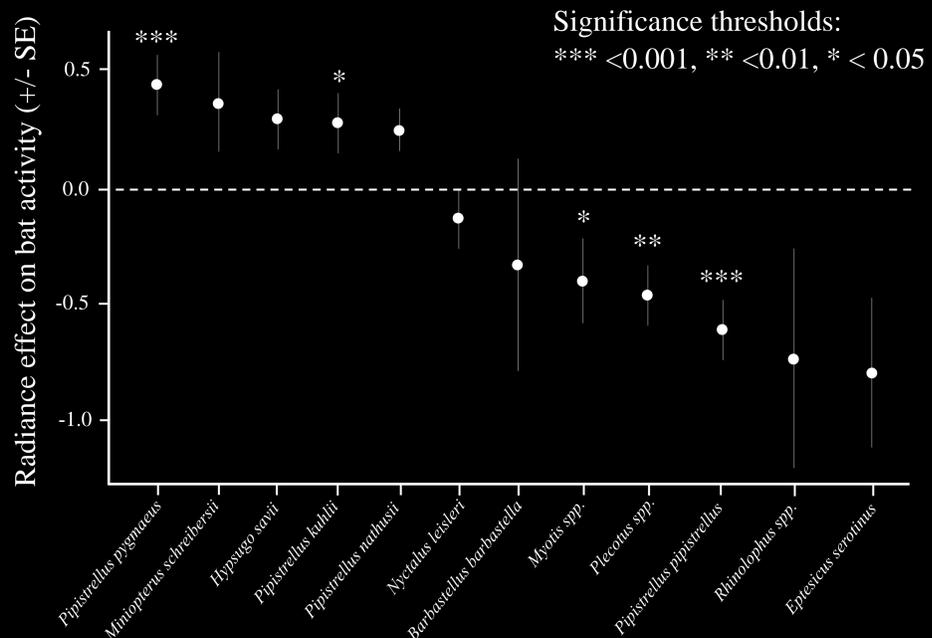
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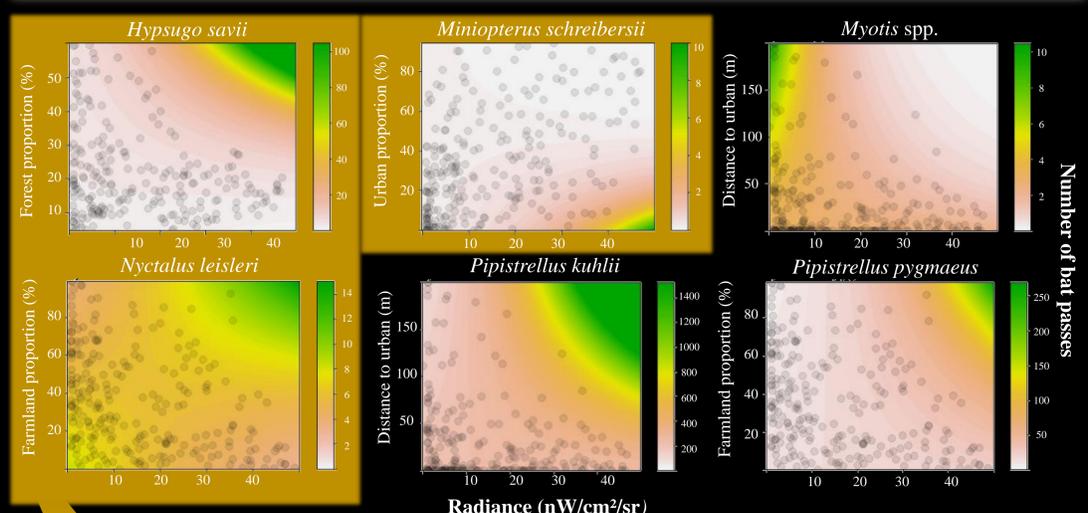
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Results



Interactions with the landscape composition



10 significant interactions (6 presented)

Some non-significant average effects* are hidden in landscape interactions, occurring only in given landscape compositions

Artificial light may change flight patterns of bats near bridges along urban waterways

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Keywords

acoustic localisation; artificial light; Chiroptera; ecological corridor; flight behaviour; light pollution; microphone array; rivers.

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Abstract

Artificial light at night (ALAN) is considered as a major threat to biodiversity, especially to nocturnal species, as it reduces availability, quality and functionality of habitats. However, its effects on the way species use landscape elements such as rivers are still largely understudied, especially the effect of crossing infrastructure lighting on bridges. These elements are nevertheless key commuting and foraging habitats in heavily urbanised landscapes for several taxa such as bats that are particularly affected by ALAN. We studied the effects of the illumination of facades and undersides of bridges on the relative abundance of pipistrelle bats, on their 3D distribution and their behavioural response (i.e. flight speed) close to bridges. We set-up an innovative approach based on a microphone-array to reconstruct positions and flight trajectories in 3D. We studied the effect of lighting on bats in the close proximity of six similar bridges, mostly differentiated by the presence or absence of lighting (3 lit and 3 unlit). All bridges cross the same waterway, within a uniformly and highly urbanized agglomeration (Toulouse, France). We found that bat activity was 1.7 times lower in lit sites. Bats tended to keep a larger distance, and to fly faster close to illuminated bridges. These results suggest that bridge lighting strongly reduces habitat availability and likely connectivity for bats. In that case, results call for switching off the illumination of such bridges crossing riverine ecosystems to preserve their functionality as habitats and corridors for bats.

Introduction

Among the most prevalent sources of change in biodiversity state, Artificial Light At Night (ALAN) is increasingly recognized as a new threat (Koen *et al.*, 2018). ALAN impacts a wide range of taxa, from individual physiological response to ecosystem functioning, interactions between species and regulatory processes (Hölker *et al.*, 2010; Knop *et al.*, 2017; Bennie *et al.*, 2018; Salinas-Ramos *et al.*, 2020) at many

spatiotemporal scales (Altermatt & Ebert, 2016; Gaston *et al.*, 2017).

ALAN particularly affects nocturnal species such as bats. ALAN affects the availability, quality and functionality of habitats for bats, by changing environmental conditions in which bats interact with other taxa at different spatial scales: their prey, their predators and likely their competitors (Jones & Rydell, 1994; Minnaar *et al.*, 2015; Cravens *et al.*, 2017; Russo *et al.*, 2019). First of all, it affects the abundance and

the distribution of their prey, (i) by massively attracting insects around light sources at the streetlight scale (ii) and by inducing a suspected vacuum cleaner effect in the surrounding dark areas (Eisenbeis, 2006; Perkin *et al.*, 2014). ALAN also induces mortality and changes in community composition of insects (Davies *et al.*, 2012) in such a way that ALAN is suggested to be a major driver of large scale decline in insects' populations (Frank, 1988; Fox, 2013) and consequently in bat prey availability. By illuminating the scene, ALAN is also suggested to increase predation risk of bats by owls and other raptors (Jones & Rydell, 1994), and in turn bats increase their flight speed (Polak *et al.*, 2011). Bat species respond differently to these changes in interactions with other taxa according to their flight type. Slow-flying species adapted to forage on insects in cluttered vegetation, such as *Myotis* spp., *Plecotus* spp. and *Rhinolophus* spp. avoid lit areas (Azam *et al.*, 2015; Zeale *et al.*, 2018), while fast-flying species adapted to hunt insects in open space, such as *Pipistrellus* spp., may appear to benefit locally from the aggregated prey resources around streetlight (Rydell, 1992; Azam *et al.*, 2015), although at a wider scale, ALAN negatively impacts their relative abundance (Azam *et al.*, 2016; Pauwels *et al.*, 2019).

By reducing habitat availability and quality, ALAN was also suggested to decrease the functional connectivity of landscapes for bats (Laforge *et al.*, 2019) and can have dramatic impacts on their relative abundance at a larger scale (Azam *et al.*, 2016; Pauwels *et al.*, 2019). Linear landscape elements such as hedgerows and rivers play an essential role for bats commuting between roosts and foraging patches (Smith & Racey, 2008; Akasaka *et al.*, 2012; Lacoëuilhe *et al.*, 2016; Pinaud *et al.*, 2018). Such landscape elements also provide dark corridors in dimly lighted situations (full moon or distant lighting) (Zeale *et al.*, 2018; Ancillotto *et al.*, 2019) and are specifically important in illuminated urban landscape. ALAN is nevertheless worldwide increasing, in particular close to protected areas and biodiversity hotspots (Guetté *et al.*, 2018), for security, use or aesthetic reasons. This lighting hinders bats when crossing gaps in wooded linear corridors (Hale *et al.*, 2015) and reduces the number of bat commuting along hedgerows (Zeale *et al.*, 2018). Among linear landscape elements, riverine ecosystems are key habitats for bats. Their riparian vegetation and water surface are important foraging areas for many bat species and are recognized as determinants to explain bat abundance across the landscape (Grindal *et al.*, 1999; Downs & Racey, 2006; Lloyd *et al.*, 2006; Lookingbill *et al.*, 2010; Sirami *et al.*, 2013; Carrasco-Rueda & Loiselle, 2019). In highly urbanized areas rivers or waterways and their associated riparian vegetation are often the only corridors still relatively dark, and are thus of high importance for bat moving through such illuminated landscapes (Lintott *et al.*, 2015; Laforge *et al.*, 2019; Todd & Williamson, 2019). However, ecological consequences of the illumination of rivers remain largely understudied (Jechow & Hölker, 2019). Only one study to our knowledge investigated the effect of ALAN on commuting bats by recording Daubenton's bats (*Myotis daubentonii*) passing through culverts. In this study, the bat

activity was found to be unaffected by the presence of light (Spoelstra *et al.*, 2018). However, another study showed that most bat species, including *Myotis* species, significantly reduced their number of drinking and activity above water in presence of artificial light (Russo *et al.*, 2017, 2018, 2019). However, studying bats using such activity metrics from acoustic recordings does not inform on all behavioural changes (e.g. flight speed, spatial position). The development of microphone arrays allows high-resolution localization of bats using their echolocation calls, and hence tracking the animal's movement (Koblitz, 2018). Precise tracking of bats appears as an innovative and a promising method for assessing poorly studied impacts of light on flight behaviour, such as flight speed and changes in flight path.

Here, we aim to assess how the illumination of bridges over waterways affects bat activity and their flight behaviour along riverine ecosystems. We studied six bridges above a waterway in a highly urbanized area to assess the impact of facade and underbridge lighting on bats. In addition to activity measurements, we used a microphone-array to record bat positions to construct 3D bat flight trajectories in order to calculate flight speeds. When approaching a lighted structure across a riverine ecosystem, we hypothesize that bats have to deal with a trade-off that includes the benefits of foraging and commuting along this corridor, and the drawback of increased predation risk by exposure to light. In the case of bats limit the risk of exposure to light (Jones & Rydell, 1994; Russo *et al.*, 2018), we predict a decrease in passing bats through light cone and in approaches of individuals to lit bridges. Light sources at riverine ecosystems could therefore form a barrier for moving along it (Hale *et al.*, 2015). In case bats do fly through light cone, they possibly try to minimize the risk of predation by increasing their flight speed (Polak *et al.*, 2011).

Material and methods

Study sites

We carried out the study on three lit and three unlit bridges. These six bridges were across two branches of a waterway with a comparable width (around 30 m) and stagnant water (i.e. low current), at the centre of a highly urbanized area (in the city of Toulouse, France, N 43.60 E 1.43; Fig. S1). Among bridges studied, four were road bridges (two lit and two unlit) and two were footbridges (one lit and one unlit). Bridges were chosen such that these were comparable in shape (height and width; Table 1 & Fig. S1) and surrounding vegetation (Fig. S1). The lit bridges have been illuminated for many years, with all-year lighting of the facade and underside from the sunset until 1:00 a.m., while unlit bridges had no illumination at all (Fig. S1). Since all the sites were located in very dense urban areas, we assumed that background light from the surrounding city was comparable for all sites. Lit sites were on average exposed to twice as much light than unlit sites: respectively 7.4 ± 1.4 lux for lit sites and 3.6 ± 1.6 lux for unlit sites (Table 1; see Supporting information S1 for details about light measurements).

Table 1 Summary per site of study sites characteristics, sampling design and bat survey results.

Sites	Date	Lighting treatment	Bridge type (height – width in meters)	Array-bridge distance (m)	Light intensity \pm SD (Lux)	Number of 3D positions	Number of 5 seconds bat passes (buzzes)	Average bat-bridge distance \pm SD (m)	Average flight speed \pm SD (m/s)	Average imprecision on positions \pm SD (cm)
1	19/06/2018	Lit	Road bridge (7.2 – 29.7)	16.2	9.1 \pm 8.8	107	144 (0)	15.7 \pm 1.8	8.2 \pm 1.3	54.1 \pm 27.0
2	21/06/2018	Lit	Road bridge (5.5 – 17.8)	11.7	7.9 \pm 8.2	26	106 (0)	10.7 \pm 1.8	6.8 \pm 2.0	48.2 \pm 22.9
3	24/06/2018	Lit	Footbridge (6.0 – 2.5)	10.5	5.3 \pm 3.6	18	136 (0)	12.6 \pm 1.5	8.5 \pm 1.3	54.5 \pm 22.0
4	20/06/2018	Unlit	Road bridge (5.7 – 22.8)	8.5	4.7 \pm 8.8	779	179 (3)	7.1 \pm 2.9	6.5 \pm 2.3	16.0 \pm 13.8
5	22/06/2018	Unlit	Road bridge (6.5 – 29.3)	10.5	4.9 \pm 4.1	263	253 (10)	10.0 \pm 2.1	5.7 \pm 2.0	59.2 \pm 27.7
6	25/06/2018	Unlit	Footbridge (6.2 – 2.6)	6.0	1.2 \pm 0.3	994	212 (8)	5.7 \pm 3.6	6.3 \pm 2.4	12.3 \pm 14.3
1 + 2+3	/	Lit	/	14.7	7.4 \pm 1.4	151	386	14.5 \pm 2.7	8.1 \pm 1.5	53.1 \pm 25.8
4 + 5+6	/	Unlit	/	7.5	3.6 \pm 1.6	2036	644	6.8 \pm 3.5	6.3 \pm 2.3	19.8 \pm 22.5

Sampling design and 3D acoustic tracking

We studied the effect of bridge-illumination on bat activity, bat-bridge distance and associated flight speed, through comparisons between lit and unlit sites. We therefore recorded and localized bats in three dimensions on the three first hours starting from sunset during 6 consecutive nights between the 19 and 25 June 2018 (Koblitz, 2018). Weather conditions were highly stable and optimal throughout this sampling period (average temperature: 24.5 \pm 1.5 °C, average wind: 3.3 \pm 1.1 m/s, no rain and no cloud; Table S1). Between consecutive nights, we alternated each night sampling near lit and unlit bridges.

To sample bats, we used an acoustic localization system (hereafter named microphone array) designed at the Institut Langevin by Ros Kiri Ing (see Supporting Information S2 for more details about the system) (Ing *et al.*, 2016), with a detection radius of about 20 m. Arrays were placed as close as possible to the bridge where the nature of the ground allowed to install the microphone array (i.e. 16.2, 11.7 and 10.5 m from lit bridges, and 10.5, 8.5 and 6 m from unlit bridges). Consequently, the microphone array was placed at the same distance from bridges for only one pair of lit/unlit bridges (i.e. 10.5 m). We accounted for these differences in array-bridge distances in statistical analysis (see statistical analysis section).

Each position of bats was reconstructed in 3D using time differences of arrival (TDOA) (Koblitz, 2018) of one echolocation call following the Ing *et al.* (2016) approach. While relatively seldom used for bat studies, this innovative approach of acoustic localisation has already proven its worth (Polak *et al.*, 2011; Ing *et al.*, 2016; Koblitz, 2018; Götze *et al.*, 2020). We chose to discard positions with a cumulated imprecision greater than one meter on the three dimensions (i.e. the sum of the imprecision on each dimension). Spatial location of bats around the microphone array

then allowed the computation of the distance of each emitted bat call to the bridge (see Supporting information S3 for more details on calculation). We then computed flight speed (Equation 1) as follows:

$$V_i = \frac{\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2 + (z_i - z_j)^2}}{t_i - t_j} \quad (1)$$

where x , y and z represent distances to the microphone array for each of the three-dimension axis, and t is the time of call arrival to the microphone array of a given position i and its previous position j (see Supporting information S3 for more details).

Although the number of sampled sites was low due to technical constraints, the method using the microphone array allowed to measure a high number of positions with high precisions.

Assigning species to 3D positions and quantification of the number of passing bats

The microphone array continuously recorded the echolocation calls of passing bats which were stored in sound files (Ing *et al.*, 2016). These files were divided in five-second files, a sufficient interval for the average duration of a bat pass (Kerbirou *et al.*, 2019). Hereafter, a bat pass was thus defined as a single or several echolocation calls within a five-second interval. Only 0.6% of 5-second recordings contained more than one individual. Each five-second file was classified to the closest taxonomic level using Tadarida software (Bas *et al.*, 2017). We also visually inspected sound files for feeding buzzes during each bat pass, i.e. rapid sequences of short linear calls before the prey capture.

Because the identification at the species level can be problematic, we limited identification level to the species group. We limited further analysis to the *Pipistrellus* group, which includes *Pipistrellus kuhlii*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *Pipistrellus nathusii*. The other bat species groups were absent or showed only a couple of passes preventing any analyses. We subsequently linked the 3D bat position calculated for each call to the species group assigned to it by Tadarida. See Supporting information S4 and R script for more details about automated identification and assigning species to 3D positions.

Statistical analysis

We first compared bat activity between lit and unlit sites, using the number of bat passes instead of the number of bat positions, because increasing flight speed reduces the number and the precision of positions (Table 1).

To test for potential difference of bat-bridge distances between unlit and lit bridge sites, we built a Linear Mixed Model (LMM, R package *TMB*) using the bat-bridge distance as the response variable following a Gaussian error distribution (Fig. 1), and the lighting treatment (i.e. lit or unlit bridge), the array-bridge distance, the square of the array-bridge distance, and the interaction between both array-bridge distance variables and the lighting treatment as fixed explanatory variables. We used the array-bridge distance as a covariate because lit sites were sampled on average slightly closer to bridges than unlit sites due to field constraints (Table 1; Fig. S2). We included the site as a random effect in models to account for the spatial-temporal structure of the sampling design of recordings (i.e. several recordings per site, one site sampled per night).

We then tested whether flight speed changed according to the distance to light. We performed LMM using the flight speed as the response variable associated with a Gaussian error distribution (Fig. S3), the lighting treatment (i.e. lit or unlit bridge), the array-bridge distance, the bat-bridge distance (i.e. for every position for which a flight speed was computed), the square of the bat-bridge distance as fixed explanatory variables. The square of the bat-bridge distance was included as explanatory variable after visual inspection of their non-linear nature in a Generalized Additive Mixed Model using the *gamm* function (R package *mgcv*). As flight speed is expected to vary with lighting (Polak *et al.*, 2011), we also included two interaction terms between the bat-bridge distance, respectively the square of the bat-bridge distance, and the lighting treatment (i.e. lit or unlit bridge). Since flight speed was computed for positions which were part of bat individual trajectories composed of several positions (see Supporting Information S2 for trajectory reconstruction), we accounted for this individual nesting by adding a random effect on the trajectory identity. We also included the site as a second random effect. Given that imprecisions of positions were positively correlated with their distance to the microphone array and the flight speed (Pearson correlation tests: $t = 18.5$, $df = 2185$, $p\text{-value} < 0.001$ and

$t = 17.2$, $df = 1349$, $p\text{-value} < 0.001$, respectively), we gave to the response variable different weights according to their associated precision by adding a weight term in LMMs (i.e. one per imprecision squared; Penone *et al.*, 2013). We then selected for models with the lowest AIC values, and with VIF values lower than 2 to avoid collinearity issues (Zuur *et al.*, 2010). We re-ran this model for road and footbridges separately to assess the potential dependence of results to the type of bridge. Finally, because the microphone array was placed at the same distance from bridges for only one pair of lit/unlit bridges (i.e. 10.5 m), we focused a last model only on positions that were located between 10.4 and 13.5 m from bridges, that is, that corresponded to the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges (see right panel of the Fig. 1). This model was identical to the previous ones but without the bat and array-bridge distance variables as it only focuses on a restricted range of distances, where there is maximum confidence in the results by limiting the array-bridge distance bias.

Finally, it was not technically possible to measure light intensity with sufficient precision for each bat position due to the presence of the waterway. We therefore used the bat-bridge distance variable assuming it could be a good proxy due to the relationship between the light intensity and the distance to light. All analyses were performed using a significance threshold of 5% in the R statistical software (R Core Team, 2018).

Results

We recorded 644 bat passes of *Pipistrellus* spp. at unlit sites (respectively 179, 212, 253 bat passes per site) while only 386 at lit sites (respectively 106, 136, 144 bat passes per site; Table 1), that is, 1.7 times less bat passes at lit compared to unlit sites. We also recorded four passes of *Myotis* spp. and 12 passes of *Nyctalus* spp. The *Pipistrellus* group was composed of 73.1% *Pipistrellus kuhlii/nathusii*, 26.4% *Pipistrellus pipistrellus* and 0.5% *Pipistrellus pygmaeus*. *Pipistrellus* spp. emitted in total 21 feeding buzzes (i.e. during 2% of all passes), all at unlit sites (Table 1). We also recorded more 3D bat position at unlit sites (i.e. 2036) than at lit sites (i.e. 151) (Table 1).

Bat positions were located significantly closer to unlit bridges than lit bridges (Table 2). At the 10.5 m array-bridge distance at which unlit and lit sites were both sampled, bats were in average 1.6 m closer to unlit bridges than to lit bridges (Fig. 1). This difference tends to become higher when sites are sampled closer to bridges (Fig. 1). Bats never approached lit bridges closer than 7.9 m while for unlit bridges they regularly flew along, over or under bridges (Fig. 2).

Bats were overall flying significantly faster in nearby lit bridges compared to unlit bridges. Flight speeds were for example 8.7 m/s for lit sites and 6.5 m/s for unlit sites on average within the range of distances between 10.4 and 13.5 m from bridges (i.e. the range including an overlap of 95% between bat positions from lit and bat positions from

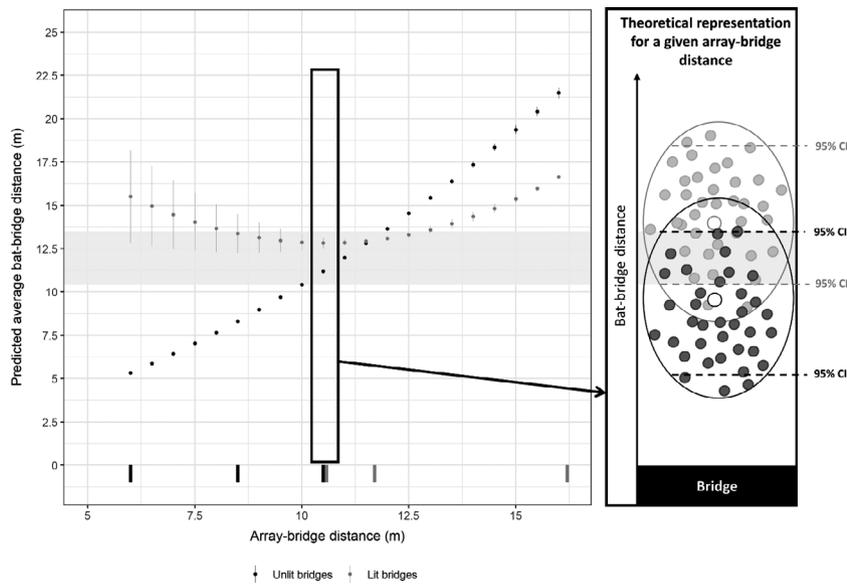


Figure 1 Predicted average bat-bridge distances in unlit and lit sites according to the array-bridge distance of sampling. This interaction comes from the linear mixed model presented in Table 2. Vertical bars at the bottom show the three array-bridge distances sampled in unlit sites (black), and the three sampled in lit sites (grey). The representation on the right panel shows a theoretical top-view of bat localisations (filled circles) and average bat localisation (blank circles) according to the lighting type of bridges, and shown for the array-bridge distance of 10.5 m shared by two sampling sites. The light grey rectangles show the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges.

unlit bridges; Table 2; Fig. 2). The relationship between the flight speed and the bat-bridge distance was thus found to strongly differ between unlit and lit bridges (Table 2; Fig. 2). Flight speed was found to significantly decrease when bats approached unlit bridges, while we found significant increasing of speeds when bats approached lit bridges (Table 2; Fig. 2). The array-bridge distance was not found to significantly influence results about flight speeds (Table 2). Finally, bats responded the same to footbridges and road bridges (Figs. S4 & S5), the results were thus independent of differences in usage, structure and lighting way.

Discussion

Results show that compared to unlit bridges, bats approaching illuminated bridges kept a greater distance, were less abundant, and increased flight speed instead of slowing down. Although these results have to be taken with cautious given the number of sampled sites (i.e. 6 bridges) due to technical constraints, we think we can be confident in their accuracy thanks to the innovative approach of 3D acoustic localisation which allowed to measure a high number of positions (i.e. 2 187) with high precisions (i.e. 22.1 ± 24.2 cm). In addition, we cannot exclude an effect of particular conditions in samples correlated to lit-unlit characteristics of sites. However, the sampling was designed to control for environmental conditions by selecting sites as similar as possible, and we found a bat activity always higher at unlit sites (i.e. 179, 212, 253 bat passes per site) than at lit sites (i.e. 106, 136, 144). Further studies with a

higher sample size to limit potential effects of inherent site characteristics would therefore be necessary to confirm our results.

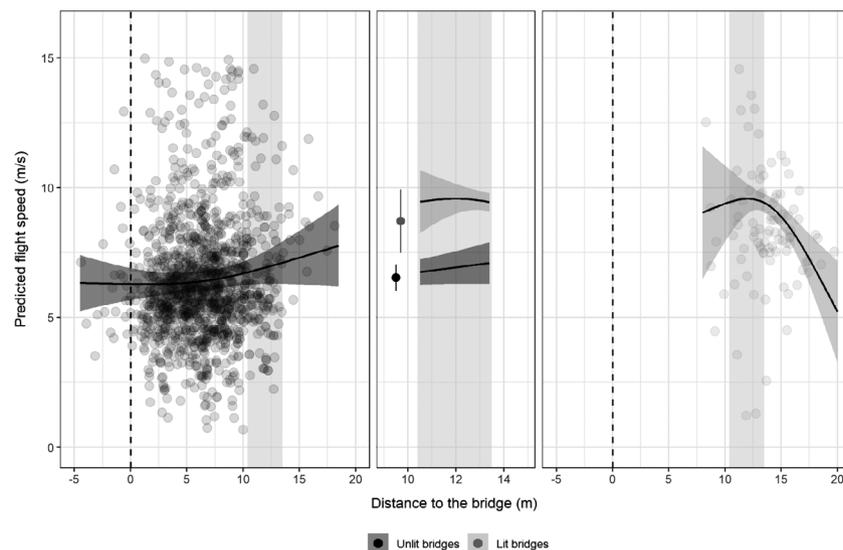
These results are also consistent with previous studies showing that for this group (i.e. *Pipistrellus* species), light at night can result in a decrease of bat activity (Azam *et al.*, 2016), can limit the presence of feeding buzzes (Kerbiouri *et al.*, 2020), reduces the crossing probability of gaps in wooded corridors within a city (Hale *et al.*, 2015), and that flight speeds are much higher in presence of light (Polak *et al.*, 2011).

Given the high importance of riverine corridors for bats in urbanized areas with little green spaces (Lintott *et al.*, 2015), our results suggest that bridge lighting reduces bat activity in an important habitat and could potentially constitute a barrier for moving along waterways by preventing individuals from approaching and crossing bridges, and hence affect the functional connectivity for bats in urban landscapes (Laforge *et al.*, 2019; Pauwels *et al.*, 2019).

The considerably lower number of bat passes found near illuminated bridges, and the increase in flight speed in response to light is particularly interesting as *Pipistrellus* species are commonly considered as light-tolerant when studied at a similar spatial scale (Azam *et al.*, 2015; Spoelstra *et al.*, 2017; Azam *et al.*, 2018; Zeale *et al.*, 2018). Indeed, as light sources used for street lighting massively attract insects (Wakefield *et al.*, 2016), *Pipistrellus* species often increase foraging activity around these and reduce their flight speed (Grodzinski *et al.*, 2009). We hypothesise that bats may increase flight speed when their fear for predators

Table 2 Bridge lighting effects on bat-bridge distance and flight speed from linear mixed models, respectively including the bat-bridge distance and the flight speed as response variables. Delta AIC is shown as a difference with respective null models.

Response variable	Explanatory variables	Estimate \pm SE	z value	P-value	Δ AIC
Bat-bridge distance	Intercept	27.230 \pm 4.527	6.015	<0.001	-60
	Unlit vs. lit bridge	-26.145 \pm 4.529	-5.773	<0.001	
	Array-bridge distance	-2.727 \pm 0.673	-4.055	<0.001	
	Array-bridge distance ²	0.129 \pm 0.024	5.315	<0.001	
	Unlit vs. lit bridge: Array-bridge distance	3.093 \pm 0.673	4.593	<0.001	
Flight speed	Intercept	-0.072 \pm 0.024	-2.964	0.003	-2565
	Unlit vs. lit bridge	8.832 \pm 2.221	3.977	<0.001	
	Bat-bridge distance	2.043 \pm 0.294	6.954	<0.001	
	Bat-bridge distance ²	-0.082 \pm 0.011	-7.573	<0.001	
	Array-bridge distance	-0.185 \pm 0.096	-1.929	0.054	
	Unlit vs. lit bridge: Distance to the bridge	-2.083 \pm 0.294	-7.088	<0.001	
	Unlit vs. lit bridge: Distance to the bridge ²	0.089 \pm 0.011	8.250	<0.001	
Flight speed in the overlap between 95% confidence intervals of positions of lit and unlit sites	Intercept	8.708 \pm 0.625	13.930	<0.001	-5.5
	Unlit vs. lit bridge	-2.175 \pm 0.677	-3.214	0.001	

**Figure 2** Predicted relationships between the flight speed and the bat-bridge distance for unlit (dark grey, left panel) and lit sites (light grey, right panel) and associated 95% confidence intervals from the linear mixed model presented in Table 2. The light grey rectangles and the focus on it in the middle panel show the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges, for which direct comparison is the most reliable. Solid dots in the middle panel show predicted average flight speeds in the overlap zone. Vertical dashed lines show the bridge location, and empty circles show raw data used in models.

outweighs the benefits of foraging at a specific location. The absence of feeding buzzes (i.e. foraging) at lit sites is consistent with this hypothesis: individuals fly faster in highly lit environments and in turn reduce foraging behaviour (Grodzinski *et al.*, 2009). This response has been observed in other mammal taxa as well (Hof *et al.*, 2012; Farnworth *et al.*, 2019). We finally show that bats decrease their flight speed while approaching unlit bridges. This is presumably linked to the bridge that forces individuals to slow down to avoid it.

Although we accounted for differences in sampling bat-bridge distances between unlit and lit sites by adding the array-bridge distance as a covariate in models, the range of array-bridge distances shared by unlit and lit sites was narrow, which calls for caution in interpreting results about bat-bridge distances for the whole lighting influence area. However, even though we lack data between zero and seven meters from lit bridges (Fig. 2), flight speed response to the distance to bridges and number of bat passes are different enough between lit and unlit sites to be confident about these results.

In our study, we were able to only explore the response of fast-flying species such as *Pipistrellus* species often described as light-tolerant at the street light scale (Lacoeuilhe *et al.*, 2014), but the response of other bat groups – such as slow-flying light-shy bats – that also rely on aquatic corridors as we tested here will be highly interesting as well. Such negative effects on *Pipistrellus* species thus raise numerous questions about less tolerant species, especially in more rural landscapes where light-shy bats are regularly more abundant than in urban landscape (Gili *et al.*, 2020). In addition, *P. pipistrellus* and *P. pygmaeus* may respond differently to light as these species are smaller than *P. kuhlii/nathusii* (Dietz *et al.*, 2009), and hence have different flight characteristics (e.g. Azam *et al.*, 2015; Azam *et al.*, 2018; Russo *et al.*, 2018). Further studies are needed to assess species-specific changes in flight patterns due to artificial light.

Our results highlight that even for the most common bat species in urban habitat, which is considered as light-tolerant in direct response to light, we found a strong impact of light on the relative abundance near bridges, and on the spatial distribution and flight behaviour. The effects we report here call for keeping bridges dark to preserve the functionality of river corridors and to limit habitat loss for bats.

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Author's contribution

K.B., I.L., C.K., R.K.I. and K.S. conceived the ideas and designed the methodology. K.B. and S.C. collected the data. K.B. and Y.B. prepared the data and wrote R scripts. K.B., C.K. and I.L. analysed the data. K.B., I.L., K.S., C.K. and Y.B. led the writing of the manuscript. All authors gave their final approval for publication.

Data Availability Statement

Data and R scripts used to prepare data are available at the following link <https://doi.org/10.5281/zenodo.3929723>.

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Supporting information

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RESEARCH

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Bats seek refuge in cluttered environment when exposed to white and red lights at night

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Abstract

Background: Artificial light at night is recognized as an increasing threat to biodiversity. However, information on the way highly mobile taxa such as bats spatially respond to light is limited. Following the hypothesis of a behavioural adaptation to the perceived risks of predation, we hypothesised that bats should avoid lit areas by shifting their flight route to less exposed conditions.

Methods: Using 3D acoustic localization at four experimentally illuminated sites, we studied how the distance to streetlights emitting white and red light affected the Probability of bats Flying Inside the Forest (PFIF) versus along the forest edge.

Results: We show that open-, edge-, and narrow-space foraging bats strongly change flight patterns by increasing PFIF when getting closer to white and red streetlights placed in the forest edge. These behavioural changes occurred mainly on the streetlight side where light was directed.

Conclusions: The results show that bats cope with light exposure by actively seeking refuge in cluttered environment, potentially due to involved predation risks. This is a clear indication that bats make use of landscape structures when reacting to light, and shows the potential of vegetation and streetlight orientation in mitigating effects of light. The study nevertheless calls for preserving darkness as the most efficient way.

Keywords: Acoustic localization, Artificial light, Flight behaviour, Chiroptera, Microphone array, Streetlight

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Background

Artificial light at night (ALAN) is recognized as a prominent and growing threat to global biodiversity [1] and hence there is an urgent need to expand scientific knowledge on its effects on ecosystems, and a demand for efficient solutions to reduce these [2]. ALAN impacts a wide range of taxa, at different spatiotemporal scales [3, 4]. Effects vary from the individual level to the disruption of ecosystem functioning by altering interactions between species and regulatory processes [5–7].

ALAN also affects spatial behaviour by disorienting species and forming barriers in the landscape. For instance, artificial light disorients migrating birds [8] and obstruct toads [9] and highly mobile taxa such as bats [10]. However, the impact of ALAN on species movement across nightscapes remains poorly documented, in particular underlying mechanisms such as changes in spatial behaviour and movement (e.g. flight speed, flight route) of bats in response to light [11] which potentially affects energetic cost and fitness of individuals [12].

This topic is all the more important given that bats are mostly nocturnal and well known to be impacted by ALAN in term of activity [13]. Depending on species, ALAN positively or negatively impacts bat activity (e.g. *Pipistrellus* spp. and *Nyctalus* spp., respectively *Myotis* spp., *Plecotus* spp. and *Rhinolophus* spp.) at the streetlight scale [14–16], while evidence is also accumulating that ALAN negatively impacts activity of these groups at larger scales [17–19].

ALAN also affects bat movement, for example by keeping individuals from crossing of lit gaps in wooded corridors [10] or lit bridges along waterways [20] in urban environments. It was also shown that different spectra reduce commuting activity along hedgerows and that light shy species switch to the unlit side [21].

Among possibilities to reduce these impacts, light spectrum, intensity, directionality, light spill and the duration of lighting are parameters that potentially can be used to reduce negative effects [22]. For instance, light-shy bats such as *Myotis* and *Plecotus* spp. appear to be equally active close to red streetlights and at unlit sites [23]. However, highly light averse species such as *Rhinolophus hipposideros* have shown to avoid all spectra tested for, including red light [21]. Specific part night lighting schemes, with lights turned off from midnight to 5 am, were not found to substantially mitigate effects of light at night as they were still on during the activity peak of bats [14]. Moreover, information on impact distances are also essential to prevent negative effects of lighting setups and allow biodiversity friendly urban planning. However, how the response of bats relates to the distance to light sources – and hence light intensity – is still relatively unknown. Thus far, the only study available on how the response of bats varies with distance

reveals clear species dependent differences between 10 and 50 m from a light source [24]. For *Eptesicus serotinus* no difference in effects were shown between 0 and 10 m from the streetlight, however strong negative effects were present between 25 and 50 m from the streetlight [24]. These findings suggest the response of bats to light is intensity dependent.

All these effects of ALAN and possible measures for reduction of impact on bats remain so far mostly studied using activity metrics (i.e. indicators of abundance). However, the level of activity close to a light source does not provide information on how light level affects the behaviour of bats. Indeed, using a single microphone only allows the assessment of average bat activity within an acoustic detection range of approximately five to over 100 m, depending on species specific call amplitude [25].

Therefore, to assess respective effects of light intensity and spectrum on bats, there is a need for the assessment of species-specific changes in flight behaviour (e.g. changes in flight paths). Acoustic localization in three dimensions (3D) is an effective tool for the assessment of flight paths [26]. In a study using this technique, authors found that bats reduce flight height and increase flight speed in presence of artificial light [11]. The attraction of insects by light [27] creates foraging opportunities for bats [28] which should cause bats to reduce flight speed [29]. However, studies found that light increases flight speed, probably due to an increased fear of predation [11, 20]. An alternative solution to reduce predation risk is to avoid open spaces when exposed to light. Hence, we hypothesize that bats that have the opportunity to fly closer to vegetation (i.e. when flying close to the forest edge) seek shelter in the vegetation while getting closer to lights. This hypothesis is supported by the fact that typically highly light-averse species [14, 23, 30] such as *Myotis* and *Plecotus* species, are adapted to fly in cluttered habitats (hereafter named narrow-space foragers) by flying slower and hence more vulnerable to predation by hawking birds. We also hypothesize this behavioural response (i.e. flight closer to vegetation) to begin at least 10 m from the light source as shown by Azam et al. [24]. Indeed, distances from the light source at which behavioural responses (avoidance or attraction) are detected vary according to species, and approximatively lie around 50 m for bat species mostly flying in open space (hereafter named open-space foragers) such as *Eptesicus serotinus*, 10 m for bat species mostly flying at wooded edges (hereafter named edge-space foragers) such as *Pipistrellus* species and at up to 25 m for narrow-space foragers such as *Myotis* and *Plecotus* species [24]. Such distance thresholds correspond to light intensities lower than one lux for narrow-space foragers and between one and five lux for open-space and edge-space foragers [24].

In this study, we hypothesize the distance dependent behavioural response of open, edge and narrow-space foraging bat species to streetlights emitting different spectra. Specifically, in comparison with unlit sites we expect bats to fly closer to the vegetation when getting closer to the light, and as much for spectral composition close to white. Using 3D acoustic localization near experimental light posts in forest edges, we first investigated the probability of bats flying inside the forest versus open habitat in relation with the distance to the light. We studied whether this relationship varies around light posts (e.g. the back and front side, and above and under the lights) in order to determine the potential of impact reduction by light orientation (i.e. shielding by the light armature).

Methods

Experimental sites

The study was done at four experimentally illuminated sites in The Netherlands, each with four rows (separated by 204 ± 17 m) with five four-meter-tall lampposts (separated by 25 m and the central one at forest edge) placed perpendicular in forest edge habitat (Fig. 1). Each row was randomly assigned to emit white, green or red light (Fortimo white, ClearField red, and ClearSky green light, Philips, Amsterdam, The Netherlands), with one of the rows kept dark (just poles). In this study, we only used the white, red and dark rows. We choose not to study green lights as these have not shown to be an option to reduce impact of light on the activity of bats (and other nocturnally active species) in earlier studies at these sites (Spoelstra et al., 2015, 2017 [23, 31]), and hence to allocate our time and efforts to white and red light. All lights are switched on at sunset, and off at sunrise since spring 2012. All experimental lights emit light in the full spectrum range at low intensity; green lamps have an increased blue and reduced red light emission, and red lamps have an increased red and reduced blue emission (Fig. 1). All light colours have negligible UV emission (see Spoelstra et al. [31] for spectral compositions). The light beam of each light is directed downwards by Philips Residium FGS224 (1xPL-L36WHFP) armatures to project light in preferential directions. The light intensity at ground level is on average 8.7 ± 3.0 lx, which is comparable to the illumination levels of countryside roads (Fig. 1; see Spoelstra et al. [31] for a further description of these experimental sites). For more detail about light intensity in relation with the distance to the lamp and the orientation of the lamp, see Additional file 1, Appendix S1.

Sampling design and 3D acoustic localization

Bats were acoustically tracked in three dimensions during the first 3 h after sunset for 12 nights between the 10th and 22nd of July 2018. As we could deploy only one microphone array at the time, we unable to

simultaneously sample different light treatments, so we sampled white light, red light and dark control during separate nights. In order to limit variation in bat behaviour linked with inter-night environmental variations, we always sampled a different light colour between consecutive nights (Additional file 1: Table S1). All nights were sampled under highly favourable and constant temperatures (average=16.2 °C, Standard Deviation=1.7 °C) and wind speed conditions (average=1.3 m/s, SD=0.8 m/s) (Additional file 1: Table S1). In total four dark control, four red and four white lights were sampled. White light, red light, and dark control were uniquely sampled in two of the four experimental sites, and combinations of the two spectra (dark control and red, and dark control and white, respectively) were sampled in the two other experimental sites. Within the row of light posts, we always sampled the light post right in the forest edge (i.e. at the border of the forest and the open area; see Fig. 1).

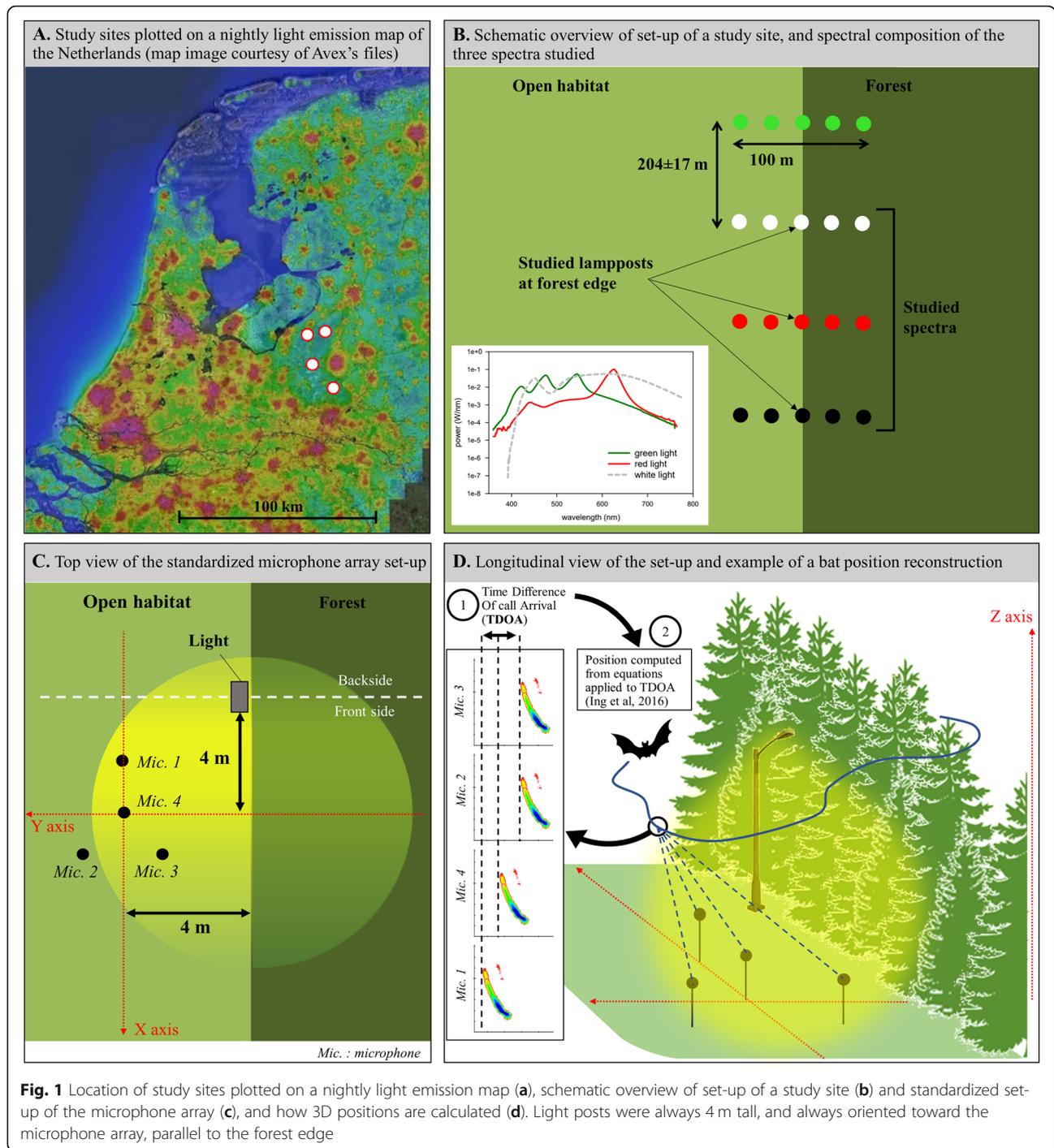
To reconstruct 3D positions of bats, we used a trajectory system (hereafter named microphone array) designed at the Institut Langevin (Paris, France). The system uses echolocation calls recorded in a frequency range from eight to 160 kHz at four microphones (FG 3329, Knowles Acoustics, Itasca, IL USA; see Additional file 1, Appendix S2 for more details about sound recording and triggering of echolocation calls). Microphones were arranged in a horizontal triangle form (i.e. three in the corners and one in the middle; Fig. 1). The microphone array was set up similarly near each row: the four microphones were placed in a horizontal plane above the ground surface, with the central microphone in the open space at four meters horizontal distance to the forest edge and to the streetlight axis perpendicular to the forest edge. The microphone array was always placed on the same side of the light (Fig. 1). Bat positions in the detection range of the microphones were continuously assessed using the time of arrival difference (TOAD) of bat echolocation calls between microphones in the array, using the call waveform [26]. Further details about the recording setup, the conversion of bat call arrival times into 3D positions, assigning positions to trajectories and the precision of these can be found in Ing et al. [32] and Additional file 1, Appendices S2 and S3.

Calculation of the distance from 3D positions to the light and accounting for imprecision

To calculate the distance between each bat position and the light, we used the following equation (D , Eq. 1):

$$D_i = \sqrt{(x_i - 4)^2 + (y_i - 4)^2 + (z_i - 4)^2} \quad (1)$$

where x , y and z represent distances to the microphone array for each of the three-dimension axis of a given position i . The microphone height was corrected for by entering the actual height of the microphones as placed in the field (i.e. 0.82 to 1 m) in the position calculation



software. Since lights were located at the forest edges and were at four meters height, and given the microphone array placement, we subtract four meters to x , y and z axis, in order to compute the real distance to the light (Fig. 1).

Since the imprecision was expected to increase with the distance to the microphone array, we calculated

the cumulated imprecision of 3D positions (I , Eq. 2) as follows:

$$I_i = \sqrt{(dx_i)^2 + (dy_i)^2 + (dz_i)^2} \tag{2}$$

where dx , yx and zx represent the standard deviation of distances to the microphone array estimated for each of

the three-dimension axis of a given position i [32]. We choose to discard positions with a cumulated imprecision of more than one meter (Fig. S1) and those not included in any bat individual trajectory (i.e. composed of several positions; for details on trajectory reconstruction see Additional file 1: Appendix S3), which led us to keep 28,646 positions on the 35,067 recorded.

Assigning species to 3D positions

Individual bat calls used to reconstruct 3D positions were saved by continuously recording sound files. In a second step, sound files were segmented into five-second intervals which is sufficient to cover the average duration of a bat pass [33]. Each of 25,195 five-second files were then classified to the closest taxonomic level using the Tadarida software [34]. Because the identification by echolocation to the species level is difficult, we limited identification to following species groups: the *Eptesicus/Nyctalus* group including *Eptesicus* sp. and *Nyctalus* sp., the *Myotis/Plecotus* group including *Myotis* sp. and *Plecotus* sp., and the *Pipistrellus* group including *Pipistrellus* sp. These three groups respond differently to light: *Eptesicus/Nyctalus* group (i.e. open space forager) are usually considered as light opportunistic or light shy (context dependent), species in the *Myotis/Plecotus* group (i.e. narrow space forager) are light shy, and species in the *Pipistrellus* group (i.e. edge space forager) are light opportunistic.

In a third step, we linked the 3D positions in each 5 s file to the species group found by Tadarida. In case calls of different species groups were found within the same 5 s file, we were able to assign the correct species group to separate series of calls by making use of sequential 3D positions and the peak frequency.

Statistical analysis

We assessed whether the probability of bats flying inside the forest (PFIF) differed according to the distance to the light, and whether this relationship differed between spectra (i.e. dark control, red and white lights). The relationship between the PFIF and the distance to the light allowed us to define the Flight-Path Switch Distance (FPSD) as the distance at which bats on average flew as much inside as outside the forest. We performed Generalized Linear Mixed Models (GLMM, R package *TMB*), using the PFIF as a binomial response variable where zero corresponded to positions located in the open habitat, and where one corresponded to positions located inside the forest (Fig. 1). We used as explanatory variables the distance to the light, the spectrum type, and the interaction between them to assess the effect of spectra on FPSD. To account for a part of the pseudo-replication (i.e. an average of 15.4 ± 10.1 positions per trajectory; Additional file 1: Fig. S2), we included a

random effect on the trajectory identifier. We also included the date as random term in models to control for potential inter-site (i.e. one site sampled each night) and inter-night variations of bat behaviour in relation with lights. Note that weather conditions were highly favourable to bats and stable throughout the sampling period, and that habitat composition was similar between sites (see Sampling design and 3D acoustic localization section and Additional file 1: Table S1).

Given that imprecisions of positions were slightly positively correlated with the distance to the light for *Eptesicus/Nyctalus* group ($r = 0.05$, $t = 2.0$, $df = 1786$, p -value = 0.045; Pearson's correlation test), we adapted the weight of response variables to the associated precision of positions (i.e. inverse of the imprecision squared [35]) by adding a precision weight term in GLMMs.

Lights were oriented toward the ground and the armature parallel to the forest edge, which results in a heterogeneous distribution of light in horizontal and vertical planes (Fig. 1). Thus, in order to assess the dependence of light effects on bats to their spatial position around a streetlight, we built one model per species group for (i) all positions around the light, for (ii) positions under the light (i.e. $z < 4$ m), for (iii) positions above the light ($z > 4$ m), for (iv) positions at the backside of the light (i.e. $x > 4$ m) and for (v) positions in front of the light (i.e. $x < 4$ m) (Fig. 1). All GLMMs exhibited much smaller Akaike Information Criteria (AIC) than null models. We assessed for each model the goodness of fit by computing the percentage of variance explained by models using the r^2 function (R package *sjstats*). We checked residual plots of models using the R package *DHARMA*. All analyses were performed using a significance threshold of 5% in the R statistical software [36].

Results

3D acoustic localization

Bat calls within the 25,195 five-second files recorded allowed the assessment of a total of 28,646 (3D) positions, with an imprecision of less than one meter. Of all positions, 91.3% were assigned to the *Pipistrellus* group, 6.2% to the *Eptesicus/Nyctalus* group and 2.4% to the *Myotis/Plecotus* group (Additional file 1: Table S2). The number of locations was higher at the white-light poles, followed by red and then dark control poles for *Eptesicus/Nyctalus* and *Pipistrellus* groups, but higher around red-light poles followed by white and then dark control poles for *Myotis/Plecotus* group (Additional file 1: Table S2). Overall, the cumulative imprecision for each location varied between 0.10 and 0.39 m on average, and was dependent on species group, but similar between the three light treatments although slightly lower for all groups in red sites (Additional file 1: Table S2). More than 70% of positions had a cumulative imprecision lower than 0.2 m (Fig. S1).

Effect of spectrum on the flight behaviour

Overall, the average probability of bats flying inside the forest (PFIF) was significantly higher near red and white light posts compared to dark control poles for *Pipistrellus* group, while only significantly higher near white light posts for *Myotis/Plecotus* and *Eptesicus/Nyctalus* groups (Table 1). All bat groups were found to have a greater PFIF when getting closer to the light. The increase in PFIF when getting closer to the light was stronger for red and white light posts compared to dark control poles for *Pipistrellus* and *Eptesicus/Nyctalus* groups, and only stronger for white light posts for the *Myotis/Plecotus* group. The increase in PFIF when getting closer to the light was even stronger for red compared to white light posts for the *Pipistrellus* group, and even stronger for white compared to red light posts for *Eptesicus/Nyctalus* (Table 1; Fig. 2). Irrespective of these differences, white lighting increased the Flight Path Switch Distance (FPSD) for *Eptesicus/Nyctalus* group (i.e. 6.1 m), red lighting generated a greater FPSD for *Pipistrellus* group (i.e. 2.0 m), and white light generated a FPSD of 5.5 m for *Myotis/Plecotus* group (Additional file 1: Table S3; Fig. 2).

At three to five metres from the light, the PFIF for *Myotis/Plecotus* and *Eptesicus/Nyctalus* groups even reached 100% for white lighting treatment, while the usual PFIF at such distance in unlit sites was under 1% (Fig. 2). Similarly, the PFIF for *Pipistrellus* group reached more than 85 and 50% at one meter from red and white lights respectively, while close to 0% in unlit conditions whatever the distance (Fig. 2).

Variation of responses according to location around lights

All species groups increasingly flew inside the forest when getting closer to the light. For both spectra, this effect was only present at the front side of the light, except for *Eptesicus/Nyctalus* group around red lights (Table 1; Fig. 3). For this group, the response was furthermore limited for bats flying above light posts of both spectra. For the *Pipistrellus* group, this response was unrelated to flight height (Table 1; Fig. 3).

Concerning the distance dependency, Flight Path Switch Distance (FPSD) was greater for *Eptesicus/Nyctalus* flying above and at the front side of white compared to red light poles (5.1 m and 7.0 m versus 4.0 m and 0.2 m, respectively), and was greater for *Myotis/Plecotus* flying at the front side of white light poles (6.7 m versus no prediction possibility due to insufficient PFIF, respectively) (Additional file 1: Table S3; Fig. 3). The FPSD was also higher under and at the front side of red-light poles compared to white light poles for *Pipistrellus* group (3.2 m and 2.4 m versus no prediction possibility due to insufficient PFIF, respectively) (Additional file 1: Table S3; Fig. 3).

Finally, fixed effects of models overall almost always explained a large part of the variance (0.11–0.90 r^2 ; Additional file 1: Table S3).

Discussion

We show that artificial light located at forest edges significantly increases the Probability of Flying Inside the Forest (PFIF) for open-, edge- and narrow-space foragers (*Eptesicus/Nyctalus*, *Pipistrellus* and *Myotis/Plecotus* groups, respectively) regardless of light spectrum.

For open- and edge-space foraging bats that take advantage of around light accumulated insects, the presence of cluttered habitat (i.e. forest in our case) could further facilitate foraging around streetlights by providing shelter against predators. This result is also consistent with the antagonist effects of ALAN at different spatial scales for open- and edge-space foragers. At the streetlight scale these groups can appear light-opportunistic [13, 14, 21, 23, 24], however, at a larger scale these species are negatively impacted by ALAN [17–19]. The observation that light-opportunistic open- and edge-space foragers seek refuge in cluttered environment near light sources may explain this negative impact, especially in areas with little vegetation around light.

Comparable behavioural changes were expected for *Myotis/Plectus* species as they are adapted to fly in cluttered environments and are known to be light-averse [14, 23, 30]. Both red and white light increased the PFIF for *Myotis/Plecotus* group compared to dark control sites. Although the effect of red lights was much less important compared to white lights, this finding is important as red light has been reported to have limited to absent effects on the activity of these species [21, 23]. Our results thus suggest that red light may actually not be entirely effective in avoiding behavioural changes of narrow-space foragers, and even less for open- and edge-space foragers.

Overall, Flight Path Switch Distances (FPSD) were mostly longer around white lights, which is likely due to the fact that bats may perceive white light as more intense compared to red light due their spectral sensitivity [37, 38]. Such differences in FPSD could also be linked with differences in light intensity at equal distance, higher for white than red lamps we studied (4.83 more lux in average in a 5 m radius around red lights; see Additional file 1: Appendix S1 for graphical representation of light intensity in relation to the distance to white and red lights), which is known to be one of light parameters driving impacts on bats [39]. When considering the vertical location of bat positions, we found that compared to white light poles, the FPSD was higher for individuals located under (i.e. for *Pipistrellus* group) and above (i.e. for *Pipistrellus* and *Eptesicus/Nyctalus* groups) red light poles. This is likely directly related to the

Table 1 Estimates, standard errors and *p*-values of the effect of the distance to the light, the spectrum and the mutual interaction on the probability of bats flying inside the forest when unlit control (A) and white spectrum (B) were used as intercept ($***p < .001$, $**p < .01$, $*p < .05$). Results are presented for all positions, and positions above, under, behind and in front of the light (see Fig. 1 for placement definitions), and derived from generalized linear mixed models

		<i>Eptesicus/Nyctalus</i>	<i>Myotis/Plecotus</i>	<i>Pipistrellus</i>
All positions		<i>N</i> =1788	<i>N</i> =692	<i>N</i> =26,166
Dist. to light		-0.950 ± 0.020 ***	-1.864 ± 0.736 *	-0.188 ± 0.036 ***
Spectrum	(A) Unlit vs. Red	-0.679 ± 4.278	3.056 ± 4.055	5.185 ± 1.570 ***
	(A) Unlit vs. White	18.890 ± 4.004 ***	16.736 ± 7.994 *	3.522 ± 1.491*
	(B) White vs. Red	-19.569 ± 3.502 ***	-13.680 ± 8.379	1.663 ± 1.509
Dist. to light: Spectrum	(A) Unlit vs. Red	-1.013 ± 0.044 ***	-0.508 ± 0.376	-0.802 ± 0.067 ***
	(A) Unlit vs. White	-1.639 ± 0.435 ***	-1.537 ± 0.742 *	-0.385 ± 0.040 ***
	(B) White vs. Red	0.625 ± 0.055 ***	1.029 ± 0.790	-0.417 ± 0.059 ***
Vertical location: above light		<i>N</i> =1708	<i>N</i> =465	<i>N</i> =19,438
Dist. to light		-0.951 ± 0.020 ***	-1.715 ± 794 *	-0.207 ± 0.038 ***
Spectrum	(A) Unlit vs. Red	37.339 ± 8.043 ***	-4.277 ± 6.453	2.587 ± 1.690
	(A) Unlit vs. White	20.557 ± 3.787 ***	7.801 ± 8.163	2.721 ± 1.596 .
	(B) White vs. Red	16.784 ± 8.092 *	-12.078 ± 8.351	-0.134 ± 1.623
Dist. to light: Spectrum	(A) Unlit vs. Red	-6.282 ± 0.187 ***	0.783 ± 0.914	-0.477 ± 0.074 ***
	(A) Unlit vs. White	-1.487 ± 0.044 ***	-0.507 ± 1.059	-0.369 ± 0.043 ***
	(B) White vs. Red	-4.795 ± 0.190 ***	1.290 ± 0.856	-0.108 ± 0.066
Vertical location: under light		<i>N</i> =80	<i>N</i> =227	<i>N</i> =6728
Dist. to light		/	/	-0.567 ± 0.043 ***
Spectrum	(A) Unlit vs. Red	/	/	10.751 ± 2.080 ***
	(A) Unlit vs. White	/	/	5.340 ± 1.944 **
	(B) White vs. Red	/	/	5.411 ± 1.480 ***
Dist. to light: Spectrum	(A) Unlit vs. Red	/	/	-1.624 ± 0.197 ***
	(A) Unlit vs. White	/	/	-0.581 ± 0.162 ***
	(B) White vs. Red	/	/	-1.044 ± 0.128 ***
Horizontal location: backside		<i>N</i> =895	<i>N</i> =326	<i>N</i> =6433
Dist. to light		-0.520 ± 0.380	/	-0.347 ± 0.548
Spectrum	(A) Unlit vs. Red	-47.725 ± 29.775	/	-10.136 ± 7.872
	(A) Unlit vs. White	-13.521 ± 7.152 .	/	-5.289 ± 7.145
	(B) White vs. Red	-34.205 ± 28.608	/	-4.847 ± 3.978
Dist. to light: Spectrum	(A) Unlit vs. Red	1.977 ± 1.134 .	/	0.715 ± 0.588
	(A) Unlit vs. White	0.676 ± 0.408 .	/	0.429 ± 0.559
	(B) White vs. Red	1.302 ± 1.026	/	0.286 ± 0.240
Horizontal location: front side		<i>N</i> =893	<i>N</i> =366	<i>N</i> =19,733
Dist. to light		-0.748 ± 157 ***	0.959 ± 0.602	-0.555 ± 0.021 ***
Spectrum	(A) Unlit vs. Red	1.082 ± 3.269	18.784 ± 9.528 *	7.343 ± 1.893***
	(A) Unlit vs. White	6.229 ± 2.215 **	45.356 ± 20.498 *	4.534 ± 1.818 *
	(B) White vs. Red	-5.147 ± 3.384	-26.572 ± 19.127	2.809 ± 1.779
Dist. to light: Spectrum	(A) Unlit vs. Red	-0.538 ± 0.326 .	-2.587 ± 1.036 *	-1.070 ± 0.079 ***
	(A) Unlit vs. White	-0.558 ± 0.170 **	-5.466 ± 2.590 *	-0.468 ± 0.047 ***
	(B) White vs. Red	0.020 ± 0.338	2.879 ± 2.555	-0.602 ± 0.070 ***

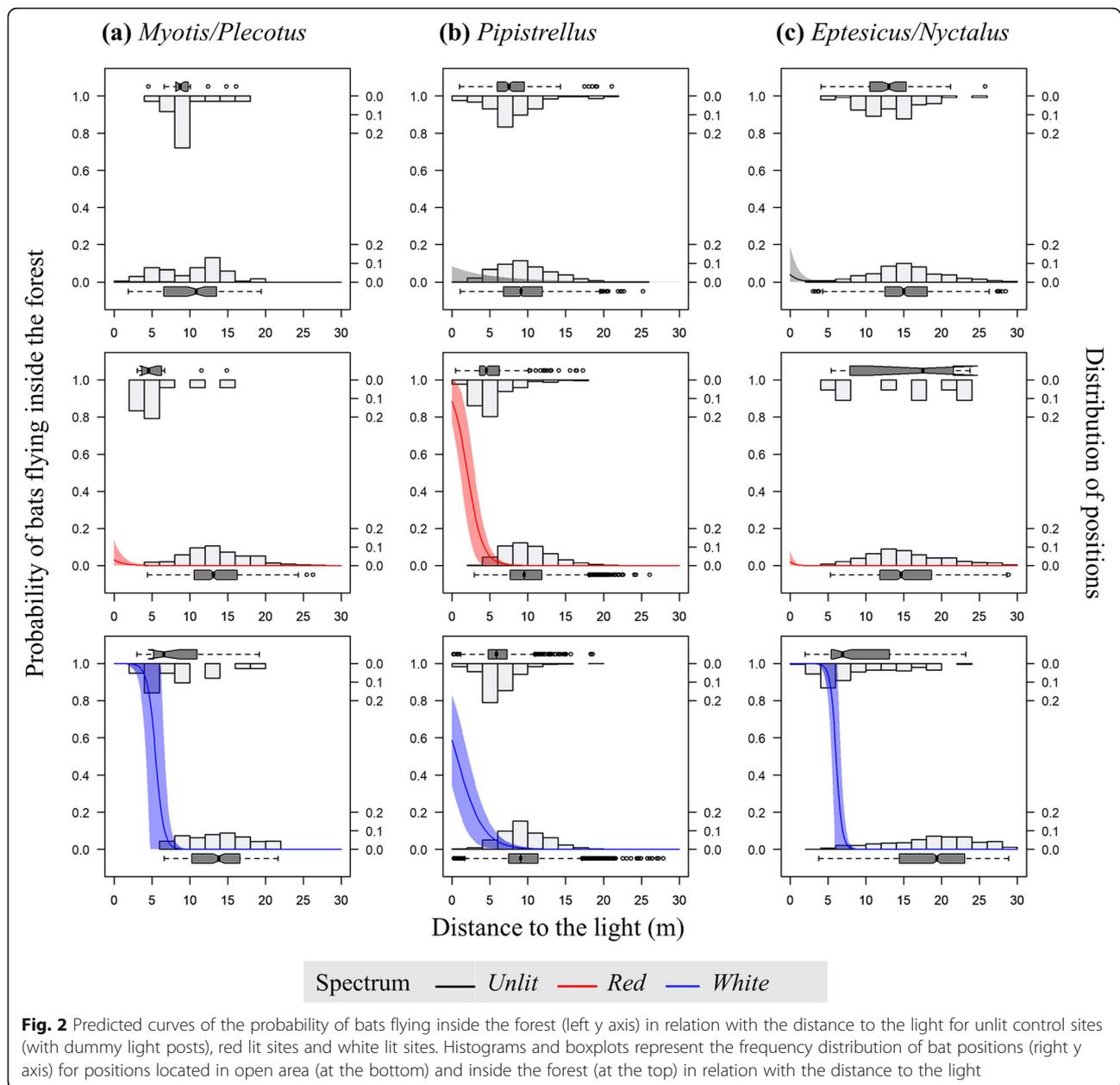
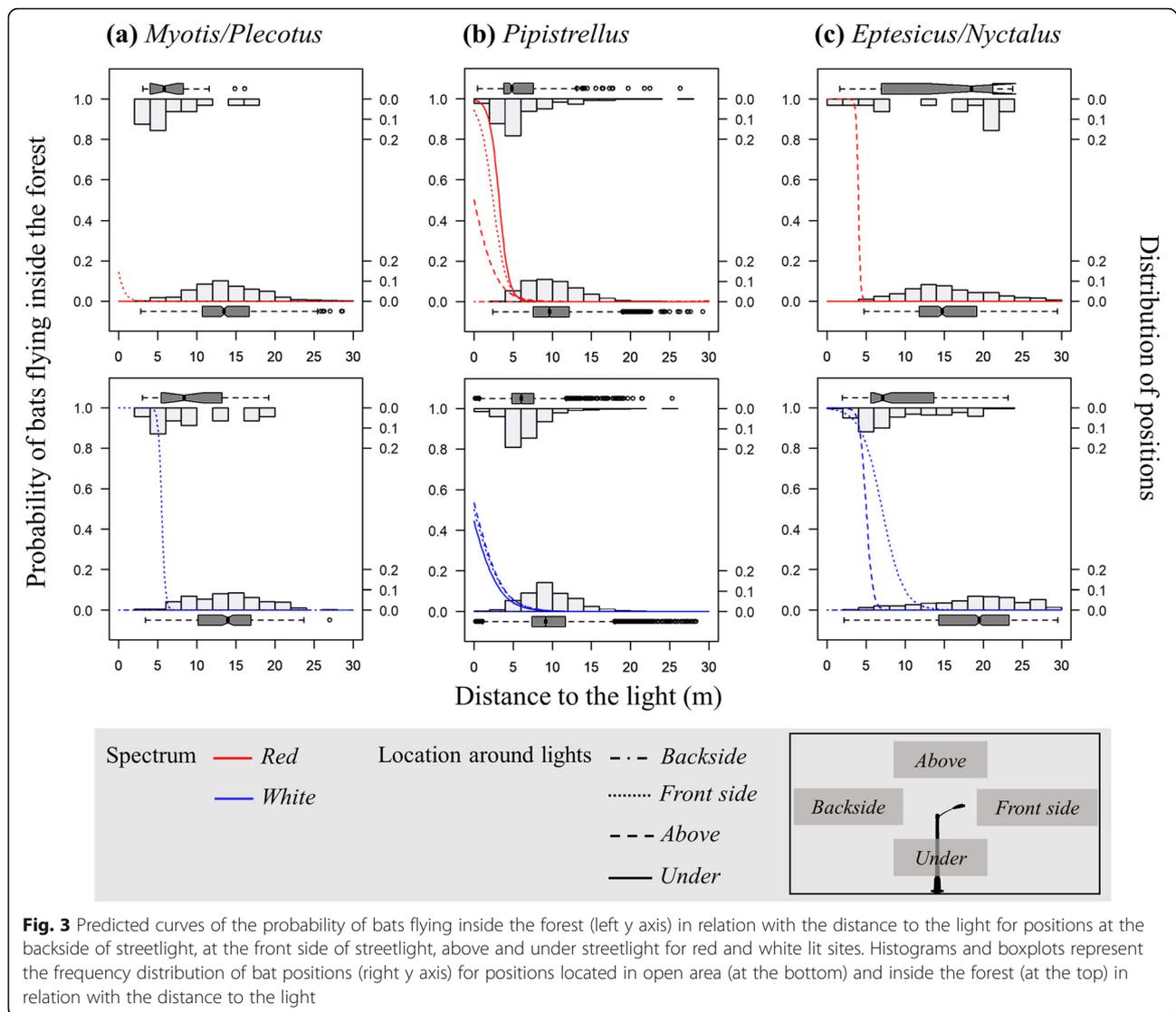


Fig. 2 Predicted curves of the probability of bats flying inside the forest (left y axis) in relation with the distance to the light for unlit control sites (with dummy light posts), red lit sites and white lit sites. Histograms and boxplots represent the frequency distribution of bat positions (right y axis) for positions located in open area (at the bottom) and inside the forest (at the top) in relation with the distance to the light

distribution of the light around the streetlights (Additional file 1: Appendix S1), and aligns with the distance relation – and hence intensity dependence – of activity reported by [24]. However, it should be noted that *Eptesicus/Nyctalus* group mainly flew above lights (Additional file 1: Table S2) which likely explain the absence of response under lights.

We also found changes in bat behaviour in front of light posts for all groups but not at the backside. Thus, the directionality of the light post matters and can be used to reduce the adverse impacts of artificial lighting on bats. In our study, we had a sharper cut-off in light at the backside of the light posts, and hence the effects there disappeared at shorter distances. Individuals could

forage at the backside of streetlights where the predation risk is low, and hence not seek refuge inside forest when getting closer to the light. Further investigations are needed to understand mechanisms involved. Concerning the overall higher effect of red light compared to white light on *Pipistrellus* group, further studies would be needed to understand why, and if they possibly turn back when getting closer to light instead of seeking refuge inside the forest. However, open-space foragers do not show the same pattern and react similarly to red and white light. We could hypothesise that their higher flight height allows for flying in or above the canopy (i.e. in a potentially more open space than for *Pipistrellus*



group) while increasing their flight speed in response to light, which could explain their different response than edge-space foragers. Further investigations are also needed to address these aspects.

Finally, depending on bat location around streetlights, Flight Path Switch Distances (FPSD) in front of streetlights overall started from 7 m and 4 m for white and red lights, respectively. These distances of impact correspond to light intensities around 6 lux for both white and red lights. However, we defined FPSD as the distance at which bats on average flew as much inside as outside the forest, but impacts likely start before this arbitrarily chosen threshold. When we look at the beginning of behavioural perturbation, i.e. when the PFI previously close to zero increases towards positive PFIs, corresponding FPSD would be around 15 m and 9 m for white and red lights, respectively. Such distances correspond to light intensities around one lux for both white and

red lights. These thresholds seem to be consistent with a study which looked at thresholds in light intensity affecting bat activity [24].

However, it is important to be cautious about the definition of safety thresholds for bats and further studies should confirm these results by testing wider distance and intensity ranges around streetlights, by sampling all spectra simultaneously, and by studying more sites and nights per spectrum. We were not able to measure forest height, thus further studies could accurately account for bat position in relation to forest canopy as open space foragers such as *Nyctalus* spp. can fly above (average flight height 9 ± 4 m; Additional file 1: Fig. S3). However, considerably lower flight heights recorded for *Pipistrellus* (5.8 ± 2.8 m) and *Myotis/Plecotus* groups (5.2 ± 2.5 m), and light effects generalized to under and above light positions for *Pipistrellus* group support these findings (Additional file 1: Fig. S3).

Conclusion

Our study demonstrates that spectrum type, intensity and directionality of streetlights has an effect on the flight behaviour of all bats, including light-opportunistic species, highlighting the need to consider simultaneously all these characteristics when studying ALAN impact on bats. In contrast to the absence of changes in bat activity in response to red light reported earlier, we here show that bats can have a comparable change in flight behaviour in response to red and white light. This finding first shows that bats actively seek refuge in cluttered environment when getting closer to light sources. This is a clear indication that bats make use of landscape structures when dealing with light, and shows the potential of vegetation in mitigating negative impacts of artificial light at night, but calls for preserving darkness as the most efficient way.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-020-00238-2>.

Additional file 1.

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Authors' contributions

K.B., I.L., C. K. and K.S. conceived the ideas and designed the methodology; R.K.I. built the microphone array; K.B. and K.S. collected the data, K.S. set up experimentally illuminated sites; K.B. and Y.B. analysed the data and wrote R scripts; K. B., I. L., C.K. and K. S. interpreted results; all authors led the writing of the manuscript. All authors contributed to the drafts and gave their final approval for publication.

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Availability of data and materials

R scripts and data used for analyses are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.4036279>.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

We declare we have no competing interest.

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Synthesis

Grasping darkness: the dark ecological network as a social-ecological framework to limit the impacts of light pollution on biodiversity

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ABSTRACT

Artificial light at night (ALAN) is nowadays recognized as a major anthropogenic pressure on the environment on a global scale and as such is called light pollution. Through its attractive or deterrent effects, and its disruption of the biological clock for many animal and plant taxa, ALAN is increasingly recognized as a major threat to global biodiversity, which ultimately alters the amount, the quality, and the connectivity of available habitats for taxa. Biodiversity conservation tools should, therefore, include ALAN spatial and temporal effects. The ecological network, i.e., the physical and functional combination of natural elements that promote habitat connectivity, provides a valuable framework for that purpose. Understood as a social-ecological framework, it offers the opportunity to take into account the multiple uses of nocturnal spaces and times, by humans and nonhumans alike. Here we present the concept of “dark ecological network.” We show this concept is able to grasp the effects of ALAN in terms of habitat disturbances and integrates temporal dimensions of ecological processes into biodiversity conservation planning. Moreover, it is also intended to trivialize the practices of darkness protection by turning them into the ordinary practices of land use planning. From an operational point of view, the challenge is to translate the levers for reducing ALAN-induced effects into a political method for its “territorialization.” To achieve this objective, we propose a course of action that consists of building an interdisciplinary repertoire of contextualized knowledge (e.g.,

impacts on wildlife, human/lightscape relationship, existing legal tools, etc.), in order to deduce from it a number of practical supports for the governance of the dark ecological network in response to societal and ecological issues.

Key words: artificial light at night (ALAN); darkness; ecological network; land-use planning; light pollution; multilevel approach; participatory processes; social-ecological systems

INTRODUCTION

Habitat destruction, reduction, transformation, and/or isolation profoundly affect the dynamics of populations, communities, and ecosystems, as well as underlying ecological processes and in turn biodiversity levels (Soulé and Oriens 2001). Based on this observation, many studies have highlighted the need to move from the conservation of only a few remarkable habitats and species to the conservation of more ordinary ones (Margules and Pressey 2000, Hansen and De Fries 2007, Thompson et al. 2011). Moreover, to promote ecologically functional habitats, ecological planning must focus on appropriate spatial scales to account for habitat connectivity (Fischer and Lindenmayer 2007). The concept of ecological network has emerged in response to this need for renewed conservation policies and spatial design (Opdam et al. 2006, Boitani et al. 2007). It is intended to grasp the ecological conditions necessary for individuals and populations to maintain in a fragmented habitat, for example, by maintaining a sufficient diversity, size, shape, and connection of favorable habitat patches according to considered species or communities. The strength of this concept, developed on the basis of island biogeography theories (MacArthur and Wilson 1967) and population dynamics (Levins 1969), allows for “a shift away from the “topologic” approach to conservation, involving only protected areas, and to the landscape “chorological” approach, involving the whole territory” (Battisti 2003:241).

It is therefore essential to approach ecological networks from a twofold pragmatic perspective and within the framework of integrated conservation (McShane and Wells 2004): to combat landscape homogenization and habitat fragmentation on the one hand (Jongman 2002), and to integrate conservation theories into landscape and land use planning practices on the other (Opdam et al. 2006). On this last point, Battisti (2003:241) insists that “this planning must take into account the “real world”, whose interpretation needs a multidisciplinary approach (Haila 1985, Soulé 1986): applied ecologists and wildlife managers will have to interact with landscape planners and politicians, although their languages are different.” In this perspective, the concept of “ecological network” has established itself in the field of nature conservation (Bischoff and Jongman 1993).

There are debates on the effectiveness of ecological networks within the scientific community (on that issue we can compare the words of Boitani et al. 2007 or Lévêque 2017 with what Rientjes and Roumelioti 2003 or Samways and Pryke 2016 for instance, had to say about that). Yet, the concept has nevertheless achieved unprecedented social and political success (Jongman 1995), particularly in Europe, in a landscape context under heavy human domination (Vimal et al. 2012). The introduction of this scientific concept into the political arena has resulted in the Pan-European Biological and Landscape Diversity Strategy. It was initiated in 1995 by the European Ministers of the Environment in association with the United Nations and the Council of Europe (Jongman et al. 2004). This strategy’s primary objective was to create a Pan-European ecological network (Jongman and Pungetti 2004, Jongman et al. 2011): a homogeneous and coherent network from a geographical and ecological point of view, consisting of core areas, corridors, restoration areas, and buffer zones. Since the late 1990s, many European Union (EU) member states have implemented a national ecological network planning policy (Bennett and Wit 2001, Jongman and Kristiansen 2001). The EU is now seeking to harmonize these national policies. It is working on the establishment of a green infrastructure (GI), defined as “a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services. It incorporates green spaces (or blue where aquatic ecosystems are concerned) and other physical features in terrestrial (including coastal) and marine areas. On land, GI is present in rural and urban settings” (European Commission 2013:3). Member states currently trying to implement such networks have to compromise between scientific knowledge on the one hand and local political and social issues on the other (Alphandéry et al. 2012).

Current approaches to building ecological networks do not explicitly integrate ecosystems’ temporal dynamics: they are only based on a daytime perception and on material causes of habitat fragmentation. However, although their planning claims to take into account the “real world” (Battisti 2003), ecological networks should also consider the nocturnal dimension of ecosystems. Indeed, in this “real world”, when it comes to repelling the daily descent of darkness, societies deploy specific techniques, such as artificial light at night (ALAN) and more particularly outdoor spaces lighting (Brox 2010). ALAN is a space planning tool that responds to multiple social uses, e.g., security enhancement of goods and people, nighttime economy activities, architectural aestheticism, city marketing and promotion. However, the degradation of the darkness generated in and around urban areas is nowadays understood as a source of pollution in its own right, so-called “light pollution” (Riegel 1973). Street light sources or other public light sources are of course not the only ones responsible for light pollution; it has recently been shown that many other privately operated sources, e.g., illuminated signs, can play a non-negligible role in the emission of artificial light from urban areas (Kyba et al. 2020). ALAN negative effects are therefore at the heart of the complex interactions that occur between the environment and societies within anthropized nocturnal space-time.

Several recent studies have pointed out that environmental protection tools do not include the issues raised by ALAN-related impacts (Schroer et al. 2020). For example, this major anthropic pressure is not taken into account in the network of Natura 2000 sites, the European policy flagship tool for the preservation of biodiversity. As a consequence, conservation planning tools urgently need to account for ALAN effects on habitat loss and fragmentation, namely examples from highly mobile taxa such as bats (Laforge et al. 2019, Pauwels et al. 2019). Hence, it is essential to retain and develop “dark ecological networks.” Global ecological networks would benefit from specific dark ecological networks because they share specific features. First, ecological corridors such as wooded edges and rivers (classically part of global ecological networks) are also often constrained by ALAN (Spoelstra et al. 2017, Barré et al. 2020),

hence highly important in lighting reduction schemes. Second, a great number of ecological communities composing global ecosystems, i.e., nocturnal and diurnal, are expected to be influenced by ALAN because 28% of vertebrates and 64% of invertebrates are nocturnal worldwide (Hölker et al. 2010). Then, ALAN affects parts of trophic chains not limited to night and affects other neighbor ecosystems (Manfrin et al. 2017). However, it is also necessary to articulate to what degree ALAN affects ecological processes and the scales of ALAN management by institutions. This articulation represents a challenge traditionally encountered in the treatment of environmental problems (Cumming et al. 2006). This challenge is made worse concerning ALAN because of the diffuse nature of light pollution, the plurality of its effects, as well as the uncertainties that remain about its effects at various geographical/temporal scales and/or ecological levels. This results in a current mismatch between scales of knowledge and scopes of action.

The purpose of this article is twofold. Based on the conceptual framework of ecological networks, the first objective is to present the concept of dark ecological network and to clarify its aims, particularly from ecological and geographical points of view. The second objective is to highlight the challenges involved in translating the dark ecological network as a concept defined by scientists—both in its theoretical and practical dimensions, for example when discussing and defining its shape, structure, or components (Boitani et al. 2007)—into an action-oriented tool. To meet these two objectives, we highlight the global dimension of the various problems caused by light pollution. We show the intertwining of the spatial and temporal dimensions of ALAN ecological effects. We also define the scientific concept of dark ecological network. We emphasize the intrinsically socio-ecosystemic dimension of this concept. That concept dimension makes it possible to grasp the multiple facets of darkness preservation as a resource in its own right. More particularly, we show that this concept permits us to envision a junction between practices that have until now been implemented in a disjointed way—the development of protection and enhancement areas of the starry sky on a large scale, and the spatiotemporal management of lighting on a fine scale. Finally, we outline some of the issues raised by the translation of the dark ecological network as a scientific concept into the dark ecological network, understood as an action-oriented tool. In other words, we are discussing the transition from a scientific method to an unavoidable political compromise for the “territorialization” of darkness protection.

LIGHT POLLUTION, A GLOBAL ENVIRONMENTAL PROBLEM

Tightly linked to urbanization, outdoor lighting has grown by between 3% and 6% per year during the second half of the 20th century (Hölker et al. 2010). Even today, ALAN is increasing in most parts of the world. Between 2012 and 2016, Earth’s artificially lit outdoor surface area increased by 2.2% per year, with a radiance growth of 1.8% per year. As for the brightness of continuously illuminated areas, it has increased by 2.2% per year (Kyba et al. 2017). De facto, light pollution affects 23% of the global land surface, including 88% of the European surface area (Falchi et al. 2016). Under the influence of aerosols suspended in the atmosphere, ALAN spills beyond urbanized areas over to protected surroundings and biodiversity hotspots (Guetté et al. 2018). Moreover, ALAN represents a significant part of global energy consumption, with 20% of global electricity consumption and, on the same scale, 6% of CO₂ emissions (UNEP 2012), and about 3% of global oil demand (UNEP 2017). In the United States of America alone, International Dark-Sky Association estimates that at least 30% of all outdoor lighting is wasted. Still according to this NGO, this waste costs up to US\$3.3 billion a year and emits 21 million tons of carbon dioxide over the same period (see <https://www.darksky.org/light-pollution/energy-waste/>). This growing anthropogenic pressure contributes to global environmental changes through multiple mechanisms related to health, culture, and ecology.

The health implications of ALAN

From a health point of view, the natural alternation between light and darkness is the most powerful exogenous synchronizer of the master clock of peripheral clocks. This central clock controls all circadian biological rhythms, both for humans and wildlife (Gaston et al. 2017). The degradation of darkness by ALAN disrupts the synchronization of the central circadian clock, modifies sleep architecture, and inhibits melatonin secretion. These responses depend on several interacting factors: intensity (Cajochen et al. 2000, Zeitzer et al. 2005), duration (Chang et al. 2012), timing (Khalsa et al. 2003), temporal patterns (Rimmer et al. 2000, Gronfier et al. 2004, Najjar and Zeitzer 2016), and the spectral composition (Brainard et al. 2001, Thapan et al. 2001, Najjar et al. 2014) of the light stimulus. For instance, it has recently been shown that ALAN intensities between 2 and 10 photopic lux are sufficient to inhibit melatonin secretion and to disrupt the circadian clock in humans (Prayag et al. 2019). These intensities are far lower than those we are exposed to on a daily basis, via multiple domestic lighting systems, and are comparable to those generated by “intrusive light” (Falchi 2018) in a bedroom without shutters in an urban context.

The socio-cultural implications of ALAN

In socio-cultural terms, the loss of natural darkness deteriorates several scientific (Riegel 1973) and cultural amenities (Gallaway 2010, Stone 2017, Challéat and Poméon 2020). ALAN “closes the window” on the starry sky (Isobe and Hirayama 1998)—one-third of humanity can no longer make out the Milky Way (Falchi et al. 2016). ALAN erodes darkness and reduces the relationship to this inexhaustible historical, literary, philosophical, religious landscape or artistic resource, which participates in our individuation, in the constitution of our being, and in our relationship with other humans and nonhumans (Galinier 2010, Le Gallic and Pritchard 2019, Lam 2020). ALAN thus contributes to the extinction of the experience of nature (Pyle 1978, Miller 2005, Soga and Gaston 2016) and fuels generational environmental amnesia (Kahn 2002). In addition, cultural geography studies emphasize the extent to which darkness makes possible original forms of conviviality and intimacy, the occupation of public spaces, and the perception of the world through senses other than sight (Edensor 2013, 2015, Shaw 2018). In other words, whatever the types of space involved, darkness preservation provides access to an array of experiences for the sensorial apprehension of the world.

The ecological implications of ALAN

Finally, ALAN produces many ecological disturbances (Rich and Longcore 2006, Sanders et al. 2021) and constitutes one of the least understood sources of perturbation affecting biodiversity (Gaston et al. 2015). Altering natural light and dark patterns in ecosystems, especially day/night rhythm (Gaston et al. 2017), ALAN impacts a wide range of taxa from the molecules level to ecosystems, interactions between species, and regulatory processes (Hölker et al. 2010, Gaston et al. 2017, Grubisic et al. 2017, Knop et al. 2017, Bennie et al. 2018a). ALAN plays a major part in the activity and energy metabolism of taxa by altering energy expenditure (e.g., Welbers et al. 2017, Touzot et al. 2020). Such a physiological consequence of ALAN may have a long-term negative effect on individuals' fitness across populations (Touzot et al. 2020). ALAN also fragments habitats, altering the functional connectivity of landscape for many species (Laforge et al. 2019). Indeed their avoidance-attractiveness mechanisms at more local scales (Barré et al. 2020) greatly depend on the species sensitivity according to their traits, e.g., fast-flying vs. slow-flying species, and light parameters, e.g., intensity and spectrum (Spoelstra et al. 2017, Azam et al. 2018). Such fragmentation due to ALAN has genetic implications that have recently been argued as a driver of evolution contributing to population differentiation across urban-rural landscapes (Hopkins et al. 2018). Species response to ALAN heavily depends on spatial scale, with, for example, positive effects on some bat species activity within the range of the surrounding streetlight (Azam et al. 2018), while with seriously negative effects at the national scale (Azam et al. 2016; Fig. 1). These authors have even shown that, for these taxa, ALAN poses a threat equivalent to others such as soil artificialization and the proportion of intensive agriculture on a large scale (Azam et al. 2016). Such spatial and temporal perturbation of habitats and species is suspected in turn to profoundly affect the functioning dynamics of populations, communities, and ecosystems (Falcón et al. 2020).

THE INTERTWINED SPATIAL AND TEMPORAL DIMENSIONS OF ALAN ECOLOGICAL EFFECTS

The spatiotemporal dimensions of ALAN effects

Habitat fragmentation constitutes a central concern about ALAN effects on biodiversity. The first purpose of the dark ecological network is to identify solutions to mitigate impacts. ALAN results in habitat fragmentation through two main mechanisms. The first one is the spatial barrier effect, which can be produced by individuals' physical or temporal isolation. Specifically, ALAN can generate illuminated areas that are more difficult for individuals to pass through than unlit areas, e.g., for bats (Lewanzik and Voigt 2014, Hale et al. 2015, Barré et al. 2020) and toads (van Grunsven et al. 2017). It induces direct spatial barriers for moving and results in habitat losses. ALAN also generates indirect spatial barrier effects because of temporal asynchronies inducing mismatches between lit and unlit areas, e.g., in the timing of grass species flowering later under artificial light (Bennie et al. 2018b) and producing less fruit (Knop et al. 2017). Indeed, such temporal asynchronies can induce a spatial differentiation between populations driven by the spatial distribution of artificial light (Altermatt and Ebert 2016), and ultimately a spatial barrier through evolutionary changes in populations (Hopkins et al. 2018). Such spatial or temporal isolation of populations could even ultimately limit gene flow and increase genetic drift as advocated by Hopkins et al. (2018). The second main mechanism through which ALAN causes habitat fragmentation is through its attractiveness to taxa. Indeed, light sources promote the accumulation of individuals of many species, such as arthropods in lit areas (Rydell 1992) and their depletion in unlit areas (Eisenbeis 2006). Artificial light also attracts predators such as insectivorous bats (Stone et al. 2015) or seabirds (Rodríguez et al. 2017) and could cause top-down and bottom-up trophic effects, as demonstrated, e.g., on invertebrate populations (Bennie et al. 2018a). ALAN also disrupts migration, alters fly paths, migration activity (Van Doren et al. 2017), and migratory stopover selection by birds (McLaren et al. 2018). Such attractive effects can thus generate modifications in the spatial use of habitats and ultimately compromise the life cycle achievement of species, e.g., access to reproduction sites or mates.

Temporally fixed and local scale solutions used so far to reduce effects

Much scientific knowledge is available and has already been used to reduce the impacts of ALAN. For instance, lights that contain the most blue and UV wavelengths, i.e., high and low-pressure mercury, metal-halide, and white light-emitting diodes, attract a higher number of arthropod species than other lights, i.e., low and high-pressure sodium, discharge lamps and amber LED (van Langevelde et al. 2011). However, although high-pressure sodium lights attract much fewer arthropods than lights containing more blue and UV wavelengths, they remain 27 times more attractive than dark conditions (Perkin et al. 2014). Taxa responses to light, regardless of whether they are positive or negative, are also known to be spectrum-dependent such as in birds (de Jong et al. 2015), reptiles (Witherington et al. 1991), toads (van Grunsven et al. 2017), or mice (Bird et al. 2004). It was also shown that red spectrum lights were equivalent to dark conditions for global activity of insectivorous bats (Spoelstra et al. 2017). Besides, although light from high-pressure sodium lamps or red LEDs, for example, attract fewer insects, it still has negative impacts on bat commuting (Stone et al. 2009, Zeale et al. 2018). However, it should be noted that spectrum-related effects remain highly diverse, either in bats (Voigt et al. 2018), in insects (van Grunsven et al. 2019), and more generally in flora and fauna (Schroer and Hölker 2017).

Toward solutions to reduce ALAN effects at different spatiotemporal scales

However, such measures that aim at modifying streetlight attributes remain focused on the local scale and, although useful, they are most often not sufficient. Indeed, it has been shown that light pollution can remain a concern for natural ecosystems far away from city centers owing to light halo phenomena, which can be exacerbated in periods of cloudy nights (Secondi et al. 2017). Furthermore, following the example of bats and despite some positive effects at local scale for some species, ALAN shows a severe negative effect at larger spatial scales for all European guilds (Azam et al. 2016). Maintaining and increasing unlit areas likely remains the most efficient solution: reducing the trespass of lighting could keep habitat heterogeneity, which provides dark refuges. In the same way, decreasing lighting intensity limits skyglow and impacted areas (Gaston et al. 2012). Some studies, however, found that current lighting schemes

using switch-off strategies were not a promising solution for bats because they do not match with peaks of activity (Azam et al. 2015). More drastic options, i.e., using lamps that switch off between 00:00 and 04:00 am, were not fully effective, though they do reduce the number of taxa impacted for grassland invertebrate assemblages (Gaston et al. 2017). At conurbation scale, Laforge et al. (2019) tested different light-reduction scenarios and found that their efficiency to improve landscape connectivity for bats depends more on the type of land use, i.e., habitat, where light reduction is applied than on the total area impacted by it.

These results confirm that both ALAN effects on biodiversity and the efficiency of mitigation measures (such as light reduction/extinction) depend on the spatial context. For instance, it was recently shown that the probability for greater horseshoe bats of crossing a gap in an ecological corridor, e.g., a hedgerow, substantially decreased from 38 meters (Pinaud et al. 2018), which constitutes key knowledge to mix with lighting schemes. In addition, it has been recently demonstrated that bats avoid streetlight at up to 50 meters (Azam et al. 2018). Coupled with knowledge about landscape connectivity such as Pinaud et al. (2018), it could help the implementation of an efficient dark ecological network. These results suggest that existing ecological networks could integrate such information as a framework to develop dark ecological ones.

The literature also suggests that ALAN effects on biodiversity depend on the temporal context. First, as explained in the introduction, species depend on regular day and night alternation that shapes their daily biological cycle. Perturbations of daily light cycles impact biological events such as singing for birds, daily movements, foraging, sleep, and recovery, documented about a wide range of taxa (Gaston et al. 2017). Then, at the peak of species abundance, foraging activity and breeding periods strongly depend on seasons (e.g., Newson et al. 2015, Salvarina et al. 2018, Lučan and Radil 2010). That is why species are affected differently by artificial lighting, according to time of year, e.g., response of avian daily rhythms to light intensity (de Jong et al. 2016). Monthly and seasonal regimes of lunar sky brightness also shape biological timings and spatial repartition of species, e.g., for zooplankton's vertical migrations, and can be masked or even very negatively impacted by the skyglow generated by the extent of artificial lighting sources (Davies et al. 2013, Ludvigsen et al. 2018). Finally, ALAN can generate long-term impacts. Indeed, ALAN can change community assemblages including diurnal ones, e.g., for invertebrates (Davies et al. 2012, 2017). ALAN can even have genetic impacts, as shown for a moth species in which individuals in lit areas had reduced flight-to-light behavior compared to those in unlit areas (Altermatt and Ebert 2016). Concerning solutions to mitigate such impacts, no studies, to our knowledge, have tested the efficiency of lighting schemes focused on long-term and seasonal impacts. However, accurately including long-term temporal processes in decision making to establish dark ecological networks appears essential to ensure the coexistence of humans and biodiversity in an increasingly urbanizing world (Secondi et al. 2017).

THE DARK ECOLOGICAL NETWORK, A CONCEPT FOR MATCHING SCALES AND LEVELS OF DARKNESS PRESERVATION

On a large scale, the starry sky as the main horizon for an anthropocentric utilitarian protection of darkness

At the international level, the fight against light pollution is carried out in different ways and supported by different actors. In its most advanced territorial form today, it can be seen in the protection of the starry sky through new zoning. It is built on a classic center-periphery logic: a high protection core area is surrounded by a buffer zone, but no environmental protection is expected outside. This logic, which has historically prevailed in the planning of many national and nature parks (Shafer 1999*a, b*, Dudley 2008), is the one currently used to implement "dark sky places" around the world (Charlier and Bourgeois 2013, Bénos et al. 2016).

Initiated in 1993 in the United States with the creation of the Dark Sky Preserve at Lake Hudson (Michigan), this territorial dynamic of starry sky protection really took off at the end of the 2000s. It is based on a labeled zoning logic, supported by various associations from the dark sky movement (Challéat and Lapostolle 2014, Challéat 2019). The International Dark-Sky Association is top of the list. Just over 140 territories are currently labeled by the latter. Its International Dark Sky Places (IDSP) status initially made it possible to distinguish high places of astronomical observation, and is now sought by conventional protected areas (according to the International Union for Conservation of Nature typology), hence extending to the starry sky the scope of their protection measures (Collison and Poe 2013). The main labeling criterion here is the existence of a remarkable starry sky. It can be easily mobilized in different valorization strategies (Rodrigues et al. 2015, Challéat and Poméon 2020). For example, the development of dark sky tourism and other territorial marketing strategies can lead to a purely utilitarian understanding of the starry sky as a new assessable economic good (Mitchell and Gallaway 2019). In this logic, the aesthetic or utilitarian criteria and considerations often muddle the ecological and health stakes of preserving darkness as a resource (Blundell et al. 2020, Lapostolle and Challéat 2021). Acting this way, in a field that should be a new front in the construction of conservation policies, proves to be a methodological step backwards with regard to the convergence efforts made since the 1990s in the field of conservation and the creation/evolution of protected areas. However, the articulation between territorial development issues and environmental protection matters is subject to local compromises. Guidelines are currently shifting thanks to their effects.

On a fine scale, "getting lighting right" using knowledge of spaces' nocturnal characteristics as a slow paradigm shift

The geographical concept of "nocturnal territoriality" (Raffestin 1988, Lapostolle and Challéat 2021) underscores the role of nighttime darkness in the change in our daily relations with the places we experience. Knowing nocturnal territorialities implies grasping in a situated way the daily practices and uses in and of the nighttime (Challéat and Lapostolle 2018). Taking into account the many different uses and approximations of nocturnal characteristics means partially moving away from technocratic prescriptions of what spaces should be (how a priori it should be planned), by giving back a role to do-it-yourself approaches with a view to adding other knowledge and experiences, i.e., other than those of experts, into the mix. This is essentially a form of land-use planning democratization. In

addition to defining space in terms of the production of figures and procedural standards, it takes into account actual uses and experiences of spaces as two elements that contribute to shaping the sense of places (Chapin and Knapp 2015, Hausmann et al. 2016). Knowledge of nocturnal territorialities enables us to move toward the “right way of lighting” (*éclairer juste*), a set of practices condensed into a new urban lighting doctrine that seeks a settlement between our needs for artificial light and the set of ecological, health-based, and socio-cultural needs for darkness (Challéat 2019, Lapostolle and Challéat 2021). In France, for example, these new practices are brought together within the *éclairer juste* doctrine, which includes integrating environmental constraints into the economic logic of many lighting professionals. This doctrine is promoted on a national level by various dominant stakeholders in the lighting and energy sectors, like the *Agence de l’environnement et de la maîtrise de l’énergie* (ADEME), the *Association française de l’éclairage*, and the *Syndicat de l’éclairage*, a national syndicate that brings together national and international manufacturers of lamps, luminaires, candelabras, and electronic components used in the lighting industry (ADEME et al. 2010).

From the public lighting policies point of view, it is important to note that considering nocturnal territorialities is not in itself a fight against light pollution, but rather a fight against unnecessary expenditure, i.e., financial and energy savings (Franchomme et al. 2019). However, the “right way of lighting” doctrine is proving to be a frame of reference for action permeable to new environmental considerations. In other words, if considering nocturnal territorialities does not necessarily mean placing the fight against light pollution at the foundation and heart of the renewal of lighting practices, it nevertheless opens the way for integrating this issue into the production of tomorrow’s urban lighting. It is in this frame of reference that the new public lighting regulation practices take place. For instance, in France, in the early 2010s, local-authority budget cuts and pressure to meet energy-transition targets placed new constraints on urban lighting. As a result, an increasing number of municipalities, most often in rural areas, but also, increasingly, in (peri-)urban areas, have reduced or switched off public lighting at certain times of the day and/or certain periods in the year. But these actions remain spatially scattered, and politically uncoordinated: there is no interterritoriality for their implementation or, in other words, no articulation between the different organizational levels of action.

The dark ecological network, a concept to strengthen the protection of darkness

No reticular thinking presides over the implementation of IDSP-type zoning on the one hand, and of “right lighting” policies on the other. Although they are locally efficient to reduce light pollution and to increase awareness and concern about the multiple issues related to the preservation of darkness (Silver and Hickey 2020, Lapostolle and Challéat 2021), these initiatives and practices too often remain disjointed and are not networked. Moving from mere starry sky protection and/or from plain energy costs reduction to the preservation of all the benefits of darkness requires mobilizing a holistic protection tool such as the ecological network. In what is thus becoming a dark ecological network, IDSPs are “macro-reservoirs of darkness,” i.e., core areas of darkness among others, linked by the other structural components of the network: dark landscape corridors, dark linear corridors, dark buffer zones, and dark stop-over sites (Fig. 2). In addition, the multiscale structure of the dark ecological network enables it to protect the darkness needed for ecological processes by capturing the multiple effects of ALAN on various scales, from the light footprint generated by a sole luminaire to the one generated by (mega)cities’ skyglow.

Unlike IDSP-type zoning, the network has no center, no periphery, no clear boundary between inside and outside, but relies on its components’ connectedness and connectivity. This structural characteristic provides it with lability, a property that is particularly effective in terms of preserving darkness. The habitat fragmentation caused by ALAN differs from the physical obstacles of linear transport infrastructure: the obstacle can be temporarily removed by switching off the lights. In addition, and contrary to issues encountered in agricultural environments, for example, where land and property rights matters require the mobilization of a complex set of actors, technical intervention on interconnected public lighting systems only involves a relatively small number of operators. These two specificities related to technical lighting systems make it possible to temporarily activate some elements of the dark ecological network according to seasonal ecological issues, first and foremost the dark (landscape) corridors and the dark stop-over sites. Here, following radically different spatial scales, we can start with the migratory passage or maiden flight of birds particularly ALAN sensitive (Horton et al. 2019), or the spring pollination in areas where the local economy is heavily dependent on fruit growing. Given this network’s lability, isolated and scattered actions that already exist could be linked to the dark ecological network, such as Houston Audubon Lights Out Action Alerts in the USA (see: <https://houstonaudubon.org/conservation/bird-friendly-communities/lights-out.html>), or *Les nuits sans lumière* (Nights without light, renamed *Les jours de la nuit*, Days of night) in the Réunion Island (see: <https://www.lesjoursdelanuit.re>). These operations consist in generating alerts or asking individuals, businesses, and communities to turn off the lights, during the passage of migratory birds in the USA, or during the ocean-ward maiden flight of the young Barau’s Petrels (*Pterodroma barau*) in the Réunion Island.

For and through the implementation of the dark ecological network, it is, therefore, a matter of deepening and extending darkness protection. Faced with the urgent need to preserve biodiversity, the dark ecological network enriches the tools for territorial action in the fight against light pollution. In other words, it is no longer just a question of protecting the starry sky or a few remarkable species, but of protecting the ordinary biodiversity and what we could call, by analogy, the ordinary darkness, i.e., the darkness whose protection does not depend on the implementation of zoning that establishes a specific protection status. Extending the fight against light pollution means spreading the protection of darkness and biodiversity beyond protected areas alone, symbolically represented by areas overhung by an exceptional starry sky, even in ordinary areas. The reticular approach proposed via the dark ecological network takes this twofold ecological and geographical direction: it aims to make the protection of the darkness/biodiversity couple a new guiding principle for land use planning.

FROM A SCIENTIFIC CONCEPT TO AN ACTION-ORIENTED TOOL: FACING THE TERRITORIALIZATION CHALLENGE

By emphasizing the importance of darkness as a new dimension of ecological connectivity, the concept of dark ecological network operates nothing less than a radical reframing of the fight against light pollution. It requires a shift in darkness preservation views and objectives, from a vertical, aesthetic, and quasi-pictorial landscape—the nightscape and its “artialized” (Roger 1997) starry sky, contemplated like a painting in a way that is dissociative from the self—to a horizontal and holistic landscape. This holistic landscape is part of the “real world” (Battisti 2003) and thus becomes the boundary object (Brand and Jax 2007) between the modality of scientific analysis and the modality of public action. Achieving this change in perspective is the challenge of the territorialization of the dark ecological network, whose practical implications stem from this holistic and geographically situated approach of the nocturnal social-ecological systems.

Territorialization, a multilevel process to counteract scales mismatches

According to Dessein (2015:108), “we use the notion of ‘territorialization’ to describe the dynamics and processes in the context of regional development that are driven by collective human intentionality; these stretch beyond localities and fixed regional boundaries (Horlings et al. 2015).” De facto, any territorialization process involves a multiscale, multiactor, and multisector approach. The problem of mismatch between the scales of ecological processes and the stakeholders responsible for their management is well known (Borgström et al. 2006, Cash et al. 2006, Cumming et al. 2006, Folke et al. 2007). This problem is particularly acute when dealing with diffuse pollution such as light pollution, radically multiscale in both its causes and consequences. Here, and as Borgström et al. (2006) and others since the 1990’s (Lee 1993, Holling and Meffe 1996, Hobbs 1998) point out, “the scale of monitoring and decision making often does not match ecological spatial, temporal, or functional scales.” These scale mismatches result in a mismanagement of natural resources. Among mitigating solutions, Cumming et al. (2006) emphasize the “institutional changes at more than one hierarchical level” and show that these changes are dependent on “social learning and the development of flexible institutions that can adjust and reorganize in response to changes in ecosystems.”

We understand territorialization as the process of situated objectification that organizes the pairing of positivist and constructivist epistemologies at the service of environmental action. The territorialization process confronts scientific knowledge with institutional struggles and cooperation, but also with vernacular knowledge and other forms of attachment to places (Sébastien 2020) in order to make them operational. In a logic and context of uncertainty, territorialization thus aims at articulating the knowledge scales—understood as “the temporal and spatial extent and character of knowledge held by individuals and collectives” (Ahlborg and Nightingale 2012)—to the spatial, institutional, and temporal scales. Thus stated, the territorialization process is close to both adaptive governance (Folke et al. 2005)—whose relevance to solving the scales mismatch within social-ecological systems has been demonstrated by Termeer et al. (2010)—and multilevel governance. However, territorialization is more critical with regard to foundations and the meaning of pre-existing governance systems. In other words, territorialization leaves open the possibility of questioning the institutional governance frameworks, because it considers the meaning of places and relationships to lived spaces as facts that must be taken into account when defining instruments for preserving biodiversity. For this reason, we argue that debate and the proximity of decision making and citizen involvement are then consubstantial with the territorialization of the ecological network.

Building repositories of contextualized scientific knowledge

The territorialization process is necessarily a situated and action-oriented approach. It is situated because it takes into consideration the different dimensions that structure the territory and the distinctiveness of places for sustainable development, e.g., cultural, historical, political, physical, or ecological dimensions (Horlings 2015). It is action-oriented because it focuses on bringing together researchers, residents, politicians, practitioners, user groups, environmental associations, and experts.

Thinking about the protection of darkness beyond protected areas alone poses the difficulty of confronting the multiple nocturnal uses and the planning choices that have been made at different territorial scales. The transition from a scientific concept to a territorial and political project is therefore a problematic situation, in that it places scientific and territorial constraints under stress. Negotiations and arbitrations, particularly in terms of artificial lighting management, respect for human uses, and choice of species to be protected, preside over the production of the dark ecological network and reflect its socio-ecosystemic complexity. The territorialization and operationalization of the dark ecological network require a reflexivity effort on the part of both scientists and territorial actors. It is reflected in a change in practices on both sides. This reflexivity effort can be illustrated by the cartography of the dark ecological network. This work relies on combining the “knowledge, techniques and realities of the territory in order to organize the transition from the concept to the development of concrete projects” (Vimal and Mathevet 2011). In concrete terms, the cartographic definition of the ecological network must integrate value systems and representations linked to territories’ historical, social, economic, political, and symbolic dimensions (Mascia et al. 2003, Blicharska et al. 2016). Social sciences tools and methodologies make it possible to probe this territorial thickness by analyzing connections between the spaces and actors involved in the protection of the darkness and biodiversity couple (Challéat and Lapostolle 2014). By examining, as well, the mediation logics at work in lighting policies local redefinitions (Lapostolle et al. 2015, Lapostolle and Challéat 2021), the integration of biodiversity issues into public controversies and debates, social, economic, and scientific issues related to the protection of nocturnal spaces and species, or pioneering practices that foreshadow new forms of organizing nocturnal socio-ecosystems.

However, while objective knowledge of territorial specificities is necessary to inform action, it is likely not sufficient. The experiential relationships to nature expressed by inhabitants and users, i.e., vernacular knowledge, must be integrated into the repertoire of situated

scientific knowledge, in order to guarantee the balanced governance of the dark ecological network.

The experience of nature as the basis of dark ecological network governance

Public policy decision making is based on different knowledge repositories. In the perspective of classical evidence-based policy making, the repertoire of objective knowledge predominates. Now, because we wish to territorialize public environmental policies, several recent studies show that it is necessary to integrate into their governance the actors holding other knowledge repositories: citizens, resource users, policy makers, and practitioners, for example (Cornell et al. 2013, Leach et al. 2013, Díaz et al. 2015). This is the challenge of the multiple evidence-based approach developed by Tengö et al. (2014, 2017), which recognizes as complementary different knowledge systems with distinct epistemic properties, and aims to link them in action. This approach requires a broader construction of the “public of the problem” (Dewey 1927) and the creation of conditions for participation in its governance (Zask 2011). This “common decision-making process” is the meaning we give to the dark ecological network as a political method to recognize the diversity of nature experiences (Skandrani and Prévot 2015). Considered this way, the dark ecological network is no longer just a scientific concept, but becomes the preferred vehicle for restoring within our everyday lives the experience of darkness in ordinary places (Miller 2006), even in (peri-)urban spaces. In other words, and whatever the types of spaces considered, darkness preservation gives access to a range of experiences that permit a sensitive understanding of the world.

Such sensitive understanding of the world is permeable to environmental issues. Therefore, and even in urbanized spaces, night appears as the daily scene of multiple experiential dimensions of nature and biodiversity (Bogard 2008, 2013, Challéat 2019), as well as to oneself. Emotional dimensions include some of our atavistic fears (Painter 1996, Schaller et al. 2003, Koslofsky 2011), but also sensory, memorial, analogical, or utilitarian dimensions (Prévot et al. 2016). These experiences are a tangible basis for debating artificial light at night in the face of darkness. These multiple dimensions make darkness a multifaceted resource, e.g., naturalistic, poetic, literary, philosophical, religious, landscape, scientific, or artistic, that participates as much in our individuation and in the constitution of our relationship to the world as in the fabric of the territories (Challéat et al. 2018). It thus gives meaning to places (Barreteau et al. 2016, Sébastien 2020). However, the governance of artificial light at night, by neglecting these different meanings of the resource, spatially and temporally erodes darkness and impoverishes the relationships that our societies maintain with the nocturnal environment. In this way, it deprives itself of a number of solutions to preserve darkness and to support consensus on how to preserve it at local level (Fig. 1).

In order to work, this holistic, integrated, and situated approach of darkness conservation must be built within hybrid forums (Callon et al. 2001) allowing the expression of the plurality of experiential relationships. The teachings and lessons learned from the difficulties encountered in the territorialization of other forms of public environmental actions or policies ought to be heeded (Franchomme et al. 2013). In other words, learning effects (Baird et al. 2014) should be carefully considered in order to better “bring science into democracy” (Latour 2004), especially with respect to “new” environmental problems such as light pollution. In France, for example, when identifying biodiversity reservoirs and ecological corridors at the territorial level as part of the *Trame Verte et Bleue* (TVB) policy, the French strategy to operationalize the concept of ecological network (see <https://www.ecologique-solidaire.gouv.fr/trame-verte-et-bleue>), several studies have highlighted “the difficulty of involving field actors alongside modeling experts. The mobilization of the latter’s sophisticated tools has not been accompanied with consideration for other forms of knowledge or a contradictory debate, despite the criticisms and limitations pointed out by the actors in the field about the method used” (Alphandéry and Fortier 2012). The local anchoring of the TVB has been built through different communication, translation, and advertising processes involving different stakeholders, in order to become accessible and appropriable by the greatest number of people. Political action is complex here. The lessons learned from the implementation of the TVB policy can be valuable for the dark ecological network territorialization. More particularly to bridge the gap between scientific knowledge and action and to deepen the links between multilevel governance and participatory processes. The territorialization of the dark ecological network aims to considerably change the living environment of the inhabitants and users of the spaces. It must therefore be debated in arenas whose access is not restricted to scientists. Moving beyond the technical approach to the problem and initiating a real project approach (Janin et al. 2011) to darkness conservation can, for example, involve transdisciplinarity. This makes it possible to (re)integrate research, action, and policy (Leach et al. 2013). By creating the conditions for participation, transdisciplinarity brings together researchers, residents, politicians, practitioners, user groups, environmental associations, and experts.

At the European level, we can see the embryos of these transdisciplinary practices within Interreg programs (Interreg Europe “Night Light,” Interreg Poctefa “Pirineos La Nuit,” or Interreg Großregion “Smarth Light Hub”). These programs experiment with the implementation of conferences-debates, hybridization, and cocreation workshops, or the setting up of demonstrators for the inhabitants and elected officials of the territories. More broadly, these experimental transdisciplinary approaches could be applied to changes in lighting practices in and around Natura 2000 sites, which currently do not consider the issue of light pollution. Indeed, although European texts are clear on the need for member states to ensure the ecological connectivity of their sites, they are not very prescriptive on how to achieve this. Taking into account the issues raised by ALAN-related impacts in the Natura 2000 policy would be an opportunity to clarify its territorialization framework. These approaches could then provide a pragmatic basis for regulating this area of public action. It would address scientific and technological issues, providing they allow, on the one hand, diverse stakeholders’ involvement in the local production of the dark ecological network and, on the other hand, researchers’ commitment to the democratic and political process (Fischer 2000, Reed 2008; B. V. Lewenstein 2004, unpublished manuscript, <http://hdl.handle.net/1813/37362>). What matters then is not to abandon a method that establishes facts and recognizes territories’ singularity (Vimal et al. 2012) without giving way to the performative dimension of public policy instruments in general and of the dark ecological network in particular.

CONCLUSION

Building on the ecological network framework, the dark ecological network aims to consider artificial light at night as a driver of habitat fragmentation, to further integrate the nocturnal dynamics of ecological processes into biodiversity conservation planning, and to deepen and extend the fight against light pollution to ordinary biodiversity and familiar areas. The dark ecological network success is therefore dependent on including the logic of preserving darkness in the ordinary practices of environmental planning and development of all territories. Such trivialization of darkness protection gives rise to new needs. It requires the deployment of integrated darkness conservation, paying attention to the multiple uses, both human and nonhuman, of nocturnal space and time or, in other words, the deployment of a conservation method that falls within the realm of political ecology and fits in with the concept of ecological solidarity (Mathevet et al. 2016) as a profound consideration of “the ‘community of destiny’ between humans, society and its environment” (Mathevet et al. 2010:426 [our translation]). This approach to darkness protection can only be deployed within a relational thinking framework that, within the preservation of living diversity systems, integrates the interaction of ecological systems on the one hand, and social systems on the other. In other words, the trivialization of the darkness/biodiversity couple protection through the dark ecological network is a radically social-ecological approach that aims to (re)define the nocturnal living space that a society agrees to share with the nonhumans among which it evolves. It provides a relevant framework for pragmatic action, which “requires establishing and organizing social relationships, while communicating and discussing values, ends and means” (Mathevet 2012:150 [our translation]) that underlie the geographically situated action.

Various experiences designed to define and implement the dark ecological network in France show that issues of protecting darkness to meet biodiversity challenges are gradually being addressed in land use planning policies (Challéat et al. 2018, Franchomme et al. 2019). However, passing from these experiments in a few pioneering territories to their transcription into the ordinary areas is a long way down the road. It requires rethinking both terms when analyzing the relationship between societies and the environment, as well as the conditions in which land use planning is implemented. A serious approach is emerging, which brings together the tradition of ecological research with the common practice of social geography in territories (Barreteau et al. 2016). In other words, experimental sciences and social sciences are making progress in bringing their analytical questions and methods closer together, thus catalyzing the translation of scientific ecology into political ecology (Devictor 2018a, b). Interdisciplinary social-ecological approaches are emerging as a new scientific paradigm. However, the challenge remains: how to go about it, i.e., applying these analyses to territorially situated planning policies. Here, knowledge production methods (participatory sciences, citizen sciences, action research, and engaged research) are shaking up (because they question them) the social significance of scientific knowledge and the practical experience of land use planning professionals. Yet, here as elsewhere, the “inescapable distinction between emic and etic, or between learned and common sense, should not mean superiority of one over the other or ignorance of one by the other” (Olivier de Sardan 1988:536 [our translation]). Doing so, they highlight the need for a more general appropriation of ecological transition and biodiversity protection policies. It is a paradigm shift that requires recognizing that scientific controversies and sustainability are political issues and, as such, requires an inclusive debate and a plurality of voices (Leach et al. 2013).

RESPONSES TO THIS ARTICLE

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AUTHOR CONTRIBUTIONS STATEMENT

Samuel Challéat and Kévin Barré share joint first authorship of this work.

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