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Light pollution & biodiversity: What are the levers of action to limit the impact of artificial lighting on nocturnal fauna?

Julie Pauwels

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THESE

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Julie Pauwels

Le 11 octobre 2018

Light pollution & biodiversity:

**What are the levers of action to limit the impact of
artificial lighting on nocturnal fauna?**

Sous la direction de : **Dr. Isabelle Le Viol, Dr. Christian Kerbiriou et Pr. Emmanuelle Porcher (HDR)**

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ABSTRACT

The spatial extent of artificial light is increasing rapidly and significantly on Earth surface hence changing the nocturnal lightscape and threatening an important part of ecosystems. The rise in nighttime light levels induces a perturbation of the circadian rhythm and thus a modification of nocturnal, but also some diurnal, species behavior and interactions between species. Despite the spread of light pollution being of major concern, the knowledge gaps in this field limit the creation of regulations to reduce the impact of nighttime lighting on biodiversity. Therefore it is urgent to produce clear and practical information to build tools and define recommendations for land managers.

In this context, the aim of the PhD thesis is to study the impact of light pollution on nocturnal fauna through two spatial scales in order to propose methods to evaluate and manage artificial light. We used bats as a model species as they are long-lived and nocturnal and thus highly impacted by light pollution. In addition, it has been shown that their population trends tend to reflect those of species lower in the trophic chain which makes them even more sensitive to anthropic pressures.

First, we studied the effect of light pollution within cities. This spatial scale is both coherent with bats distance of movement and with the reality of public lighting management. Although some urban-adapted species living within large cities are considered to benefit from artificial light, this work showed that, at a scale including all aspects of bats daily travels, light has a negative effect on bats activity level. Also, even if a large part of light pollution is due to public lighting, the results show that private lighting should not be neglected. Beyond the impact on bat activity, artificial light can have a barrier effect when individuals are transiting and thus reduce the landscape connectivity. Whereas environmental policies are promoting the development of ecological corridors, not considering light pollution could significantly reduce their efficiency for nocturnal species. Modelling the link between biological data and landscape variables including light level allowed us to build adapted corridors for nocturnal species. This lead to the development of a tool to evaluate lighting scenarios that could be used prior to the implementation of a lighting plan in order to predict the impact it would have and hence adapt it to the local biodiversity issues.

At a finer scale, it is necessary to understand which light characteristics are the most relevant levers of actions to formulate recommendations to limit light pollution impact on biodiversity. We carried a field work experiment in a protected area where conservation issues on bat species are even higher as the species most sensitive to light are protected there, together with their habitat, at the EU level. We worked at the interface between urban and semi-natural areas and showed that the illuminance was the most important light characteristic. Hence it is on this parameters that regulations should be applied in priority to limit the impact of light on areas that could potentially be used as corridors or dark refuges for sensitive species.

RÉSUMÉ

L'emprise de la lumière artificielle s'étend de manière importante et rapide à travers le monde entier et est en train de changer le paysage nocturne menaçant ainsi une large part des écosystèmes. L'augmentation des niveaux de lumière la nuit entraîne une perturbation du rythme circadien et par là une modification des comportements des espèces nocturnes mais aussi diurnes et des interactions entre espèces. Malgré l'importance de l'enjeu que représente la pollution lumineuse, le manque de connaissances dans le domaine limite la création de réglementations pour réduire l'impact de l'éclairage nocturne sur la biodiversité. Il est donc urgent d'apporter des éléments concrets pour construire des recommandations et des outils d'évaluation à destination des gestionnaires du territoire.

Dans ce contexte, l'objectif de cette thèse est d'étudier l'impact de la pollution lumineuse sur la faune nocturne à deux échelles paysagères afin de préconiser des méthodes d'évaluation et de gestion de l'éclairage artificiel. Nous avons utilisé les chauves-souris comme modèle d'étude car elles sont longévives et nocturnes et donc fortement affectées par la pollution lumineuse. De plus, il a été montré que les tendances de leurs populations tendent à refléter celles d'espèces plus basses dans la chaîne trophique, les rendant ainsi d'autant plus sensibles aux pressions anthropiques.

Dans un premier temps, nous avons étudié l'effet de la pollution lumineuse à l'échelle de villes, une échelle paysagère en cohérence à la fois avec les distances de déplacement des individus et avec une réalité de gestion de l'éclairage. Malgré que les espèces anthropophiles vivant toujours dans les grandes villes soient considérée comme bénéficiant de l'éclairage artificiel, ce travail a montré qu'à une échelle regroupant tous les aspects des déplacements quotidiens des individus, l'effet global de la lumière est négatif. De plus, bien qu'une part significative de la pollution lumineuse soit due à l'éclairage public de par sa permanence et son étendue, l'étude montre que l'éclairage privé n'est pourtant pas à négliger. Au-delà d'un effet sur le niveau d'activité, la lumière artificielle peut avoir un effet de barrière dans le déplacement des individus et ainsi réduire la connectivité du paysage. Alors que les politiques environnementales sont en faveur du développement de corridors écologiques, la non-inclusion du facteur pollution lumineuse pourrait réduire significativement leur efficacité pour les espèces nocturnes. Un travail de modélisation mettant en lien des données biologiques d'activité avec des aspects paysagers mais aussi lumière a permis de construire des corridors adaptés pour les espèces nocturnes. Cela a aussi mené à des outils d'évaluation de scénarios d'éclairage qui peuvent être utilisés en amont d'aménagements afin de prédire l'impact d'un changement et de les adapter aux enjeux de biodiversité.

A une échelle plus fine, il est nécessaire de comprendre quelles caractéristiques des points lumineux sont les plus pertinents à maîtriser afin de formuler des recommandations pour limiter l'impact sur la biodiversité. Nous avons mené une étude de terrain dans un espace protégé où les enjeux sur les chauves-souris sont d'autant plus importants que les espèces les plus sensibles à la lumière y sont protégées, ainsi que leurs habitats, à l'échelle européenne. En travaillant à l'interface entre urbanisation et habitats semi-naturels, nous avons pu montrer que c'est la quantité de lumière émise qui ont l'effet le plus notable. C'est donc ce paramètre sur lequel il faut travailler en priorité pour limiter l'impact de la lumière sur des zones pouvant servir de corridor ou de zone refuge aux espèces sensibles.

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“What if we woke up one morning only to realize that all of the conservation planning of the last thirty years told only half the story - the daytime story?”

Rich & Longcore 2006

GENERAL INTRODUCTION

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1. Global land-use change

The Earth is undergoing such dramatic and global environmental changes that it may have entered a new geological epoch, the Anthropocene, characterized by a human domination of the environment (Lewis & Maslin, 2015). Since the industrial revolution, the rate of global land use change greatly increased (Newbold et al., 2016; Venter et al., 2016). The rapid growth in the world population from less than two billions in 1900 to 6 billion in 2000 and a predicted rise to 10 billion by 2050 (Population Reference Bureau – www.prb.org) induced an intensification of the pressure on the biosphere's resources (Foley, 2005). Half of the planet's surface has been disturbed due to human activities and nowadays more than one-third of the global land surface is used for agriculture (Goldewijk & Ramankutty., 2009). This global change in land use is considered as a major driver of global biodiversity loss and ecosystems functions alteration (Newbold et al., 2016; Venter et al., 2016) through the loss, modification and fragmentation of habitats (Pimm & Raven, 2000). Moreover, the proportion of humanity living in urban areas increased dramatically (Grimm, Faeth, et al., 2008). Whereas only 10% of the world population were urban dwellers in 1900, currently, this percentage exceeds 50% and is predicted to rise to 66% by 2050 (Population Reference Bureau – www.prb.org) although urban areas represent less than 3% of the global terrestrial surface (Millenium Ecosystem Assessment, 2005). The shift in the human population's distribution toward urban areas provoked a major growth in cities size in terms of inhabitant number and spatial extent (Grimm, Foster, et al., 2008). It is also accompanied by the development of transport infrastructure to convey goods and people (Dulac, 2013). For most of the 20th century, the ecology of urban areas was little studied but recently, urban ecology gained attention (Grimm, Faeth, et al., 2008). Indeed, it may be of particular importance to preserve urban ecosystems as an increasing

proportion of the population and particularly children are less and less likely to have direct contact with nature thus reducing their willingness to conserve biodiversity (Keniger et al., 2013; Soga et al., 2016). In addition, the “extinction of experience” of nature (Pyle, 1993) might constitute a global health problem as several studies showed that the relatedness with nature is associated with a better health and general well-being (Kahn, 2002; Louv, 2005; Dean et al., 2018). Urbanization is one of the more lasting types of habitat loss (McKinney, 2002) and as the proportion of urban dwellers grows and with it the pressures on natural resources, it becomes increasingly important to raise people’s attention to the fundamental necessity to preserve nature (Savard, Clergeau, & Mennechez, 2000).

Biodiversity concerns in relation to urban areas are twofold: those considering the inner city scale and those considering the impact of urban areas on adjacent ecosystems (Savard et al., 2000). At the local scale, urban areas are often characterized by an intense fragmentation of the landscape with a few small vegetation or aquatic habitat areas embedded in a dense impervious matrix (Savard et al., 2000). Fragments of vegetation may be too small or too isolated to be used as habitats (Savard et al., 2000). At a larger scale, the expansion of cities toward rural landscapes generates pressures on adjacent ecosystems through changes in soils, the construction of structures and the development of transport infrastructures (Filippi-Codaccioni et al., 2008; Grimm, Faeth, et al., 2008). In cities, urbanization tends to reduce species richness (Grimm, Faeth, et al., 2008) and on a gradient from urban to rural landscapes, urban cores have the lowest species diversity (McKinney, 2002). Urbanization has been qualified as “one of the most homogenizing of all human activities” (McKinney, 2006). Indeed cities are built to fulfill only human needs and are hence similar throughout the world. This causes urban-adaptable species to become widespread and abundant in cities across the planet (McKinney, 2002) whereas species dependent on natural habitats are excluded. This shift favors generalist species over specialist species and alters biological communities toward biotic

homogenization (McKinney, 2006; Le Viol et al., 2012). As urban areas impact extends beyond administrative borders, urbanization could also reduce species diversity at regional and global scales (Grimm, Faeth, et al., 2008). Although the outward impact of urban areas mostly concerns rural and semi-natural landscapes, the distance between protected and urban areas decreases over time (McDonald, Kareiva, & Forman, 2008). Moreover, in Europe, the majority of protected areas include a significant part of human activities (European Environment Agency, 2012) thus making them more prone to suffer the impacts of urbanization.

In addition to soil sealing, the urbanization process is accompanied by the emission of environmental stressors such as chemical, noise and light pollution. Their impact on biodiversity is not always assessed although they could be cumulative with the effects of soil sealing (Gaston et al., 2014) and their consideration may be essential to produce effective land-use planning strategies (Grimm, Faeth, et al., 2008). Amongst these pollutants, light pollution was identified as an emerging (i.e. new and poorly known) threat to biodiversity (Hölker, Moss, et al., 2010; Hölker, Wolter, et al., 2010; Stanley et al., 2015).

2. Light pollution

During the 20th century, the shift toward a more urban population was accompanied by the development of electric lighting. With the growth of urban settlements, transport infrastructure and economic activities increased leading large areas of the globe to be subjected to artificial light (Bennie et al., 2014). Nowadays, artificial lighting is estimated to consume 0.72% of the world gross domestic product and about 6.5% of the world primary energy (Tsao & Waide, 2010). The widespread use of artificial light at night (ALAN) has enhanced human quality of life and is commonly associated with a sense of security, wealth and modernity (Hölker, Wolter, et al., 2010). However, the rapid multiplication of light points considerably transformed the nocturnal landscape worldwide. This change can be appraised both

quantitatively with a yearly 6% increase in light emission (Hölker, Moss, et al., 2010) and qualitatively through the change in color spectra (Elvidge et al., 2007). Globally, 80% of the world population lives under light-polluted skies (Falchi et al., 2016). And whereas most of the population lives in the 3% of the global land surface representing urban areas (Grimm, Faeth, et al., 2008), over 20% of the world land surface experience light-polluted nights (Falchi et al., 2016). Artificial light is mainly associated with human constructions such as cities, plants and transport infrastructures (Hale et al., 2013) but it can diffuse way beyond urbanized landscapes and could affect an important proportion of surrounding ecosystems (Kyba & Hölker, 2013). Indeed, although light can be seen as a point source that affects its close environment, it can also have a far reaching impact through skyglow (Kyba & Hölker, 2013). Light reflected upward and light emitted above horizontal is scattered in the sky and rebounds on particles hence being redirected toward the Earth and creating a halo of light kilometers away from their source point (Kyba et al., 2015). The impact on nocturnal landscapes is so intense that it can be seen from space (Fig. 1) and due to its extent and continuous increase, it can be considered as a global change.



Fig. 1. Composite image of the Earth at night made using data from satellite imaging (VIIRS) (source: NASA)

Astronomers were the first to state that artificial light degraded the human view of the night sky by reducing the visibility of celestial bodies (Smith, 2009) and named this phenomenon astronomical light pollution (Riegel, 1973). Recently, several other negative effects have been recognized in ecology, human health and well-being (Catherine Rich & Longcore, 2006; Navara & Nelson, 2007). Ecological light pollution (henceforth, light pollution) is defined as the artificial light that alters the natural spatial and temporal patterns of light and dark in ecosystems (Longcore & Rich, 2004). Hence, one of the main impacts of light pollution is the disruption of the circadian rhythm, arguably one of the most important organizational cue in the biological world (Bradshaw & Holzapfel, 2010). Daily and seasonal light cycles have driven the development of biological phenomena from molecules to ecosystems, including metabolic and physiological pathways, behavior and spatial distribution of species and ecosystem cycles (Bradshaw & Holzapfel, 2010; Gaston, Gaston, et al., 2015; Gaston et al., 2017). Endogenous biological clocks are essential for individuals' anticipation and adaptation to the daily and seasonal light-dark cycles in their environment as it allows them to optimally time their metabolism, physiology and behavior (Navara & Nelson, 2007). For example, individuals can adapt their reproductive rate and timing based on changes in day length throughout the season (rodents: Ikeno, Weil, & Nelson, 2014; bird: Dominoni, Quetting, & Partecke, 2013a); many taxa adjust their foraging activity according to changes in lunar cycle (birds: Brigham & Barclay, 1992; rodents: Kotler, 1984; bats: Saldaña-Vázquez & Munguía-Rosas, 2013; marine mammals: Horning & Trillmich, 1999); and the daily variation of light and dark is also essential for the regulation of hormonal systems in a large array of taxa including bird (Dominoni, Goymann, et al., 2013), rodent (Atkinson & Waddell, 2008), fish (Brüning et al., 2015), and human (Haim & Zubidat, 2015a). The apparition and wide spread of artificial light dramatically altered a thousands of years old cycle on a significant proportion of the world's land surface hence impacting biodiversity and ecosystems (Navara & Nelson,

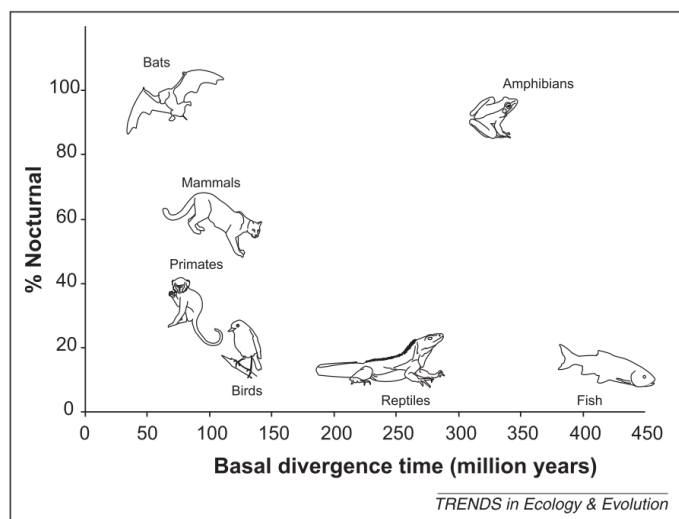


Fig. 2. Percentage of extant nocturnal species within different vertebrate classes and orders (extracted from Hölker, Wolter, et al., 2010).

2007). Among all organisms, nocturnal species might be the most impacted by ALAN and they represent a large proportion of biodiversity. Indeed, 30% of all vertebrates and over 60% of all invertebrates are nocturnal (Hölker, Wolter, et al., 2010) (Fig. 2). Over two decades (1992-2012), the mean light intensity increased in the ranges of the majority of mammals worldwide and

nocturnal species were more likely to experience this increase (Duffy et al., 2015). Moreover, although protected areas end to be darker than non-protected lands, they still suffered a low increase in ALAN in recent years (Gaston, Duffy, & Bennie, 2015; Guetté et al., 2018). Actually, light pollution is important in the direct surroundings of protected areas potentially isolating them from one another (Guetté et al., 2018). This alarming observation suggests that the importance to manage artificial lights is underestimated. Indeed, light pollution is seldom considered as a criteria to designate protected areas (Gaston, Duffy, et al., 2015) although the International Dark-Sky Association is leading an initiative to create dark sky reserves to facilitate and promote celestial bodies observation (Welch & Dick, 2012).

3. Light pollution's impacts on biodiversity

Light is the main source of energy of most primary producers and a crucial factor in the control of a large number of physiological and behavioral processes (Schroer & Hölker, 2016; Gaston et al., 2017). Light can be a signal for growth, hormonal secretion, spatial movements, orientation and communication. It has a central role in structuring communities and ecosystems

through its influence on trophic, social and competitive interaction and in shaping seasonal and daily rhythms (Schroer & Hölker, 2016).

3.1. Diversity of perception of a fundamental cue

Throughout evolutionary times, species acquired a temporally differentiated niche often associated with a specially adapted eyesight (Hölker, Wolter, et al., 2010). In the animal kingdom, a large range of adaptations of the vision exists to navigate in the environment with different light levels and color spectra (Warrant, 2004; Davies et al., 2013). However the rapid expansion of artificial light worldwide (Hölker, Moss, et al., 2010) will induce profound changes in nighttime light level and spectra potentially rendering ineffective adaptation acquired through thousands of years of evolution. An important number of animal species are able to see at light levels way below the necessary level required for humans to see properly (Gaston et al., 2013). Moreover, while humans perceive light between 400 and 700 nm as visible light, other animals can have a significantly different sensitivity both in range and perception depth. For example, birds and reptiles have four different photoreceptors (mammals only have two) hence increasing the information content of the color perception across a large part of the spectrum (Osorio & Vorobyev, 2008). In addition, birds, fish and invertebrates are sensitive to ultraviolet (UV) light (10-400 nm) and snakes and beetles can detect emissions in the infrared range (700-1000 nm) that are not perceived by the human eye (Rowse et al., 2016). Depending on organisms' spatial and temporal niche and on their sensory abilities, ALAN can enhance, disrupt or not affect their perception of light with potential downstream physiological, behavioral and ecological effects (Gaston et al., 2013).

3.2. Effects of light on daily biological events

The alteration of the natural light level by ALAN modifies the perception of day length for both nocturnal and diurnal organisms. Indeed artificial light has been shown to modify the pattern of daily activity of birds (de Jong, Jeninga, et al., 2016) but without modifying their internal biological clock when considering short time period of exposition (6 to 14 days) (Kamiel Spoelstra et al., 2018). However a longer exposition (4 to 14 weeks) changed the expression of a circadian clock gene in rodents and it also changed the expression of genes implicated in the regulation on the hormone melatonin (Ikeno et al., 2014). Melatonin has a central role in the regulation of the circadian rhythm and is involved in seasonal processes for many taxa (Dominoni, Goymann, et al., 2013). It is secreted cyclically being released at night and suppressed by daylight and regulates daily timing such as sleep and body temperature (Dominoni, Goymann, et al., 2013). Artificial light inhibits the secretion of melatonin in a large array of taxa (birds: Dominoni et al., 2013; insects: Durrant et al., 2015; mammals: Haim, Zubidat, & Haim, 2015; fish: Brüning et al., 2016) hence disrupting sleep (Yorzinski et al., 2015; Stenvers et al., 2016; Raap et al., 2017) and activity patterns (Letallec, Théry, & Perret, 2015; de Jong, Jeninga, et al., 2016; Hoffmann, Palme, & Eccard, 2018). As presented thereafter, these modifications may have significant impacts on individuals fitness and health (M. Jones et al., 2015; Ouyang et al., 2015).

Artificial light can have important impacts on foraging timing in two ways. First, light can modify the timing of the foraging activity onset. For example, lighting bats' roosts entrance delays their emergence time (Downs et al., 2003; Boldogh et al., 2007) and may hence miss the peak activity of insects therefore reducing their foraging efficiency and decreasing their reproductive success (Fig. 3; Boldogh et al., 2007). On the contrary, several diurnal bird species extend their foraging time into the night when in the vicinity of a light source (Fig. 4; Da Silva, Diez-Méndez, & Kempnaers, 2017) and can increase their reproductive success (Stracey et al., 2014) and reduce their energy expenditure (Welbers et al., 2017) although it does not necessarily influence their body condition (Russ, R uger, & Klenke, 2015) (Russ et al., 2015). Light can also modify individuals' ability to detect preys and hence reduce (Buchanan, 1993) or increase (Santos et al., 2010; Dwyer et al., 2013) their food intake.

The most damaging effects of light pollution might be its influence on organisms at low levels of the trophic chain. The diel migration of zooplankton is sensitive to very low levels of

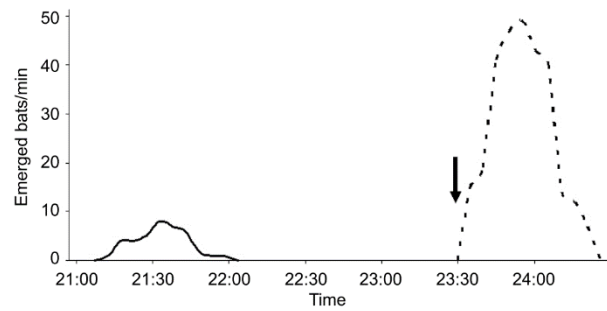


Fig. 3. The nightly emergence activity of *M. emarginatus*, in an illuminated (dashed line) and a non-illuminated roost (continuous line) during the same night. Arrow shows the time when lights were switched off at the illuminated roost (extracted from Boldogh et al., 2007)

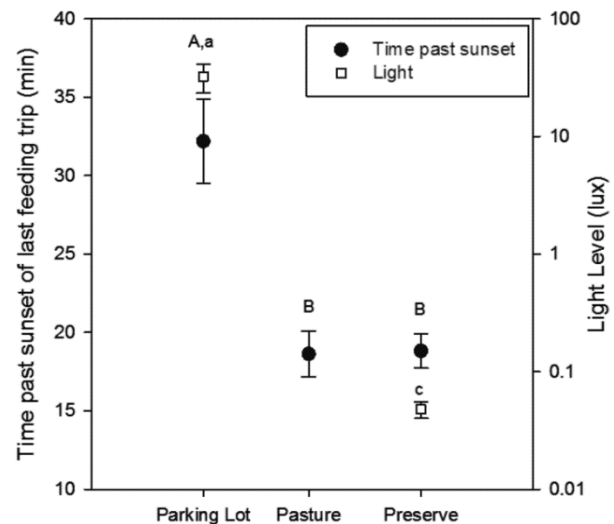


Fig. 4. Average minutes past sunset of last nestling feeding trip and average light level at night within a 20-m radius of nests (adapted from Stracey et al., 2014).

lights and can be significantly reduced both in amplitude (height in the water column) and magnitude (number of individuals) (Moore et al., 2000). Another example are plants which heavily rely on light as a resource and as an information signal for many physiological processes. Plants have a wide range of photoreceptors to respond to light quality, quantity, direction and duration presenting a diversity of sensitivity from large variation to light levels barely perceivable by the human eye (Briggs, 2006).

3.3. Effects of light on seasonal biological events

Depending on the latitude, day length varies significantly throughout the year providing a vital biological cue allowing the anticipation of changes in resource availability and climatic conditions. In urban areas, as artificial lighting is used to facilitate human activities by night, lights are turned at the beginning and end of the night. Hence dawn can be perceived as starting earlier and dusk to last longer thus potentially impact species physiology and even more so at high latitude (Gaston et al., 2017). Most studies evaluating the influence of artificial light on seasonal phenomenon focus on reproduction as it is a key event for population viability. A large array of effects on the both the timing and the success of reproduction have been demonstrated in a variety of taxa.

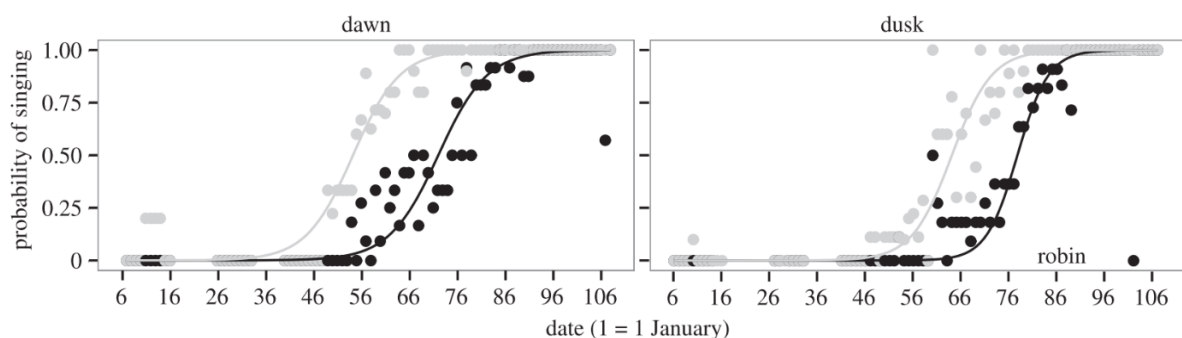


Fig. 5. Observed and predicted daily probability of singing at dawn and at dusk for the European robin at sites with artificial night lighting (grey dots and lines) and for non-lighted sites (black dots and lines) (adapted from Da Silva, Valcu, & Kempenaers, 2015)

Artificial light tends to elicit an earlier start of the reproduction in diurnal songbirds through an advance in dawn and dusk chorus (Fig. 5 ;Da Silva et al., 2015), in gonadal development (Dominoni, Quetting, et al., 2013a) and in laying date (Kempnaers et al., 2010). A disruption of the reproduction timing was also found in nocturnal mammals but in opposite ways by advancing of the estrus for mouse lemurs (Letaltec et al., 2015) and retarding birth in wallabies (Robert et al., 2015). Similarly, plants flowering time can also be modified by the presence of light stimuli. Different plant species can respond to light of different spectra and intensity in completely different ways and flowering can be either induced, suppressed, increased or reduced by light pollution depending on the species sensitivity (Briggs, 2006; Bennie et al., 2016). These changes in timing may have significant effects on reproduction success as they could cause mismatches in the timing of interdependent life history events (Helm et al., 2013).

Light can alter the reproductive success through many mechanism such as an alteration in mating partner detection (glow-worms: Bird & Parker, 2014) and attractiveness (newts: Secondi, Lepetz, & Théry, 2012) or a deregulation of reproductive hormonal secretions in birds (Schoech et al., 2013). A more drastic effect is the complete inhibition of reproduction (van Geffen et al., 2015). For example, a 2-years-long exposure to low light levels at night (0.3 lux) inhibited the development of the reproductive system of male blackbirds with an absence of testicular size and testosterone concentration increase during the reproductive season (Dominoni, Quetting, & Partecke, 2013b). Such dramatic effect may have profound impacts on population dynamics. A similar inhibition phenomenon was shown in coral's with light altering genes expressions and thus inhibiting coral mass spawning (Kaniowska et al., 2015). As corals reproductive success is crucial for the maintenance of coral reef ecosystems, light pollution could have major cascading effects.

In addition to influencing the onset and the proceeding of reproduction, light can disturb individuals' growth and development. Nestlings of great tits subjected to artificial light in their nest boxes had a reduced rate of body mass increase compared to nestlings in natural light (Raap, Casasole, Costantini, et al., 2016) and had lower levels of molecules implicated in the development of the immune system (Raap, Casasole, Pinxten, et al., 2016). Moth development is also altered by light through the inhibition of pupal diapause which could both reduce their fitness and increase mortality rates (van Geffen et al., 2014). Similarly, toads early stage development was modified by the presence of ALAN, reducing the metamorphic duration and their post-metamorphic growth rate by 15% (Dananay & Benard, 2018). A nation-wide study showed that plant development phenology can also be modified by anthropogenic light emissions. Indeed, it showed that deciduous trees budburst is advanced by up to 7.5 days in brightly lit areas (ffrench-Constant et al., 2016). Moreover, there has been several independent



Fig. 6. Defoliated *Betula pendula* except in the light cone of high-pressure streetlight (Image taken in Berlin, Germany, December 2015, by Sibylle Schroer)

observation of deciduous trees keeping leaves close to a light source longer than those that were further away in autumn (Fig. 6 ;Bennie et al., 2016). Both budburst and leaf fall timings are determinants of tree's exposure to frost damage and fungal pathogens (Bennie et al., 2016) thus early budburst and late leaf loss due to light pollution may have deleterious implications for deciduous trees.

Most studies evaluating the influence of light on seasonal events concentrate on reproduction however other physiological

phases could be impacted such as hibernation or migration. Indeed, exposition to ALAN has been shown to alter swans wintering behavior and advance their departure for spring migrating (Longcore, 2010).

3.4. Effects of light on movements and spatial distribution

Many animal species that move by night use celestial bodies as cues for direction (Gaston et al., 2017). For example, nocturnal insects can navigate using moonlight and the pattern of polarized celestial light (Dacke et al., 2003) and migrating birds are thought to calibrate their inner magnetic compass through the detection of polarized light patterns during sunset and sunrise (Muheim, 2006). In addition, bird migration direction is dependent on magnetoreception through photoreceptors and red light can disrupt this mechanism (Wiltschko et al., 1993). The increase in nocturnal light emissions may hinder stars visibility thus disrupting individual's orientation (Kyba et al., 2011). Nocturnal animals may also need low light levels for their eyesight to function properly (Buchanan, 1993). On the opposite, some species such as little penguins can take advantage of ALAN to navigate nocturnal landscapes more easily (Rodríguez et al., 2018) and shorebirds and waders can benefit from light through improved visibility to exploit lit areas for foraging (Santos et al., 2010; Dwyer et al., 2013).

The widespread attraction of insects to light have long been documented and exploited through light-trapping for their capture. This flight-to-light behavior exists in at least seven insect orders (Altermatt, Baumeier, & Ebert, 2009; Roy H. a van Grunsven et al., 2014; de Medeiros, Barghini, & Vanin, 2017) and can be elicited at distances of more than 100 m (Frank, 2006). The attraction reach is dependent of the species, the type of lamp and the light intensity thus different lamps will attract different species in different magnitude (Roy H. a van Grunsven et al., 2014). Ultraviolet emissions are particularly impacting. Indeed, the number of moths

captured at UV emitting mercury vapor lamps can be four to 100 times higher than at sodium vapor lamp emitting no UV (Frank, 2006).

Attraction to light manifests in several ways described by Eisenbeis (2006). First, insects can be disturbed in their activity by entering the attraction zone of a light source. It will then fly around the lamp endlessly and be captured by predators or fall exhausted to the ground where it will die or be caught by a predator. This phenomenon is called “fixation” or “captivity”. The second manifestation is the attraction of otherwise non-moving insects that will hence be “fixed”. This effect is called the “vacuum cleaner” as it may deplete local populations. A study found that urban moths are less inclined to be attracted to light than moth born in dark-sky

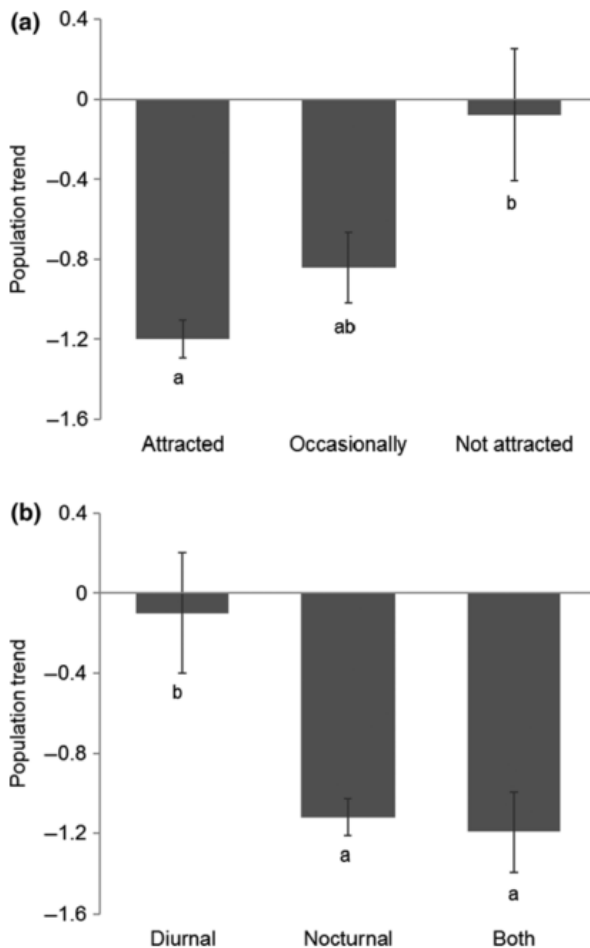


Fig. 7. Mean population trends for moth species that differ in (a) phototaxis and (b) adult circadian rhythm (extracted from van Langevelde et al., 2018).

habitats thus showing a possible evolutionary modification of their behavior (Altermatt & Ebert, 2016). However, light pollution has been suggested to possibly be an important factor of large scale decline in insects’ populations (Frank, 1988; Conrad et al., 2006). As nocturnal insects have a major role in pollination and as a primary food source for many vertebrates, important decrease in their populations would have numerous cascading effects. Despite being of primary concern (Sutherland et al., 2006), it’s only recently that study evaluated large scale effects of light pollution on insects. Wilson et al. (2018) used a 11 years dataset on 100 species of moths gathered through a

large scale moth light-trapping citizen science program to identify and quantify the role of ALAN in long-term changes in moth populations in the UK and Ireland. Their results showed that nighttime lighting could explain 20% of the variation in long-term changes in moth abundance thus bringing evidence that light pollution contributes significantly to moth species decline for the first time. In addition, another recent study demonstrated that that nocturnal moth species exhibiting positive phototaxis have stronger negative population trends than diurnal moth species (Fig. 7 ;van Langevelde et al., 2018).

Moreover, the attraction of insects to light induces a change in prey spatial distribution for insectivorous predators which can modify their foraging opportunities. Predators eating invertebrates attracted to light benefit from the accumulation of preys under lights halo as a spatially and temporally stable resource area (bats: Rydell, 1992; invertebrates: Davies, Bennie, & Gaston, 2012, van Grunsven et al., 2018; birds: Pugh & Pawson, 2016) and are therefore indirectly attracted to light (Fig. 8 ;bats: Blake et al., 1994; toads: Wise, 2007; birds: Pugh & Pawson, 2016; slugs: van Grunsven et al., 2018).

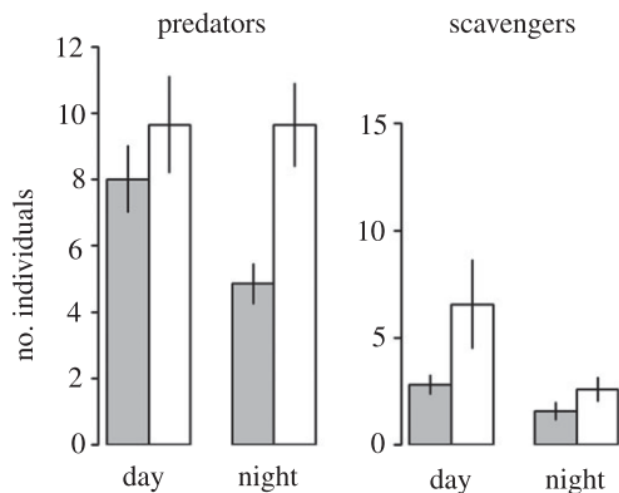


Fig. 8. The effect of high-pressure sodium street lighting on the abundance of individuals within trophic groups of invertebrates. Bars represent the average total number of individuals in each group collected from pitfall traps deployed under street lights (open bars) and between street lights (grey bars) (extracted from Davies et al., 2012).

During migration and dispersion, many species use light as an information cue to determine their direction and the presence of anthropogenic light can attract them and thus make them deviate from their original trajectory. When migrating, bats (Voigt, Roeleke, & Marggraf, 2017) and birds (H. et al., 2008; Van Doren et al., 2017; McLaren et al., 2018) can be attracted to light sources hence potentially increasing their energy expenditure and modifying their habitat selection therefore affecting their fitness. Similar effects have been found during dispersal for several turtle species hatchlings (Hetzler et al., 2016; Cruz et al., 2018) and for seabird fledglings (Rodríguez et al., 2014) with direct impacts on their survival (Rodríguez et al., 2017) and the recruitment rate in the population (Dimitriadis et al., 2018).

On the contrary, other species such as diurnal birds avoid light at night and chose nesting sites hidden from light halos (Yorzinski et al., 2015; de Jong, Ouyang, et al., 2016). Nocturnality may have been an evolutionary adaptation to avoid diurnal predators (Hölker, Wolter, et al., 2010; Russo et al., 2017) thus many nocturnal species show an avoidance response to light (Wise, 2007; Threlfall, Law, & Banks, 2013; Farnworth, Innes, & Waas, 2016; Azam et al., 2018). However the avoidance may depend on the seasonal timing such as in toads which can

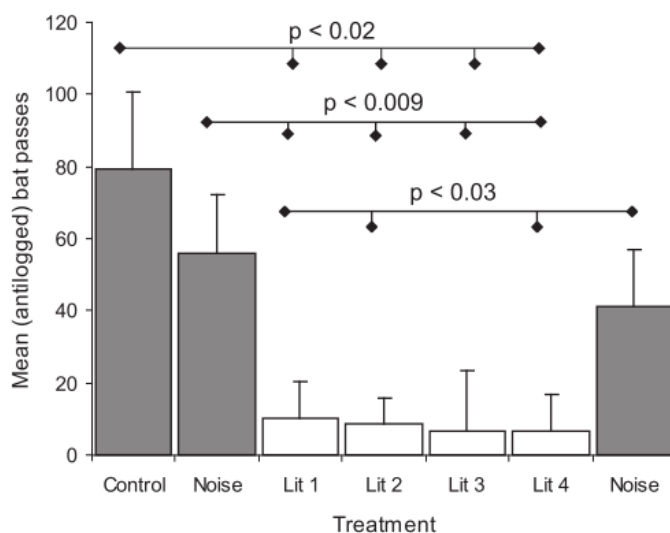


Fig. 9. *R. hipposideros* mean activity along hedgerows in relation to treatment type. Significant within-subject differences are shown with p values (extracted from Stone, Jones, & Harris, 2009).

forage under streetlights (Wise, 2007) but will avoid light during migration (Roy H. A. Van Grunsven et al., 2017). The repulsion by light may be so intense that it can be perceived as a barrier to movement. Some bat species are known to be light sensitive and will turn back if the hedge they follow as a transiting route is illuminated (Fig. 9 ;Kuijper, Schut, & Dulleman, 2008;

Stone et al., 2009; Stone, Jones, & Harris, 2012). In addition other bat species that are considered to be light tolerant can also perceive light has a barrier when an hedge they transit along in discontinuous and gaps are brightly lit which can lit to a reduction in the proportion of landscape accessible (Fig. 10 ;Hale et al., 2015). These effects on nocturnal species movement behavior have only been studied at local scales

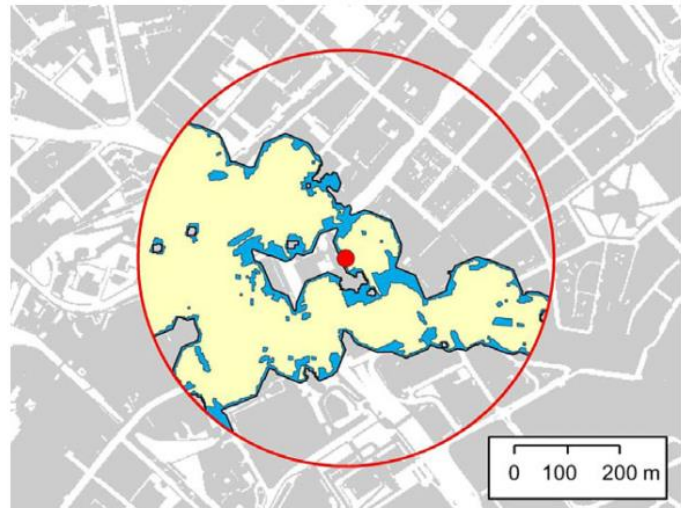


Fig. 10. Predicted areas of accessible land cover within 350 m (red circle) of an urban pond (red dot), under a scenario with no light (blue) and a scenario with normal street lighting (yellow). When no lighting is present, 44% of the local landscape is accessible from the pond, shrinking to 36% in lit conditions (extracted from Hale et al., 2015).

but they may have important consequences on individual's ability to travel through a landscape (Beier, 2006). Studies suggested that landscape connectivity could be altered by ALAN for terrestrial and flying mammals (Beier, 1995; Hale et al., 2012; Bliss-Ketchum et al., 2016) but it has never properly been tested. Due to the importance of movement for individual survival, population maintenance and ecosystem functioning (Nathan et al., 2008) the spatial extent of light pollution, the modification of species movement ability by ALAN may have far reaching consequences on species and communities.

A recent study on the influence of ALAN on bat activity at a national scale showed that bats able to forage around streetlights at a local scale exhibit an avoidance pattern when considering a large scale (Azam et al., 2016). This finding reinforce the necessity to consider the impacts of artificial light at several spatial scales in order to include different movement behaviors.

3.5. Effects of light on interactions and community composition

As a wide range of species responds to anthropogenic light and this raises concerns about the consequences for ecosystems functioning and stability (Sanders & Gaston, 2018). The avoidance behavior of certain species may lead to their absence of lit areas and therefore modify local communities. Most research focus on single species effects however it is necessary to understand how interaction networks are modified to be able to predict the overall impact of ALAN. Depending on its place and links in a network, if a single species or interaction is affected by light, it may have important repercussions on the rest of the network through direct and indirect interactions modifications (Sanders & Gaston, 2018).

Studies showed that nighttime lighting could change communities composition of terrestrial invertebrates (Davies et al., 2012, 2017), marine epifauna (Davies et al., 2015), periphyton (Grubisic et al., 2018) and plants (Bennie, Davies, Cruse, Bell, et al., 2018). All these communities represent food sources for many other organisms hence changes in species assemblage and abundance can alter trophic chains through bottom-up control. A decrease in plant flowers abundance can lead to a decrease in herbivore predator abundance (Bennie et al., 2015; Bennie, Davies, Cruse, Inger, et al., 2018) and a change in plants propriety (e.g., the toughness of grass blades) can be linked to a reduce body mass in predators hence affecting their survival (Grenis & Murphy, 2018). Light may also change the timing of plant growth (ffrench-Constant et al., 2016) and could cause a desynchronization with herbivore species which time their emergence to coincide with the apparition of leaves making them miss the peak abundance of food resource and altering their growth or survival. The modification of prey spatial distribution may also change predators foraging behavior. For example, insect preys attracted to light represent a spatially stable source of food thus locally increasing predator and scavenger abundance (Davies et al., 2012; Azam et al., 2015; van Grunsven et al., 2018) and modifying the prey items they consume in relation to their phototaxis sensitivity (Rydell, 1992).

Prey-predator relationships can be affected by the presence of light through the alteration of anti-predatory strategies such as the evasive flight maneuvers used by moths to avoid bat predation and that are less often observed when moths are flying close to a lamp (Minnaar et al., 2015; Wakefield et al., 2015). Artificial light may also trigger top-down control such as a decrease of nocturnal prey activity due to a perceived increased predation risk in lit environments (Rydell, 1992) or an increase of predators activity at lit sites hence reducing prey abundance (Bolton et al., 2017).

Although most of the interactions investigated are trophic interactions, ALAN can also alter interaction networks in other ways. It has been suggested that light could increase interspecific competition between bat species responding differently to light (Arlettaz, Godat, & Meyer, 2000). Indeed, light adverse bat species may be disadvantaged compared to bat species foraging at streetlights when competing for similar insects preys that are attracted to light. Modification in host-parasitoid dynamics also occur through direct effects of light on parasitoid or indirect effect of light through a modification in host abundance (Sanders et al., 2015).

The modification of species distribution and behavior by light pollution affects major ecosystem functions such as pollination. Moth attracted to light are more abundant at high altitudes (few meters) than at the ground level when in direct proximity of a lamp and this might disrupt their role in pollen transportation (Macgregor et al., 2017). Plant pollinated only by diurnal insects have a reduced seed production and pollen dispersal compared to plants pollinated by both diurnal and nocturnal insects (Young, 2002) hence nocturnal pollinator may have an important role in plants reproduction. A recent study showed that light reduced nocturnal pollinators visits by more than 60% compared to dark areas and it resulted in a 13% reduction in fruit set although plants were visited by diurnal pollinators (Knop et al., 2017). In addition, the structure of the interaction network between plants and nocturnal and diurnal

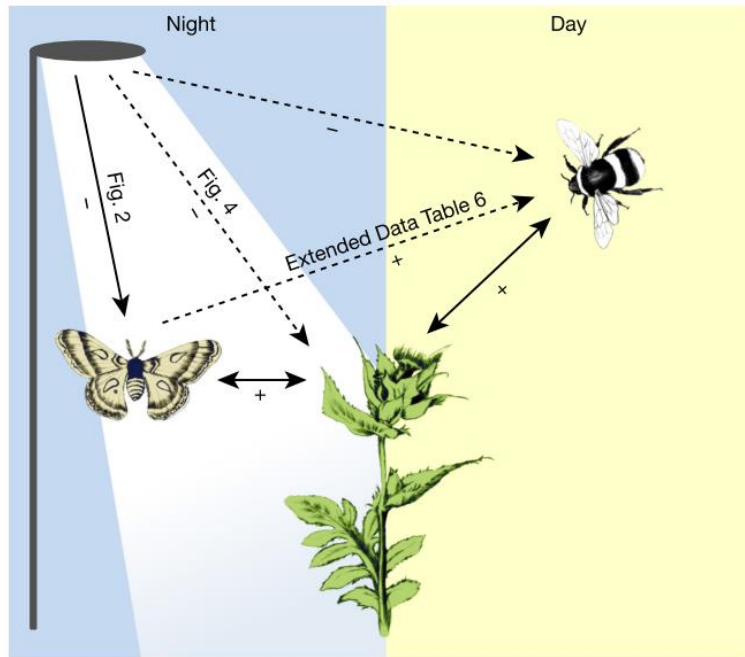


Fig. 11. Interaction web showing the pathway by which artificial light at night affects plant reproduction and diurnal pollinator communities. Solid arrows indicate direct interactions; dashed arrows denote indirect interactions. The sign (+ or -) refers to the expected direction of the direct or indirect effect (extracted from Knop et al., 2017).

pollinators tends to facilitates the spread of negative consequence of disrupted nocturnal pollination to daytime pollinators communities (Fig. 11 ;Knop et al., 2017). Indeed, as daytime pollinators may feed on plants fruit set, a reduction in their number due to disrupted nocturnal pollination could in turn negatively affect their populations. Nocturnal

pollinators are not redundant to diurnal communities and a decrease in their pollination function could have important impacts on plant diversity (Fontaine et al., 2005). In tropical areas, plants reproduction can also be altered through the disruption of seed dispersers behavior such as frugivorous bats as they tend to avoid harvesting illuminated plants (Lewanzik & Voigt, 2014).

Overall, artificial light at night affects all aspects of organisms' life history through behavioral and physiological alterations. This changes may in turn have important cascading effects on communities' composition and ecosystems' interaction networks. Studies on the impact of light pollution continue to multiply showing mounting interest and concerns from researchers. However, there is a lack of knowledge on the overall long-term impact of anthropogenic light on the spatiotemporal dynamics of population and biological communities. Nonetheless, lighting technologies continue to develop into novel lamp types and the number

of light points keeps on increasing. Very few light regulations exist to limit the effect of ALAN although there is an urgent need to develop mitigation measures to reduce the impact of this novel threat to biodiversity and ecosystems.

4. The conservation challenge posed by light pollution

4.1. Why should light pollution be a focus of environmental research in the 21st century?

In recent years, environmental scientists showed a growing concern over recognized and potential impacts of artificial light on biodiversity and ecosystems which translated in a growing body of scientific literature. As it is globally widespread, expanding and immediately and severely affects a large phylogenetic diversity of taxa, ALAN can be considered as a driver of global change (Davies & Smyth, 2017). Moreover, it has been shown that light pollution large scale impacts on bats may be of similar or larger magnitude than other well studied anthropogenic pressures such as agriculture and soil sealing (Fig. 12 ;Azam et al., 2016). The variety of organisms' sensitivity to light intensity and spectrum make the

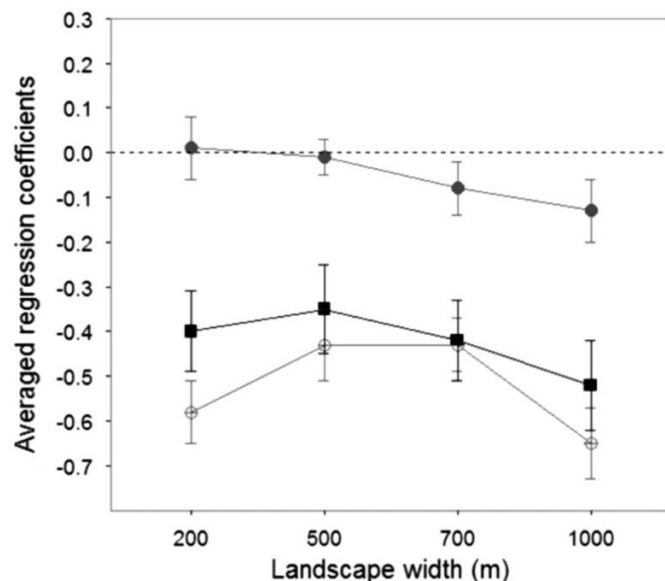


Fig. 12. Averaged standardized partial regression coefficients and associated standard errors from GLMMs model for the radiance (black squares), the proportion of impervious surfaces (filled grey dots) and the proportion of intensive agriculture (grey empty circles) for *E. serotinus* at 200, 500, 700 and 1000 m landscape scales. The 3 landscape variables have a significant effect on the probability of presence when the error bars of coefficients do not overlap with the 0-horizonal dashed line (extracted from Azam et al., 2016).

reduction of light pollution while complying with human societies a major conservation challenge. Nonetheless, it is technically easy to reverse it through light extinction. Contrarily to other pollutions such as fossil fuel combustion gas emissions, there would be no lag effect on the return of the physical environment to its dark state and the biological environment would immediately start its recovery process (Davies & Smyth, 2017). Indeed, experimentally illuminating a hedge used by light-sensitive bats as a commuting route had an immediate effect as bats stopped to taking this route but when turning off the light a few days later, bat activity was brought back to its original level (Stone et al., 2009, 2012). Moreover, although light can disturb individuals' daily activity pattern, it seems that it is a direct adaptation of their behavior to the presence of light rather than an alteration of their inner circadian clock (Kamiel Spoelstra et al., 2018). Even a change in genetic expression following a long exposition to light at night (Ikeno et al., 2014) may be due to reversible epigenetic modifications (Haim & Zubidat, 2015b). Nevertheless, all these conclusions were drawn from the study of individuals submitted to artificial light at night during a short time period and long-term exposition may have more profound effects. However, it is not unreasonable to surmise that the impact of ALAN on populations, communities and ecosystems subjected to light at night since many years might not be entirely reversible. We can speculate that the direct (e.g., increased mortality rates of insects sensitive to phototaxis) and indirect (e.g., reduced pollination due to behavioral alteration of pollinators) influence of ALAN could have such dramatic impact on populations and communities that turning off lights may not allow to return to the original state of ecosystems.

The major obstacle to limit light emissions is the acceptability by the general population. Several mitigation tools could be used to reduce artificial nighttime lighting impacts on biodiversity through land management (dark-sky reserves, dark corridors) and technical adaptation (light spectrum selection, reduction in intensity).

4.2. Current and future lighting

Most studies focus on outdoor public lighting because it is the most persistent, aggregated and intense source of lighting in urban areas (Gaston et al., 2012). Indeed light emissions from street lighting are responsible for 30 to 50% of light pollution in cities (Hiscocks & Guömundsson, 2010; Kuechly et al., 2012). Street lighting is the more pervasive source of lighting worldwide and, for example in Europe, there is one light point for each nine inhabitants (E-street, 2008). In addition, as it is managed at a relatively large scale it may be the easiest point of entry to have a global reaching reduction in light pollution by adapting its management.

The global trend tends toward an increase of artificial light at night (Hölker, Wolter, et al., 2010) and an increase in the number of outdoor lighting points (International Energy Agency, 2006). In France, this is reflected in municipalities' budget allocated to street lighting which can represent up to 45% of electricity costs (ADEME, 2011). Moreover, it is estimated that more than 20% of street lights are dilapidated and more than a third of the installations are over 20 years-old (ADEME, 2011). It is considered as opportunity to increase the energetic performance of outdoor lighting by lighting engineers. Indeed, the European Union aims at globally and drastically reducing energy consumption and greenhouse gas emissions in the near future. This foreseen change can also be seen as an occasion to include reflection on public lighting impact on biodiversity in land management.

The global energy transition contributes to an important dynamic of development of new lighting technologies such as solid state lighting (e.g., light emitting diodes - LED) that have a better energy efficiency. Such lamps also tend to have a broader spectrum than older technologies (e.g. low and high pressure sodium lamps – LPS and HPS; Fig. 13) and emit a whiter light that has a better color rendering hence enhancing visual performances for humans. These properties associated with a lower cost induce a rapid invasion of LEDs in the lighting

market (Mckinsey, 2012). Indeed in 2012, LEDs represented 9% of the market, 45% in 2016 and are predicted to reach 70% of the market in 2020 (Mckinsey, 2012; Zissis & Bertoldi, 2014). LEDs are also advocated for their numerous possibilities of tailoring in terms of spectrum, intensity and timing. Yet many environmental scientists and human health experts have raised concerns about the important proportion of blue wavelengths emitted by common LEDs as it is the most impacting part of the spectrum for numerous species including our own (Davies & Smyth, 2017).

There is an urgent need to start considering light impacts on ecosystems in lighting planning and the development of collaborations between environmental scientists and lighting engineers may help taking advantage of this transition to implement a more biodiversity-friendly street lighting.

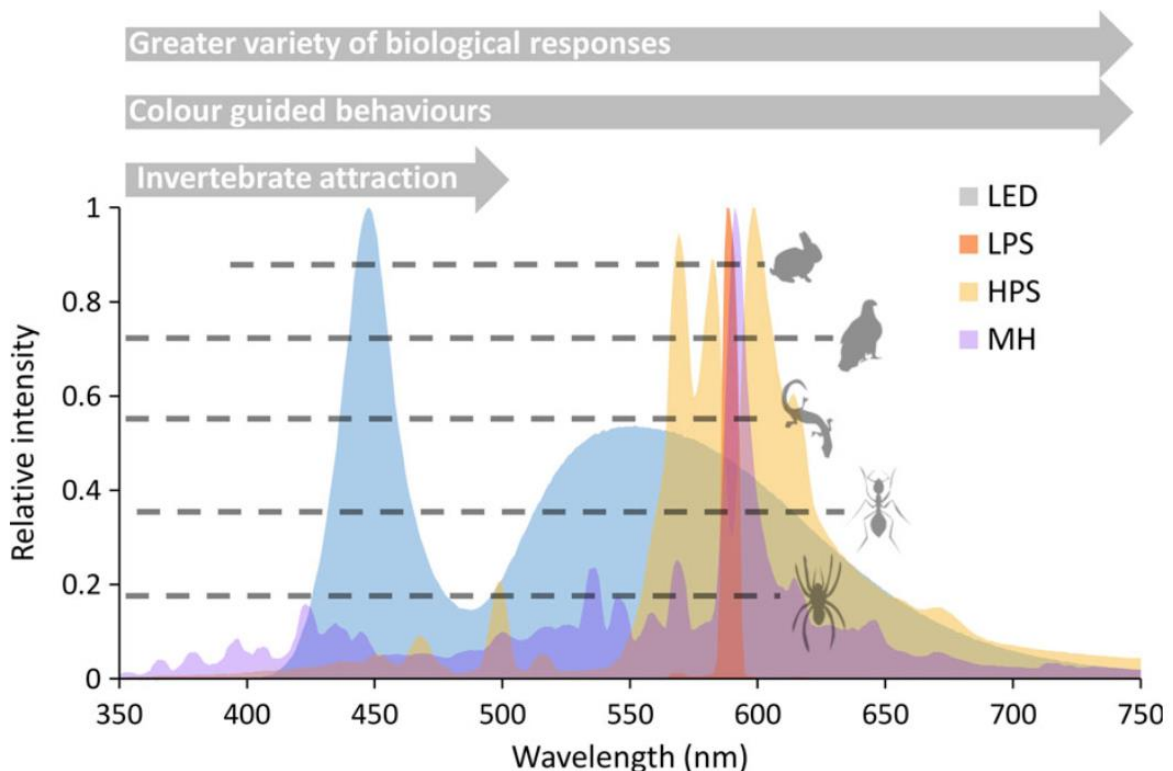


Fig. 13. The potential ecological impacts of white LED lighting compared to other light sources. Spectral power distributions are given for white Light-Emitting Diode (LED), Low-Pressure Sodium (LPS), High-Pressure Sodium (HPS) and Metal Halide (MH) lamps. Grey arrows represent the wavelength range over which different types of biological response are expected/recorded. Dashed lines represent the range of wavelengths over which mammal, bird, reptile, insect and arachnid visual systems can detect light (extracted from Davies & Smyth, 2017).

5. Management and technical levers of action

5.1. Policies gaps

Following the definition of the European Environment Agency, artificial light qualifies as a pollution however, in the same way as noise and other physical pollutions (as opposed to chemical pollutions), they are seldom considered in the legislation. Chemical pollutions of the air, soil and water are submitted to regulations to limit their potential harm to human health and ecosystems. Such regulations do not exist for light pollution although evidence is accumulating proving its potential harm to humans and ecosystems. In Europe, only Italy and Slovenia adopted laws to reduce light pollution and Croatia and France are in the process of developing national legislations (Welch & Dick, 2012). These examples demonstrate the major importance of highly motivated individuals to lead to the enactment of such legislations. In Italy, both Dr. Cinzano and Dr. Falchi, the authors of the first and the new world atlas of the artificial night sky brightness (Cinzano, Falchi, & Elvidge, 2001; Falchi et al., 2016) were determinant actors of the ratifications of the Lombardi Law on light pollution and which is enforced in two-thirds of the country (regional adoption). In Slovenia, an adaptation of the Lombardi Law led to the adoption of the strongest light pollution law worldwide with the critical impulse of Andrej Mohar, an amateur astronomer and twelve years of negotiations. In France, eight years after the adoption of a law to reduce light pollution, environmental and dark-sky preservation associations referred to the State Council as no application decree has been issued yet. All these examples show the importance of scientists and of the general population in the government consideration of the problem. One main obstacle to the adoption of local and national regulations is political actors' perceived lack of support from the population linked to perceived and realized benefits of nocturnal lighting in socio-economic activity, crime and road safety (Gaston, Gaston, et al., 2015).

5.2. Land management tools

The most common conservation tool in response to land-use changes is the creation of protected areas to preserve species and habitats. More than 15% of the world's terrestrial areas are covered by protected areas (Juffe-Bignoli et al., 2014). The main aim of protected areas is to buffer biodiversity from diverse and often intense anthropogenic pressures (Margules & Pressey, 2000). Yet light pollution is rarely considered as a criterion in the designation and management of protected areas. They tend to be darker than non-protected areas even in intensely lit regions such as Europe (Gaston, Duffy, et al., 2015; Guetté et al., 2018) and although they suffered an increase in light pollution level in recent years, it is limited compared to surrounding areas (Guetté et al., 2018). Nevertheless, the proportion of protected areas' surface considered dark is decreasing (Fig. 14 ;Gaston, Duffy, et al., 2015). In addition, when considering a 500 km buffer around protected areas, the peak in mean ALAN occurs in the first 25 km (Guetté et al., 2018). Protected areas designation is constraint by the spread of human settlements and as the distance between protected areas and urban areas shrinks (McDonald, Erickson, & McDonald, 2000), they may be increasingly impacted by diffuse pollutions.

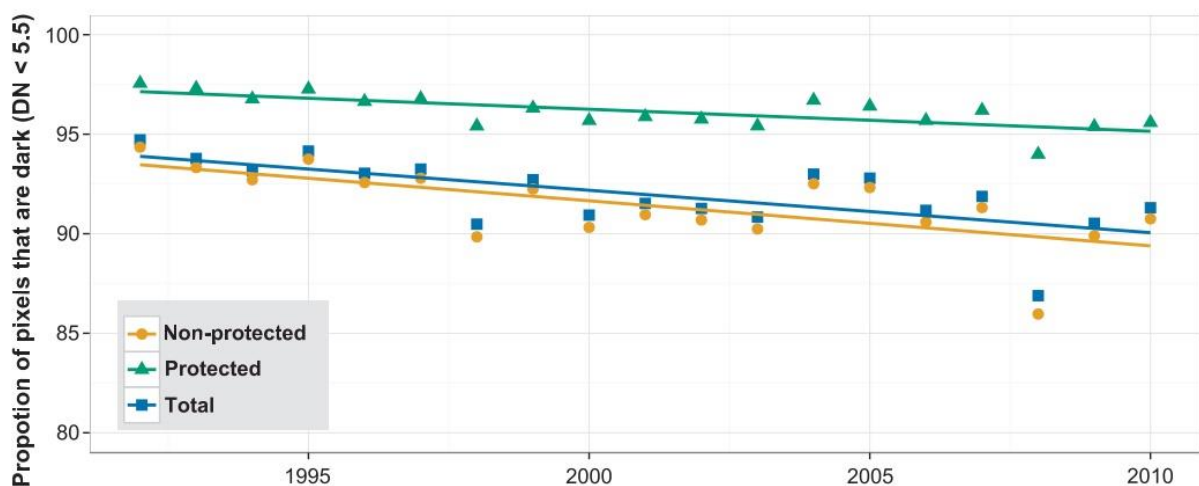


Fig. 14. Change in the global proportion of surface that is dark ($DN < 5.5$, where DN is an index of pixel brightness) in protected and unprotected areas over time (extracted from Gaston, Duffy, et al., 2015).

Astronomers' response to the increase of ALAN was the creation of the International Dark-skies Association in 1988 and the launching of a program to award dark sky places worldwide hence giving incentive for the creation of dark sky reserves. Although this program mainly aims at preserving darkness for celestial observations, it may be a potent tool to protect nocturnal biodiversity.

A more recent initiative in biodiversity conservation is the promotion of nocturnal connectivity through the definition and preservation of ecological corridors for nocturnal species. A green infrastructure policy has been developed by the European Union since 2013 to reduce landscape fragmentation at the continental scale through the development of corridor networks with countries at regional and local scales (e.g., SRCE and TVB in France). However, just like with protected areas designation, such policies seldom include artificial light as a parameter to define ecological corridors which may greatly alter their efficiency for nocturnal species movements. Moreover, green infrastructures are often mapped by landscape managers and tend to only account for the structural connectivity of the landscape (Billon et al., 2017), i.e. they do not account for species behavior in the environment and their response to landscape features. This representation of connectivity is overly simplistic and does not represent the actual functional connectivity of the landscape for the species. For example, vegetation areas are often considered as connected as long as there is no interruption in the cover (structural connectivity). However, this does not take into consideration species gap-crossing abilities. Animals such as bats indeed use linear vegetation feature such as hedges as commuting routes and depending on the species, are able to cross more or less important gaps in hedges hence increasing connectivity compared to purely structural considerations. For example, some bat species can cross gaps in hedgerows of up to 100 m although the crossing probability decrease rapidly when gaps exceed 40 m (Fig. 15 ;Pinaud et al., 2018). In addition to that, as nocturnal species, their ability to cross gaps depends on the light level within the gap. Indeed, the gap

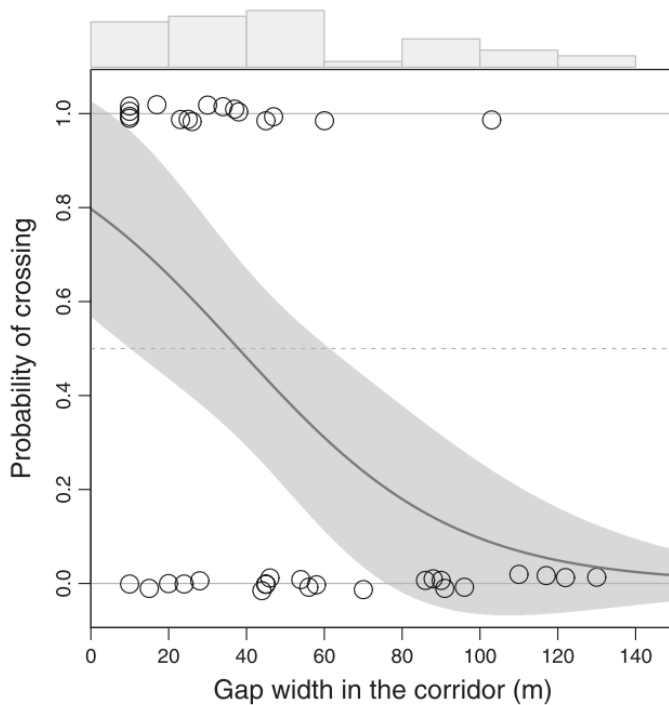


Fig. 15. Probability of crossing a gap in a connecting feature as a function of its width during commuting period for greater horseshoe bat. Top histogram in grey refers to the gap width distribution. The large, black line indicates the predicted probability from the selected binomial GLM model and the grey area indicates its 95% confidence interval (extracted from Pinaud et al., 2018).

species communities. As it is conceivable to model landscape connectivity for all possible species, some must be selected as representative of the larger community. Designating such ensembles of species is complex. An approach could be to base the selection on species functional traits as studies showed that the perception of the landscape and its connectivity is linked to functional traits (With & Crist, 1995; Penone et al., 2013).

5.3. Technical tools

A few years back, studies on the influence of light on species only characterized the light by its perceived color (e.g., Mathews et al., 2015). In addition, the quantity of light emitted was not often evaluated but when it was considered, it was frequently mistakenly called

distance bats can flight through tends to decrease with increasing light levels (Hale et al., 2015). Thus defining functional connectivity requires to account for species response to their surrounding and furthermore, it implies to include the presence of light and its characteristics for nocturnal species.

In addition, due to divergences in species perception of landscape connectivity, it is necessary to evaluate it for different species and combine the results to come up with ecological corridors that will be appropriate for

“intensity” whereas the measure represented the illuminance (e.g., Lacoeylthe et al., 2014). The need for ecology and conservation scientists to communicate their results to lighting engineers may have participated to the recent shift toward precise and detailed description of the light sources studied. Collaborations between biologists, physicists and engineers are developing to produce results with direct application perspectives. Gaston et al. (2012) proposed five light management options to reduce light pollution through the adaptation of street lights and most have subsequently been explored through experimentation.

Tailor the spectral composition of light

The spectral composition of the lamp is one of the most studied aspect of light. The qualification of the spectrum went from a simple description of its perceived color (e.g., Lacoeylthe et al., 2014) to stating lamp types (e.g., Wakefield et al., 2017) and studying different spectrum within a single type of lamp (e.g., Longcore et al., 2015). Studies are hence numerous but not always comparable and sometimes not congruent with one another. Nevertheless, globally, the highest concerns are with UV and short wavelengths that have major impacts such as an attractive effect on many insects (Eisenbeis, 2006) and a suppressive effect on melatonin secretion (Haim & Zubidat, 2015b). Although mercury vapor lamps emitting important quantity of UV have been banned in the EU due to their low energy efficiency, other lamp types emitting low amounts of UV are still widely used (e.g., metal halide lamps – MH). This is worrying as the phototaxis behavior of insects is highly sensitive to UV and seem to be independent from the amount of UV radiations emitted (Barghini & de Medeiros, 2012). In addition, the large deployment of new technologies with broad spectrum may increase the impact of light on many taxa. Indeed, depending on the species, all spectra may have consequences (e.g., mice - Spoelstra et al., 2015) or part of the spectra may be more impacting. For example, fish melatonin secretion suppression is more affected by red light than blue light

(Brüning et al., 2016b) whereas turtle are more disorientated by green light than red light (Cruz et al., 2018). Hence no part of the spectrum has no impact on any species and broad spectrum lamps (e.g., LED, MH) may affect a larger proportion of biodiversity than narrow spectrum lamps (e.g., LPS, HPS). A recent study attempted to create an index to define organismal response to lighting spectrum but it is limited to species for which action spectra are available (Longcore et al., 2018).

Limit the duration of lighting

Part-night lighting schemes are increasingly being used and likely to become widespread in regions with developed lighting infrastructures due to energy price and concerns about carbon dioxide emissions (Gaston et al., 2012). Few studies investigated the potential effect of such measures but they do not prove conclusive in reducing the impact of ALAN on bat species (Azam et al., 2015; Day et al., 2015). Indeed, street lighting is mostly important for humans activities after dusk and before dawn which coincide with the most critical hours of activity of crepuscular and nocturnal species (Gaston et al., 2012). Intelligent lighting schemes, using motion-sensors to detect users, may have more ecological benefits as they could increase the length of non-lit periods (Rowse et al., 2016) however they haven't been investigated yet.

Reduce the quantity of light

At the local scale, the quantity of light can be measured through the energy input of a lamp (power, intensity) or the light emitted (luminance, illuminance). At large scales, the quantity of light is often evaluated through remote sensing as a measure of radiance. The illuminance, measured in lux, is the most commonly employed metric as it can be easily measured in the field with low-cost equipment whereas luminance measures require expensive equipment and power and intensity can't be measured in the field, these information are held

by private companies or municipalities in charge of the outdoor public lighting. Illuminance is a photometric measure which means that it is relative to the human perception of light. Although this can be criticized as each species perceives light in a different way, this metric has the advantage of being used by lighting engineers and thus allows for direct knowledge transfer for possible lighting planning adaptations. Dose-dependent responses to illuminance have been shown in bird activity onset and human and bird melatonin secretion suppression (West et al., 2011; de Jong, Jeninga, et al., 2016). However, some species seem to be impacted by light irrespective of the illuminance level (Stone et al., 2012; Azam et al., 2018). Nonetheless, dimming schemes have the potential to improve light pollution levels at the landscape level. A study using remote sensing data of both light emissions and vegetation (as a proxy of suitable habitats) showed that a 20% reduction in light emissions mostly concentrated in rural areas (as opposed to city centers and already dark areas) in two natural reserves and their surroundings (5 km buffer) could increase the surface of dark suitable habitats by up to 46% (Fig. 16 ;Marcantonio et al., 2015).

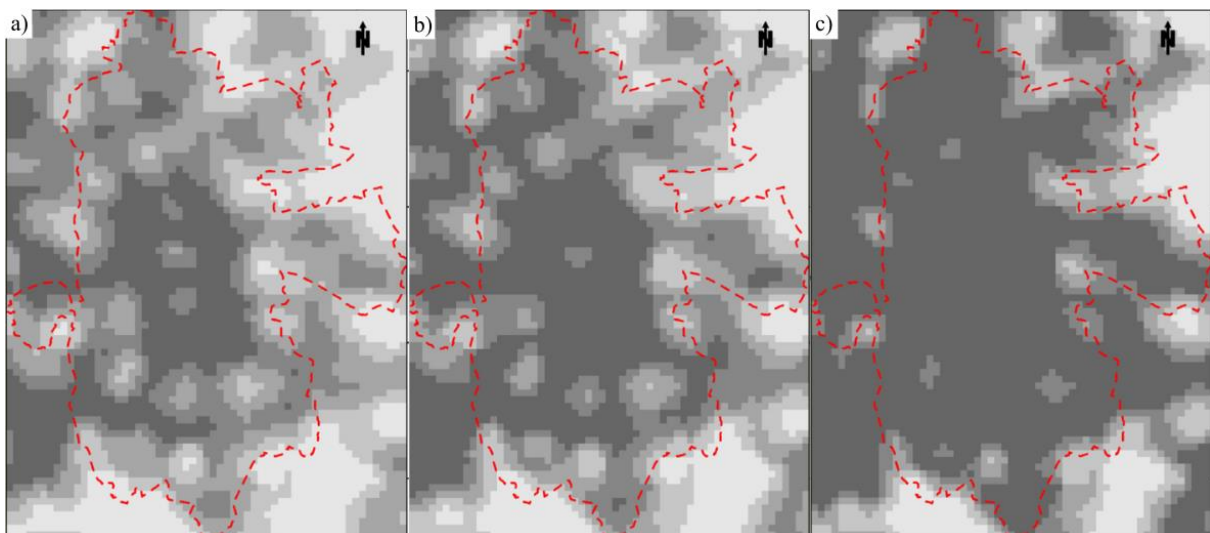


Fig. 16. Light pollution measured on a grey scale from low (dark grey) to high (light grey) in the Colli Euganei protected area (dashed red line) at the original level (a), for a 10% diminution (b) and a 20% diminution (c) in light emissions mostly concentrated in rural areas (as opposed to city centers and already dark areas) (adapted from Marcantonio et al., 2015).

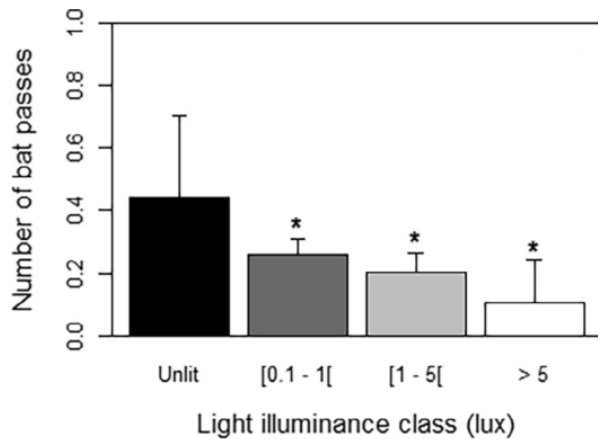


Fig. 17. Predicted *Myotis spp.* activity for four light illuminance classes. “*” indicates that light illuminance classes were significantly different from control unlit treatment ($P < 0.01$) (extracted from Azam et al., 2018).

Limit light trespass

Light trespass comprises all light which unintentionally illuminate surroundings of a light source. It is mostly due to a poor directionality of the light flux which may impact the close environment but also

have a far reach when light is emitted at horizontal or above hence highly contributing to skyglow. As organisms can be sensitive to

very low levels of light (Fig. 17 ;Dominoni et al., 2013; Brüning et al., 2016b; Azam et al., 2018), it is crucial to minimize light trespass. New lighting technologies such as LEDS produce more directional light and light fixture design can greatly participate to a better flux orientation. Position of the street light head perpendicularly to the column, shielding fixtures and correct column height can improve the flux orientation (The Royal Commission on Environmental Pollution, 2009). In addition, vegetation structures such as hedgerows can also be used as shielding to preserve dark areas.

Prevent areas from being artificially lit

The simplest approach to reduce light pollution is to restrict nighttime lighting to the minimum necessary for human use and remove installation in already light saturated areas and from areas where it is not indispensable. A good example of the harm induced by the installation of unneeded lighting is the decrease in bat colonies presence in churches due to the implementation of aesthetic lighting (Rydell, Eklöf, & Sánchez-Navarro, 2017). Unfortunately,

the global trend is not toward street light removal but toward the installation of more public lighting and the increase of private lighting due to the low cost of LEDs.

6. Knowledge gaps and thesis plan

There is a large body of literature demonstrating the numerous and dramatic impacts of artificial light at night on organisms' physiology and behavior. They suggest that a wide variety of taxa are influenced by the presence of lighting with different responses depending on the spectrum, the timing and the quantity of light. Studies' findings indicate potential major repercussions on individual's fitness and reproductive success with possible cascading effects on population dynamics, community composition and ecosystems functioning. As urban areas keep on extending, understanding, assessing and enhancing urban biodiversity is of major importance from both a conservation and a social perspective (Kowarik, 2011). Therefore, it appears important to better understand the influence of anthropogenic pressures on species inhabiting cities such as bats which are, in addition, protected at the European level (Council Directive 92/43/EEC, 1992). Therefore, during my PhD thesis, I investigated the impact of light pollution on bats (Box 1) at the local scale and at the city scale. In the first chapter, I present

Box 1. Using microchiropteran bats as model species

- > Being **insectivorous predators**, bats population trends tend to reflect those of lower trophic levels such as arthropods (Gareth Jones et al., 2009; Stahlschmidt & Brühl, 2012)
- > **Sensitive to environmental anthropogenic pressures** (Russo & Ancillotto, 2015)
- > **Present in urban landscapes** (Marnell & Presetnik, 2010; Russo & Ancillotto, 2015)
- > **All bat species are protected** at the national and European level jointly their roosts and habitat (European Commission, 1992) although there is no specifications concerning the effect of artificial light
- > As **nocturnal species**, bats are submitted to artificial light and their sensitivity to light is species-dependent

the biological and light data I used for my research. At the two scale studied, both ground-based and remote sensing data can be used to evaluate the level of light pollution. These sources of information present different advantages and drawbacks which are important to consider for their use in analyses and to interpret results. All the studies presented in this PhD are based on acoustic recordings of bat ultrasounds that can be semi-automatically identified to the species or species-group level with specific software. However the outputs of such software are not straightforward to exploit as they may include errors and false identifications. In the first study presented, I participated to the development of a methodology aiming at properly selecting bat identifications to then carry out analysis on bats response to their environment. This study intended to answer the following question:

- **How should bat acoustic data classified through a semi-automated identification software be selected to optimize their use in bat activity analysis?**

This study will be submitted for publication in *Methods in Ecology and Evolution*:

Barré K., Pauwels J., Le Viol I., Claireau F., Julien J.-F., Julliard R., Kerbiriou C., Bas Y. Robustness of using a semi-automated method to account for identification errors in bat acoustic surveys. *In prep.*

Although many studies investigated the impact of light on species activity at the local scale and few investigated large scales, none attempted to measure light pollution effects on species activity at a scale both relevant for the focus species movements and lighting management. This may be due to the scarcity of data measuring light pollution at the landscape level with a high resolution. In the second chapter of my PhD thesis, I intend to evaluate how light affects bat activity at the city scale. To carry out this work, I took advantage of biological and light data available through citizen-science programs. It allowed me to have an important amount of data on bats with a good spatial coverage (Vigie-Chiro monitoring program) as well

as high resolution nocturnal pictures taken from the International Space Station (ISS) (Cities at Night program). I intended to answer two questions:

- **How is bat activity affected by light pollution at the city scale?**
- **Which source of information is the most relevant to measure this effect?**

This study has been accepted for publication in *Landscape and Urban Planning*:

Pauwels J., Le Viol I., Azam C., Valet N., Julien J.-F., Bas Y., Lemarchand C., Sánchez De Miguel A., Kerbiriou C. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. Accepted for publication in *Landscape and Urban Planning*.

Thirdly, although the effect of light on individual's movement at the local scale was studied on several taxa, no study has evaluated its impact on daily movements at an intermediate scale. Individual's ability to travel through a landscape is crucial to comply with its daily needs such as finding food. The impediment of such movements could have important repercussions on fitness and populations maintenance (Taylor et al., 1993; Nathan et al., 2008). Although landscape connectivity has been explored for various taxa (LaPoint et al., 2015), little research focused on nocturnal species and only one considered the influence of light pollution but at a small scale (Hale et al., 2015). Hence in a second chapter, I intend to evaluate the influence of light pollution on bats daily movements in urban areas at two intermediate scales, the conurbation scale and the city scale. In addition, I intend to evaluate the potential of lighting planning to modify the landscape connectivity through the comparison of the current lighting situation with scenarios of light extinction in certain areas and scenarios of changes in lighting technologies toward the generalized use of LEDs. In this chapter I aimed at answering the following questions:

- **What is the contribution of ALAN to urban landscapes fragmentation for bats?**
- **Could localized light extinction scheme improve the connectivity at the landscape level?**
- **How would a shift in lighting technology toward LEDs affect landscape connectivity for bats?**

This chapter include two studies. The first will be submitted for publication in *Landscape Ecology*:

Laforge A., Pauwels J., Faure B., Bas Y., Kerbiriou C., Fonderflick J., Besnard A. Light reduction improves connectivity for bats in an urban landscape. *In prep.*

The second study will be submitted for publication in *Ecological Applications*:

Pauwels J., Laforge A., Bas Y., Fonderflick J., Besnard A., Valet N., Le Viol I., Kerbiriou C. Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas. *In prep.*

In the actual context of green infrastructure development, there is an urgent need for operational light-source scale recommendations adapted to local contexts in order to preserve dark corridors for nocturnal species. In particular, protected areas aim at preserving biodiversity and habitats but, in Europe, most of them include a significant part of urban activities (European Environment Agency, 2012) therefore submitting natural environment to anthropogenic pressures such as light pollution. Due to its diffuse character, light emitted in urban areas may affect surrounding semi-natural and natural habitats such as hedges which have a substantial role in landscape connectivity (Burel, 1996) and are of particular importance for bats (Verboom & Huitema, 1997). However, land managers lack information to adapt their outdoor lighting to local protected species. Thus, in the third chapter of my PhD thesis, I intend to evaluate the importance of several street light characteristics in the impact of light on a broad panel of bat

species activity around streetlights and at hedges. I designed an *in situ* experiment to answer the following questions:

- **How do streetlight characteristics influence the bat activity?**
- **What is the distance of impact of light on various bat species activity?**

The results of this study have been submitted to *Animal Conservation*:

Pauwels J., Kerbiriou C., Bas Y., Valet N., Le Viol I. Adapting street lighting to limit light pollution impacts on bats in protected areas. *Submitted in Animal Conservation.*

“[...] we are driven by our visual system and therefore tend to neglect the dark side of conservation, i.e., the protection of nocturnal animals.”

Voigt and Kingston 2016

CHAPTER 1

BIOLOGICAL AND LIGHT DATA

ARTICLE 1

Barré K., Pauwels J., Le Viol I., Claireau F., Julien J.-F., Julliard R., Kerbiriou C., Bas Y.
Robustness of using a semi-automated method to account for identification errors in bat
acoustic surveys. *In prep.*

In this PhD thesis, I undertake studies at two different scales in order to evaluate the impact of light on both bat behavior in the vicinity of streetlights at a fine scale and bat activity distribution at an intermediate scale. The second and third chapters focus on the city-scale (100 km² or less) which include all bats daily movements and allow to measure the effect of ALAN on the city landscape connectivity. This scale also corresponds to a management unit of public lighting thus results of the studies may be of direct interest for land management applications. The fourth chapter investigates the activity of several bat species at specific light sources hence concentrating on fine scale behavior. I used different types of biological and light data to explore the impacts of light at these two spatial scales.

1. Light pollution data

Most studies evaluating the impact of light on biodiversity are performed at the local scale (Stone, Jones, & Harris, 2009; Azam et al., 2018). This arose from the will to investigate and measure visible phenomenon such as the attraction of insects to light. It may also be linked to the greater difficulty to perform large scale studies and the necessity to access light data for an entire landscape. Indeed although punctual measured of light can be done fairly easily, mapping large-scale night sky brightness is more complex. In the field experiment described in the third chapter, the lamp type could be determined visually and checked with a measure of the spectrum and the quantity of light at the sampled location could be evaluated through the measure of the illuminance with a luxmeter. However, for the city-scale studies it would not have been feasible to make such measures for each light source. In order to measure cities nighttime lighting, we tested several potential sources of information on light emissions (chapter 2; Fig. 18). Ground-based data such as the location of streetlights are more and more accessible online and can be used as a proxy of light distribution although this type of data does not account for private lighting and light characteristics (spectrum, quantity, directionality).

Several sources of remote sensing data such as DMSP-OLS and VIIRS DNB satellite imaging from the National Oceanic and Atmospheric Administration (NOAA) are freely available online. Both are representations of the global light emissions with yearly and monthly updates. The radiance level is measured on a discrete grey scale and these satellite images have the advantage to have a worldwide coverage. However their coarseness make them unsuitable for city-scale studies. We used pictures taken from the International Space Station (ISS) by astronauts. These pictures are taken with regular cameras and hence can be decomposed in four color bands (red, blue and two green bands) representing the spectral distribution. The value of each pixel is proportional to the radiance emitted and thus measures the relative light emission. Such pictures are available online through the National Spatial and Aeronautic Administration (NASA) website. A recently launched citizen-science programs, Cities at Night (<http://citiesatnight.org/>), aims at classifying the thousands of existing pictures and georeference them so they can be accessible easily. Such pictures have a variable quality and resolution that can be as fine as 1 m. Yet the georeferencing is based on the recognition of light patterns hence only brightly light areas such as big cities have available picture for now. I collaborated with an astrophysicist to be able to use such picture to have a measure of the light pollution at the city scale and also to produce scenarios reflecting a change in lighting technology toward the generalized use of LED lighting.

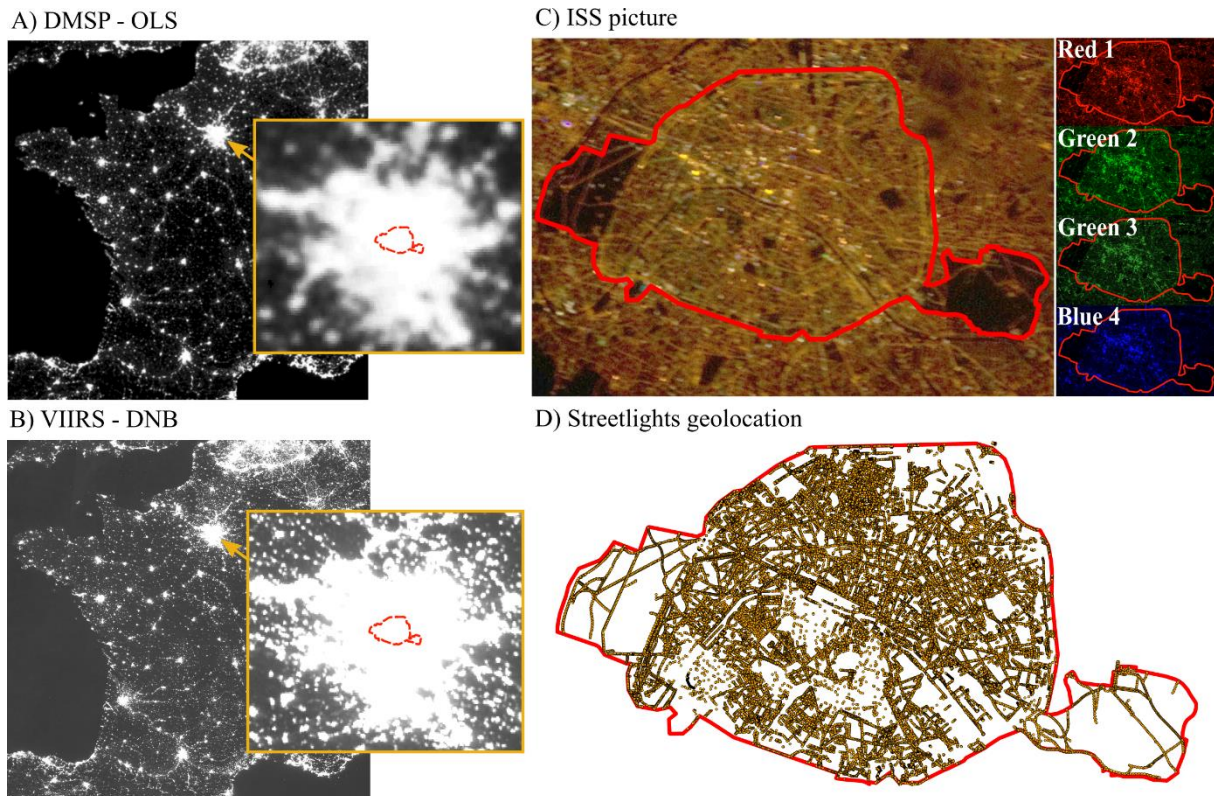


Fig. 18. Different possible sources of information on light pollution. DMSP – OLS (A) and VIIRS –DNB (B) satellite images of France with a zoom on Paris and its surrounding. The resolution of the images is too low (930 m for DMSP – OLS and 460 m for VIIRS – DNB) to see the difference of radiance emitted in Paris. The better resolution (60m) of this ISS picture of Paris (C) allows to distinguish areas with low and high radiance at a fine scale. Another source of information on light pollution is the location of streetlights (D). Each orange dot represent a streetlight (over 51 000 in Paris) (extracted from Pauwels et al. (2018) Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning*. In press)

2. Bat activity data

2.1. Bat acoustic data

While flying, microchiropterans use echolocation to detect the object surrounding them thus allowing them to navigate and forage. The recording of ultrasound echolocation calls is widely use to study bats as this method provides information on their presence in a non-invasive fashion. Bats always echolocate while flying thus recording no bat calls can be interpreted as an absence of individuals within the detection range of the microphone. Therefore bat

recordings can be used to measure the relative abundance of bats and how they use their habitat. Information on bats behavior can also be inferred from the recording of call sequences. For example while approaching a prey, bats emit characteristic sequences of calls called feeding buzzes. Foraging and transiting behavior can partly be differentiated from the characteristics of the call sequences however these two behavior are not completely separated as bats can catch insect while transiting. Echolocation calls data were used in all the studies presented in this PhD thesis.

Calls sequences can be analyzed to determine to which species they belong to although some species may have very similar acoustic signatures and can only be classified at the species group level. Moreover, individual bats from the same species cannot be differentiated on their echolocation calls. Indeed, echolocation calls are not used for communication but only for the detection of surrounding obstacles and are very similar between species and even more so between individuals. Therefore the abundance cannot be evaluated as several passages of the same individual may be recorded. Instead, acoustic data are used to assess bat activity which measures the degree to which an area is used by bats for foraging or transiting thus reflecting the suitability of the habitat. There are many ways to define bat activity (Kerbiriou et al., 2018) and for the analyses presented here, bat activity was defined as the number of bat passes per unit of time (e.g., one night) with a bat pass being a call or sequence of calls of the same species recorded within a 5 seconds interval (Millon et al., 2015). This time interval corresponds to the better compromise between the risk of multiple counts of the same individual passage and the risk of missing other individual passages (Kerbiriou et al., 2018). Indeed 5 seconds is the mean duration of calls sequences recorded (Millon et al., 2015).

2.2. Data sampling

For both scales, bat activity was evaluated through the recording of bats echolocation calls with ultrasound recorders. The city-scale studies were carried out for three large cities of France as the spatial arrangement of land cover types and the distribution of light may play an important role in the effect of ALAN on bat activity distribution and landscape connectivity. These studies required a sampling covering the entire study areas and hence a large number of recording points and I took advantage of the important database generated by the national citizen science bat monitoring program Vigie-Chiro (<http://vigienature.mnhn.fr/page/chauves-souris.html>). The fine-scale study required the sampling of selected light sources and adjacent points hence I designed a sampling plan to carry out a field experiment.

Citizen science monitoring programs aim at measuring large scale population trends by defining a sampling design representative of habitats cover and with the help of volunteers. Such programs also aim at involving citizens in the conservation of biodiversity through the appropriation of a scientific methodology. Monitoring programs represent a highly valuable source of data as they generate large-scale and long-time dataset. For the city-scale studies, I used data collected as part of the French national bat monitoring program Vigie-Chiro. The program, launched in 2006 by the National Museum of Natural History of Paris, gather data covering the entire French territory (Fig. 19) and taken following three different protocols. In the analysis presented in the thesis only two protocols are used, the pedestrian protocol and the full-night protocol. For the pedestrian protocol, volunteers take 6 minutes recording at ten points selected within a 2 km² area. For the full-night protocol, recording devices are placed at selected sites and record throughout the entire night.

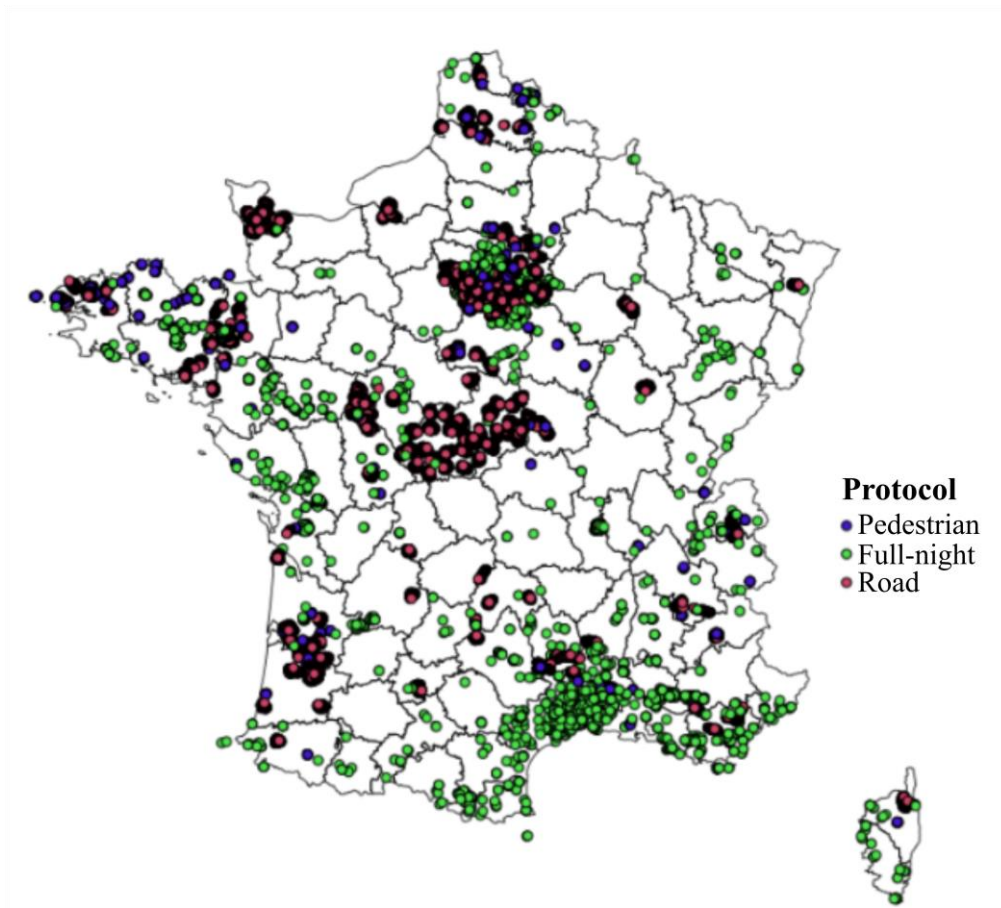


Fig. 19. Repartition of all the recordings done as part of Vigie-Chiro. The database currently contains over 4 million bat passes recorded and represent over five thousand sampling events (adapted from Bas et al. (2018) Des nouvelles de Vigie-Chiro ! Poster presented at the Rencontres nationales chiroptères de Bourges).

In order to use such data to answer another scientific question, it is necessary to verify that the spatial subset of data used covers all the possible environmental conditions encountered throughout the study areas. If the gradient of the variables of interest present in the study area is not sampled within the data available, it is not possible to carry out the analysis or it would require to modify the spatial extent to reach a better representation of the variable. To evaluate the impact of light pollution on bat activity, it was important that the sampling covered the gradient of radiance existing across the study areas and fortunately the dataset available for each city complied with this requirement.

In the third chapter, I analyze bat activity data I collected in the field. Recording locations were carefully chosen to answer my specific research question and to account for potential correlation among the variables of interest.

Until 2000, most recordings were active which means that they required the presence of an operator. Thus the quantity of data was limited by the time of investment needed for such sampling but also by the length of recordings possible. In addition, short-length recordings (6 minutes for the pedestrian protocol) produce an important number of zeros hence generating a possibly important zero-inflation in the data. More recently, passive acoustic monitoring (PAM) was developed through apparition of recorders that can now function without an operator being present all along and record for days in row. This technical evolution greatly increased the possibility to realize large samplings and investigate large scale patterns. Such methods are now widely used for field experiments and large scale monitoring such as citizen science programs and the data accumulated increased dramatically.

2.3. Bat calls identification

In order to associate a species to a bat calls sequence, several measures can be taken such as the mean frequency, the power distribution or the interval between calls (Fig. 20). Although the identification can be done manually, this implies a bias as the persons doing the identification may not all have the same level of expertise and their knowledge may evolve across time. In addition, the development of PAM and the associated increase in the quantity of data makes it virtually impossible to check all call sequences by hand. For example, the data used for the city of Montpellier included both active and passive recording data and within these data, 20 times more calls were recorded in one night (full-night protocol) than in a 6 minute recording (pedestrian protocol). Each sampling lasting one night recorded a mean number of

10 000 bat calls. Thus semi-automated identification software are being improved such as the software Tadarida (Bas, Bas, & Julien, 2017) which is developed within the CESCO lab in open source and is freely available as an online web portal to classify data recorded following the Vigie-Chiro protocols. These software allow for the rapid analysis of a large number of data and greatly reduce the time necessary for identification although they are not entirely reliable and can produce false identification. The Tadarida software computes a large array of metrics on each 5 seconds sequence of calls of a same species to allow for their identification. The identification algorithm is calibrated on a set of manually identified sequences to produce a decision tree (random forest algorithm). The decision tree is then applied to the new set of data. Each sequence detected in the data is identified to the finest taxonomic level and attributed a confidence index (CI). The CI ranges from 0 to 1 with increasing confidence in the identification. However, this index is not a probability and does not behave identically for all species. Thus it is not straightforward to use it to select the sequences identified with certitude (low number of false positive) while removing sequences with high uncertainty (high number of false positive). Indeed, it is essential to find the most optimal balance between the quantity of data kept for an analysis and the quantity of errors within the dataset to obtain correct results without losing too much statistical power. Moreover, due to the acoustic similarities between some species, inaccurate identifications can simultaneously lead to an erroneous low number of contacts for one species (false negative) while attributing them to another one (false positive).

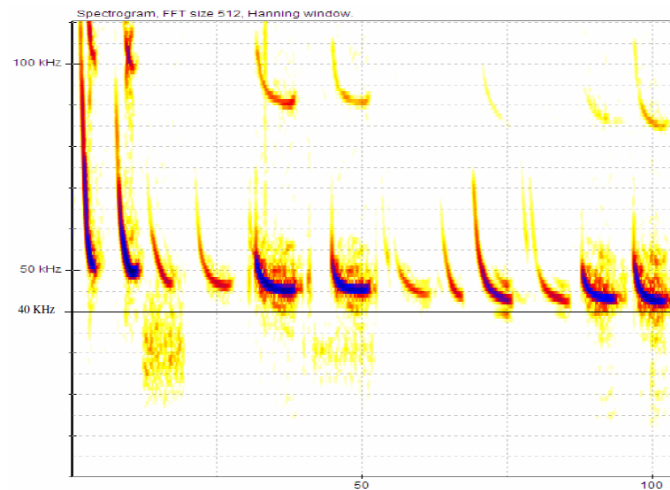


Fig. 20. Example of a spectrogram representing echolocation calls of *Pipistrellus pipistrellus* (extracted from Haquart (2009) Fiches acoustiques de Chiroptères de France et du Var)

In order to be able to discriminate between well and poorly identified bat passes, I participated in the definition of a methodology aiming at choosing CI thresholds values for each species (**Barré et al., *in prep***). The results show that it is necessary to only consider data with at least a 0.5 maximum error risk to minimize false positives and have consistent responses of bat activity to commonly used environmental variables in statistic models. This study provides new opportunities, starting with a time gain in manual checking in experimental studies and allow to generalize large-scale monitoring of bats. I adapted the methodology presented in this paper to be use it on the data I collected in the field. In the study by Barré et al., a stratified selection of the data taken in the study area were used to calibrate the algorithm. The selected data were manually checked by two experts which took several months. To identify my field data, the algorithm was calibrated using a national scale dataset that was manually identified by experts over several years thus I did not make manual identifications on my field data. Amongst the species identified in my dataset, some are acoustically very similar (e.g., *P. kuhlii* and *P. nathusii*) and there may have been misattributions of calls between species. However, my sampling sites were distributed in a fairly small area within the same biogeographic regions

thus the potential bias due to this type of misattributions is likely to be the same for all sampling sites and hence does not fundamentally change the interpretation of the results.

ARTICLE 1

ROBUSTNESS OF USING A SEMI-AUTOMATIC METHOD TO ACCOUNT FOR IDENTIFICATION ERRORS IN BAT ACOUSTIC SURVEYS

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Abstract

1. Halt threats on biodiversity and ecosystem services require large-scale and long-time studies which need to adapt monitoring methods for the understanding of biodiversity changes. Reduced costs of acoustic recorders and their huge increase of storage capacity resulted in an exponential development of Passive Acoustic Monitoring (PAM) of a very wide range of animals in a few years, in particular bats for which PAM constitutes a real efficient tool. PAM of bats lead to collect quickly a very large number of records, making manual identification increasingly time-consuming. To respond to PAM, methods for detecting sound events, extracting numerous features, and automatically identifying species have been developed. However, automatic identification can generate large rate of errors which could affect response of bats to environmental variables and pressures. This study propose a cautious method to account for identification errors in acoustic surveys without fully check records.

2. We proposed to check a representative sample of the outputs of Tadarida automatic identification software to then model the identification success probability of 10 species and 2 groups, according to the provided confidence index. We then investigated the effect of setting different Maximum error rate Tolerance (MERT) under which data should be discarded, by repeating a large-scale analysis of bat activity response to habitat variables, and checking for consistency in the results.

3. Main changes in model outputs occurred from naive (i.e. raw data) to robust analyses (i.e. MERT) with in some cases a loss of significance or an estimates inversion. Then, we did not detect major changes between 0.5, 0.4, 0.3, 0.2 and 0.1 rates of MERT, and response estimates and standard errors were highly stable.

4. We conclude that it was essential at least to sort out data with more than a 0.5 MERT to minimize the false positive rate. The method allowed to check the consistence of responses at different MERT involving various balances between quantity and quality of data, in order to enough minimize the MERT. This study provides new opportunities, starting with a time gain in manual checking in experimental studies and allow to generalize large-scale monitoring of bats improving knowledge.

1. Introduction

Despite some local successes and increasing responses, the rate of biodiversity loss does not appear to be slowing (Butchart et al., 2010), although halting this decline has been recognized as a crucial aim for humanity (Cardinale et al., 2012). In 2010, the 10th Conference of Parties to the Convention on Biological Diversity, adopted a new 2011–2020 global Strategic Plan for Biodiversity, in turn, EU launch a new Biodiversity Strategy (2011/2307). This strategy aims to halt biodiversity loss and the degradation of ecosystem services by 2020, restore ecosystems, and make a contribution to addressing global biodiversity loss. However to reach the target of reducing loss of biodiversity, the efforts undertaken by each country should be assessed, which in turn require large-scale and long-time studies which need to adapted monitoring methods for the understanding of biodiversity changes (Fisher, Frank, & Leggett, 2010). A significant increase of amount of information available on biodiversity is also needed to evaluate impact of various anthropogenic pressures.

Reduced costs of acoustic recorders and their huge increase of storage capacity resulted in an exponential development of Passive Acoustic Monitoring (PAM) of a very wide range of animals in a few years (Froidevaux, Zellweger, Bollmann, & Obrist, 2014; Kalan et al., 2015; Selby et al., 2016). Such approaches were widely used by researchers working for environmental consulting firms or government agencies (Adams, Jantzen, Hamilton, & Fenton, 2012). PAM is particularly adapted for cryptic taxa surveys such as nocturnal fauna (Delpont, Kemp, & Ferguson, 2002; Newson, Evans, & Gillings, 2015; Jeliaskov et al., 2016), for the monitoring of pristine habitats difficult to access and survey by other approaches (Gasc, Sueur, Pavoine, Pellens, & Grandcolas, 2013). PAM have been mobilized, also, in citizen science programs (Newson, Woodburn, Noble, Baillie, & Gregory, 2005), a real efficient and essential tool in implementation of large-scale biodiversity monitoring (Newson et al., 2015). Due to a

recent exponential increase in the knowledge of acoustic identification of bat species (Russo & Jones, 2002; Obrist, Boesch, & Fluckiger, 2004; Barataud, 2015), PAM have recently been widely used by bat workers. However, PAM of bats lead to collect quickly a very large number of records, which in turn had involved changes in acoustic identification procedures: before this change, acoustic identifications were mainly performed manually with software allowing visualization of spectrogram. However, manual identification was indeed increasingly time-consuming. With the arrival in the market of such new generation of acoustic recorders affordable allowing to record several hours/days straight, such amount of acoustic data could not be deal with manual procedure (Bas, Bas, & Julien, 2017). To respond to these changes several reliable quantitative methods for detecting sound events, extracting numerous features, and automatically identifying species have been developed (Parsons & Jones, 2000; Britzke, Duchamp, Murray, Swihart, & Robbins, 2011; Adams et al., 2012; Bas et al., 2017). However, automatic identification software has recently been criticised because of significant error rates, suggesting a cautious and limited use (Russo & Voigt, 2016; Rydell, Nyman, Eklöf, Jones, & Russo, 2017). Most available softwares nonetheless provide confidence indexes in the form of probabilities or other numerical indexes (Obrist et al., 2004; Waters & Barlow, 2013), and their manuals do advocate on using confidence thresholds under which data should be discarded because of error risk, e.g. SonoChiro (Biotope, 2013) or BatClassify (Scott & Altringham, 2017). Thus, the correlation between error risk and confidence indexes is an important part of the automatic identification performance so far ignored by all previous methodological studies (Fritsch & Bruckner 2014; Rydell et al. 2017). Besides that, the level at which confidence thresholds should be set is unclear to most users, limiting the use of automatic identification in bat ecological studies. A too cautious threshold could indeed lead to high false negative rates whereas a not sufficiently cautious threshold could lead to high false positive rates. Both rates have different statistical implications: false positive could lead to biases due to other species

activity while false negatives could lead to lack of power by discarding too much data. Given the fact that both rates induce different caveats, there is no straightforward way to set confidence thresholds.

In this study, we proposed to check a representative sample of the outputs of Tadarida automatic identification software to then model the identification success probability of 10 species and 2 groups, according to the provided confidence index (Bas et al., 2017). We then investigated the effect of setting different maximum error rate tolerances (i.e. confidence thresholds) under which data should be discarded, by first repeating a large-scale analysis of bat activity response to habitat variables, and then checking for consistency in the results.

2. Materials and methods

Bat survey

Bat activity was sampled through recordings of echolocation calls on 337 points over 29 localities in northwest France (Fig.1) dominated by agriculture (82%) and forest (11%) areas. Recordings were performed during 23 entire nights, from 30 minutes before sunset to 30 minutes after sunrise, from the 7th of September to the 8th of October 2016.

Among the 23 nights, 14 were dedicated to the sampling of only one locality per night, while the other 9 nights allowed us to simultaneously sample 2 localities per night (these wind farm were in average 8.1 km distant). Standardized echolocation calls were recorded using one bat detector (Wildlife Acoustic SM2Bat+) per site. The detectors automatically recorded all ultrasounds using preconized settings of the French monitoring Vigie-Chiro (trigger level set to 6 db SNR; see for further details <http://vigienature.mnhn.fr/page/protocole-point-fixe>).

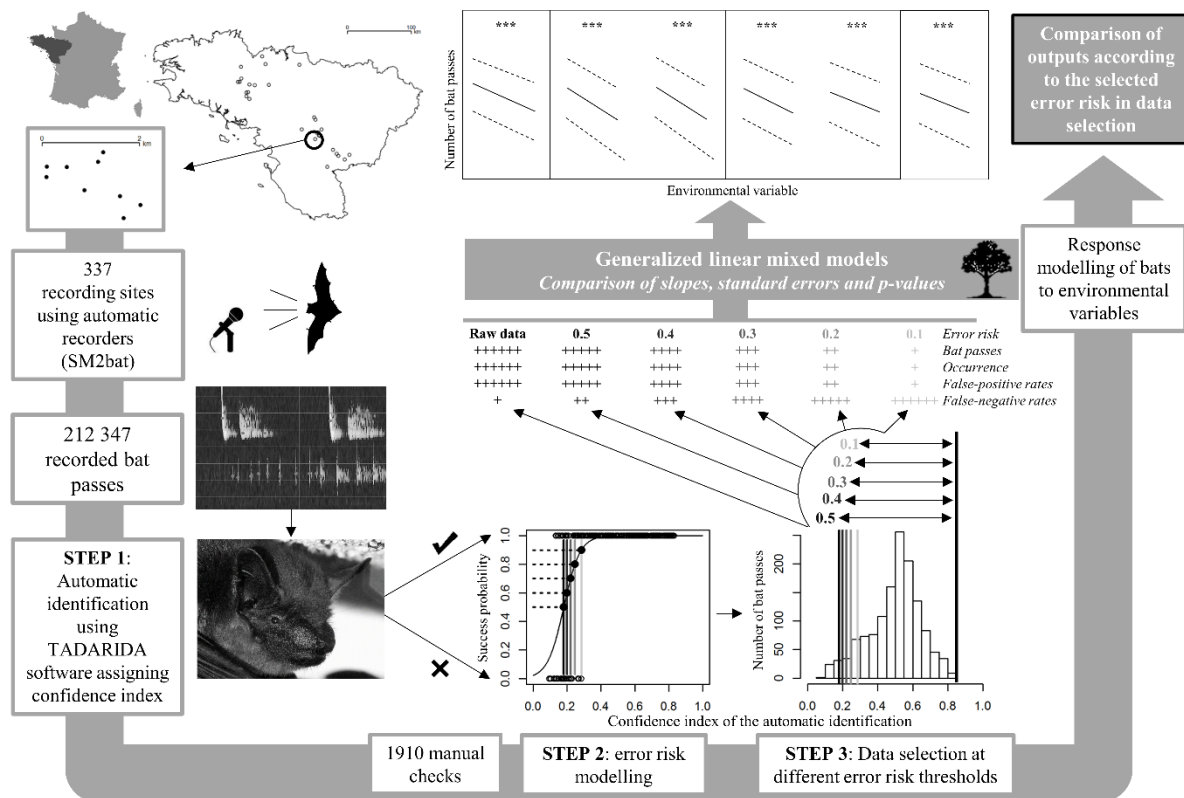


Fig. 1. Schematic and chronological representation of the steps used to study the relationship between the automatic identification errors in acoustic data and the bat activity response to environmental variables.

Step 1: semi-automated acoustic identification on a subset

We defined a bat activity metric (number of bat passes per night), where one bat pass was defined by a single or several echolocation calls during a 5 second interval which is a good compromise considering the mean duration of all bat species passes (Millon, Julien, Julliard, & Kerbiriou, 2015). The semi-automated identification process was performed in the step 1 in 2 parts (Fig. 1). In the first part, echolocation calls were detected and classified to the most accurate taxonomic level using the TADARIDA software (Bas et al., 2017) which allows to assign a species and a confidence index (between 0 and 1) to each recorded bat pass. In the second part, we randomly performed a double manual checking (KB and YB) of automatic

identifications using BatSound© and Syrinx (John Burt, Seattle, WA, USA) software for each 0.1 class of confidence index at 10 species and 2 groups (*Myotis* and *Plecotus spp.*) levels. A minimum of 25 bat passes per class of confidence index for each species and groups were checked, except for *Rhinolophus* species where all passes were checked thanks to the low total number. When the number of bat passes for a given species and confidence index class was <25, all passes were checked (Table 1). Groups were constructed because species were difficult to identify from each other, except one species of *Myotis ssp.*, *Myotis nattereri*, for which echolocation calls are very characteristics (Obrist et al., 2004; Barataud, 2015).

Step 2: error risk modelling from the semi-automated identification

From previous manual checking (i.e. a random subset of the total dataset stratified per species and per confidence index classes), we performed generalized linear models between the success/fail of the automatic species assignation (here the response variable, a binomial variable) and the confidence index of the automatic identification (explanatory variable) (see step 2 in Fig.1; Fig. 2). We selected the probit link which better fitted the binomial distribution of manual checking for all species/groups. This allowed to predict the needed confidence index from the automatic identification process to tolerate a given rate of maximum error rate: 0.5, 0.4, 0.3, 0.2 and 0.1 (Fig.1; Table 2). Then, for each of these thresholds, we calculated the false negative and the false positive rates (Table 2).

Table 1. Total bat passes assigned to each species by the automatic identification per confidence index classes, number of bat passes manually double checked and errors noted. See Table S2 for species composition in errors.

Species	Upper limits of confidence index classes of the automatic identification										Total
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1	
<i>Barbastella barbastellus</i>											
Total passes	3	52	144	242	297	671	940	1312	1596	578	5835
Checked passes	3	25	25	25	25	25	25	25	25	25	228
Errors	3	5	1	0	0	0	0	0	0	0	3.9 %
<i>Eptesicus serotinus</i>											
Total passes	1	55	102	149	268	461	218	79	10	0	1343
Checked passes	1	25	25	25	25	25	25	25	9	0	185
Errors	1	13	7	0	0	0	0	0	0	0	11.4 %
<i>Myotis nattereri</i>											
Total passes	9	166	211	223	225	411	269	180	247	47	1988
Checked passes	9	9	3	6	8	2	2	10	23	25	97
Errors	8	5	1	2	1	0	0	0	0	0	17.5 %
<i>Myotis spp</i>											
Total passes	20	534	815	770	701	1708	1132	445	258	47	6430
Checked passes	20	25	25	25	25	25	25	25	25	25	245
Errors	19	14	6	6	4	0	0	0	0	0	20.0 %
<i>Nyctalus leislerii</i>											
Total passes	3	47	41	33	11	8	9	1	0	0	153
Checked passes	3	25	25	25	11	8	9	1	0	0	107
Errors	2	16	14	13	4	0	0	0	0	0	45.8 %
<i>Nyctalus noctula</i>											
Total passes	0	113	110	82	24	43	16	6	1	0	395
Checked passes	0	25	25	25	24	25	16	6	1	0	147
Errors	0	25	23	24	23	7	0	0	0	0	69.4 %
<i>Pipistrellus kuhlii</i>											
Total passes	12	223	401	667	1142	4026	6654	10222	5240	2	28589
Checked passes	12	25	25	25	25	25	25	25	25	2	214
Errors	11	10	8	4	2	2	1	0	0	0	17.8 %
<i>Pipistrellus nathusii</i>											
Total passes	0	12	33	37	93	183	153	61	5	0	577
Checked passes	0	12	25	25	25	25	25	25	5	0	167
Errors	0	11	20	20	19	17	15	9	1	0	67.1 %
<i>Pipistrellus pipistrellus</i>											
Total passes	2	303	760	1636	3298	8311	14221	27205	83744	28024	167504
Checked passes	2	25	25	25	25	25	25	25	25	25	227
Errors	1	2	0	1	1	0	0	1	0	0	2.6 %
<i>Plecotus spp</i>											
Total passes	8	139	176	194	174	250	206	145	56	4	1352
Checked passes	8	30	26	25	28	25	25	25	25	4	221
Errors	5	19	8	2	1	1	0	0	0	0	16.3 %
<i>Rhinolophus ferrumequinum</i>											
Total passes	0	0	0	0	1	6	5	28	1	0	41
Checked passes	0	0	0	0	1	6	5	28	1	0	41
Errors	0	0	0	0	0	0	0	0	0	0	0.0 %
<i>Rhinolophus hipposideros</i>											
Total passes	0	1	1	10	8	16	26	62	4	0	128
Checked passes	0	1	1	10	8	16	26	62	4	0	128
Errors	0	1	1	7	1	0	0	0	0	0	7.8 %

Table 2. Minimum needed confidence index provided by the automatic identification to ensure a given rate of maximum error rate tolerance (0.5, 0.4, 0.3, 0.2 and 0.1), and corresponding false negative and false positive rates in the manually checked subset (1910 bat passes; steps 1 and 2 in the Fig. 1).

Species	Maximum error rate tolerance					
	Raw data	0.5	0.4	0.3	0.2	0.1
<i>Barbastella barbastellus</i>						
Confidence index	/	0.119	0.133	0.148	0.167	0.195
False negative rate	0.000	0.009	0.018	0.027	0.046	0.087
False positive rate	0.039	0.023	0.023	0.023	0.014	0.005
<i>Eptesicus serotinus</i>						
Confidence index	/	0.180	0.200	0.221	0.246	0.285
False negative rate	0.000	0.049	0.073	0.079	0.098	0.152
False positive rate	0.114	0.066	0.044	0.032	0.020	0.000
<i>Myotis nattereri</i>						
Confidence index	/	0.229	0.271	0.317	0.373	0.458
False negative rate	0.000	0.063	0.088	0.088	0.125	0.175
False positive rate	0.175	0.051	0.052	0.039	0.014	0.015
<i>Myotis spp.</i>						
Confidence index	/	0.212	0.250	0.291	0.341	0.416
False negative rate	0.000	0.071	0.112	0.153	0.194	0.281
False positive rate	0.200	0.081	0.074	0.057	0.042	0.014
<i>Nyctalus leislerii</i>						
Confidence index	/	0.286	0.342	0.402	0.476	0.587
False negative rate	0.000	0.328	0.500	0.569	0.621	0.793
False positive rate	0.458	0.316	0.256	0.138	0.000	0.000
<i>Nyctalus noctula</i>						
Confidence index	/	0.507	0.527	0.548	0.574	0.613
False negative rate	0.000	0.111	0.156	0.222	0.422	0.511
False positive rate	0.694	0.111	0.026	0.028	0.037	0.000
<i>Pipistrellus kuhlii</i>						
Confidence index	/	0.164	0.216	0.272	0.341	0.444
False negative rate	0.000	0.051	0.097	0.153	0.233	0.375
False positive rate	0.178	0.130	0.091	0.057	0.049	0.035
<i>Pipistrellus nathusii</i>						
Confidence index	/	0.668	0.756	0.853	0.971	/
False negative rate	0.000	0.582	0.800	1.000	1.000	1.000
False positive rate	0.671	0.395	0.154	/	/	/
<i>Pipistrellus pipistrellus</i>						
Confidence index	/	0.000	0.000	0.000	0.000	0.096
False negative rate	0.000	0.000	0.000	0.000	0.000	0.000
False positive rate	0.026	0.026	0.026	0.026	0.026	0.022
<i>Plecotus spp.</i>						
Confidence index	/	0.184	0.217	0.253	0.298	0.364
False negative rate	0.000	0.065	0.092	0.130	0.168	0.265
False positive rate	0.163	0.070	0.056	0.047	0.025	0.022
<i>Rhinolophus ferrumequinum</i>						
Confidence index	/	0.000	0.000	0.000	0.000	0.000
False negative rate	0.000	0.000	0.000	0.000	0.000	0.000
False positive rate	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rhinolophus hipposideros</i>						
Confidence index	/	0.385	0.398	0.411	0.427	0.452
False negative rate	0.000	0.017	0.025	0.025	0.025	0.051
False positive rate	0.078	0.009	0.009	0.009	0.009	0.009

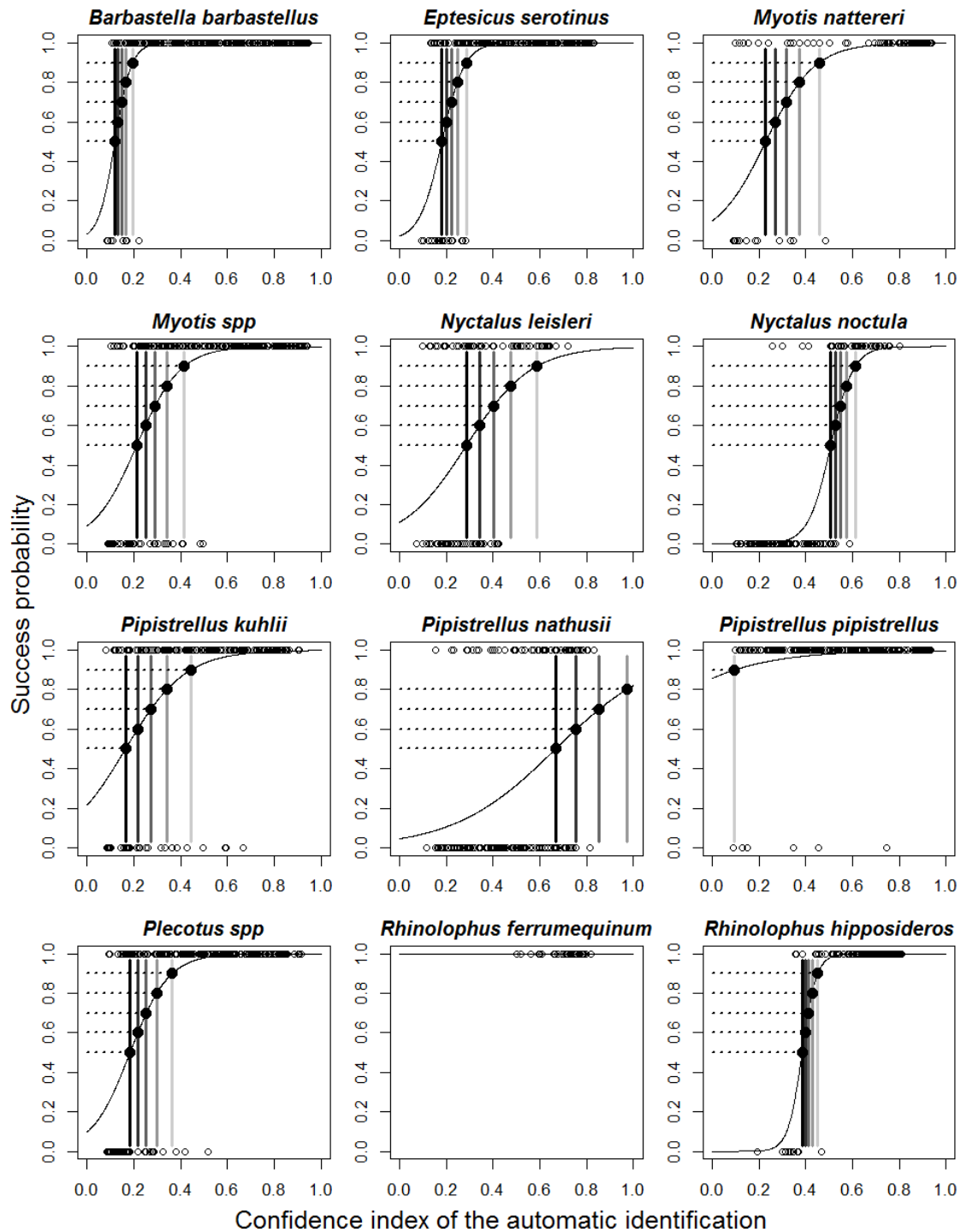


Fig. 2. Logistic regressions between the success probability and the confidence index of the automatic identification. The success probability was predicted from a subset manually checked assigning a success or fail of the automatic identification. Horizontal dotted lines show error risk probabilities (0.5, 0.4, 0.3, 0.2 and 0.1) used as threshold to select data in the total dataset above to the corresponding confidence indexes (vertical lines).

Step 3: total dataset sorting and environmental variables modelling at different error risk thresholds

After the prediction of the needed confidence index to ensure a given maximum error rate in the automatic identification, we filtered the total dataset (i.e. including the checked and non-checked bat passes) on the 5 confidence index thresholds (see step 3 in Fig.1; Fig. 3, Table 3). This filtering allowed to calculate for each thresholds on the total dataset the remaining number of bat passes, occurrences, and the expected real error rate (Table 3). In order to test if the error rate in acoustic dataset affect the response of bats (estimates, standard errors and p-values) to the 5 tested environmental variables, we performed one generalized linear mixed model (GLMM, R package lme4) per threshold of maximum error rate (0.5, 0.4, 0.3, 0.2 and 0.1) using bat activity (number of bat passes) as response variables. As an indication of how the analysis would perform if no filtering of errors were done, a sixth GLMM was fitted to raw automatic identification data.

We included in each species GLMM the 5 environmental variables as fixed effects, scaling distance and length variables. According to the sampling design (i.e. 13-15 simultaneous recordings per night), we included the date as random effect to control for inter-night variations in weather conditions and landscape context. We applied a Poisson error or a Negative binomial distribution to GLMMs. We checked there were no multicollinearity problems performing variance inflation factors (VIF) using the corvif function (R package AED; Zuur et al. 2010) on each model. All variables showed a VIF value < 1.5 , meaning there was no striking evidence of multicollinearity (Chatterjee & Hadi, 2006).

The 5 studied environmental variables are known as good predictors of bat activity: type of site i.e. hedgerow vs. open area habitat (respectively 207 sites on hedgerows and 130 in open areas located in average 86 m away from any hedgerow; Verboom & Huitema 1997; Lacoeylthe

et al. 2016), the distance in meters to forest (mean= 700; Standard Deviation=506; Boughey et al. 2011; Frey-Ehrenbold et al. 2013), the distance to urban (mean= 335; SD=170; Azam et al. 2016), the distance to wetland (mean=579; SD=363; Sirami et al. 2013; Santos et al. 2013) and the total length of hedgerows within a 1000 m radius (mean=3439; SD=1622; Verboom & Huitema 1997; Lacoëuilhe et al. 2016). The 4 quantitative environmental variables presented an important variability, and a similar gradient between sites located on hedgerows and those in open areas (Fig. S1).

This modelling allowed to check the response consistency of bats to environmental variables in relation with the different thresholds of maximum error rate. To ensure there were no acoustic biases in the bat responses, we tested the dependence of the automatic identification efficiency (i.e. success/fail by manual checks) to the environmental variables, for species with an enough error rate (>10%; Table 1) to perform models. Only one environmental variable (type of sites: hedgerow vs. open area) significantly affected the success probability of the automatic identification for only one species, *Nyctalus noctula* ($P < 0.001$; Table S1). Thus, for this species the automatic identification was less efficient for sites located on hedgerows than in open areas where calls are more steep and hard to identify (Obrist et al., 2004; Barataud, 2015).

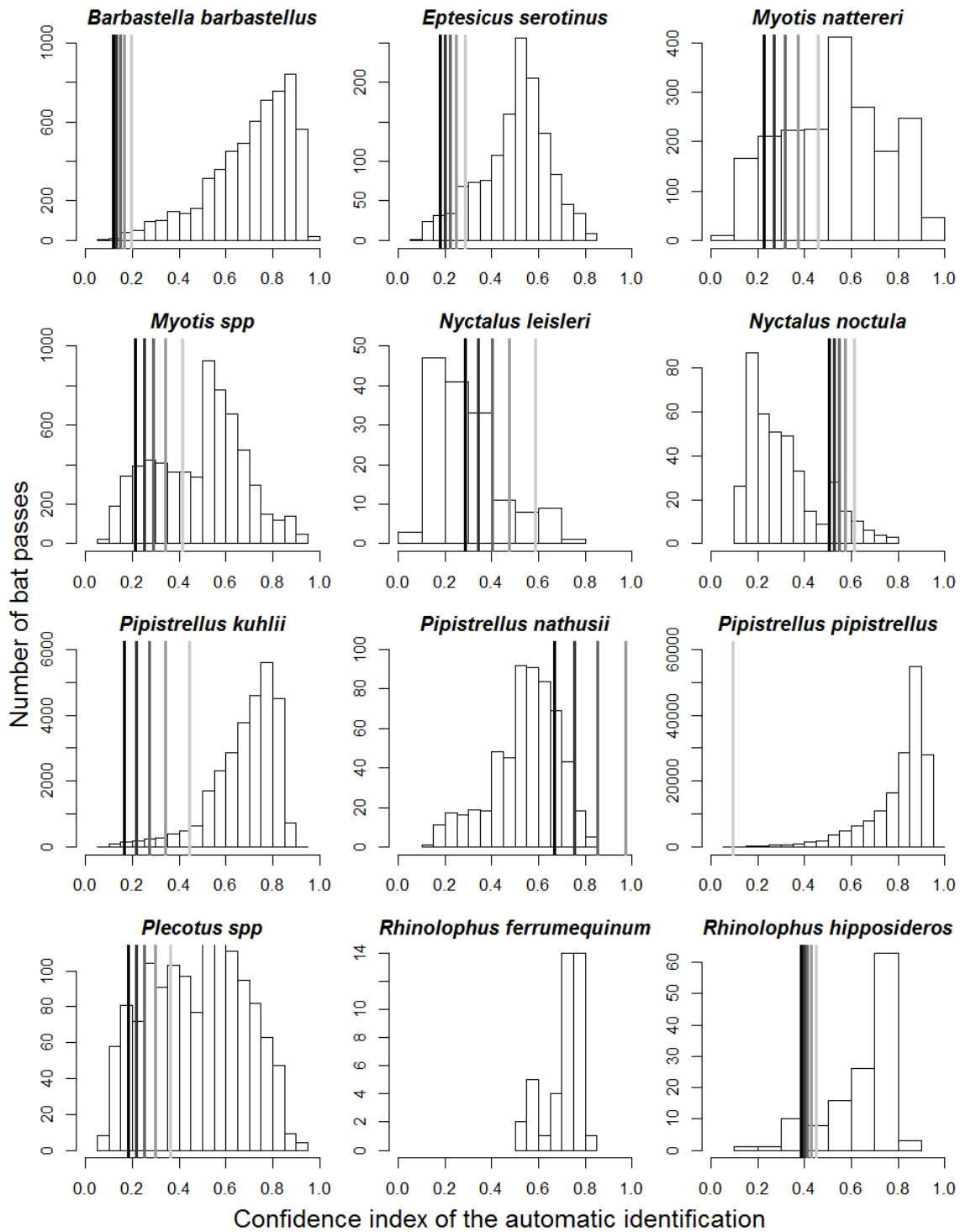


Fig. 3. Number of bat passes in the total dataset according to confidence index of the automatic identification. Vertical lines show the threshold above which data were selected to ensure a given rate of maximum error rate tolerance (from black to grey: 0.5, 0.4, 0.3, 0.2 and 0.1).

Table 3. Changes in the number of bat passes, the occurrence (presence rate among sites) and the expected error rate across the maximum error rate tolerances, calculated from a sorting of the total dataset (212 347 bat passes) on corresponding minimum needed confidence indexes presented in Table 2 (step 3 in the Figure 1).

Species	Raw data	Maximum error rate tolerance				
		0.5	0.4	0.3	0.2	0.1
<i>Barbastella barbastellus</i>						
No. of bat passes	5835	5828	5824	5822	5809	5787
Occurrences	0.694	0.694	0.694	0.694	0.694	0.694
Error rate	0.003	0.002	0.002	0.002	0.001	0.001
<i>Eptesicus serotinus</i>						
No. of bat passes	1343	1297	1287	1273	1255	1205
Occurrences	0.373	0.339	0.336	0.333	0.324	0.312
Error rate	0.044	0.022	0.019	0.015	0.012	0.006
<i>Myotis nattereri</i>						
No. of bat passes	1986	1759	1659	1562	1436	1239
Occurrences	0.688	0.648	0.624	0.609	0.578	0.529
Error rate	0.136	0.081	0.064	0.049	0.034	0.021
<i>Myotis spp.</i>						
No. of bat passes	6428	5783	5483	5135	4747	4173
Occurrences	0.798	0.792	0.786	0.774	0.765	0.716
Error rate	0.145	0.092	0.073	0.054	0.038	0.024
<i>Nyctalus leisleri</i>						
No. of bat passes	153	67	43	28	22	12
Occurrences	0.211	0.138	0.104	0.070	0.055	0.031
Error rate	0.502	0.305	0.222	0.149	0.115	0.075
<i>Nyctalus noctula</i>						
No. of bat passes	395	61	50	41	29	22
Occurrences	0.220	0.080	0.067	0.058	0.046	0.040
Error rate	0.850	0.212	0.158	0.120	0.066	0.042
<i>Pipistrellus kuhlii</i>						
No. of bat passes	28588	28456	28305	28077	27737	26854
Occurrences	0.899	0.899	0.890	0.884	0.881	0.875
Error rate	0.033	0.030	0.028	0.026	0.023	0.019
<i>Pipistrellus nathusii</i>						
No. of bat passes	577	101	18	0	0	0
Occurrences	0.404	0.116	0.031	0.000	0.000	0.000
Error rate	0.623	0.437	0.370	/	/	/
<i>Pipistrellus pipistrellus</i>						
No. of bat passes	167503	167503	167503	167503	167503	167502
Occurrences	0.954	0.954	0.954	0.954	0.954	0.954
Error rate	0.007	0.007	0.007	0.007	0.007	0.007
<i>Plecotus spp.</i>						
No. of bat passes	1352	1229	1185	1129	1034	909
Occurrences	0.615	0.599	0.596	0.596	0.584	0.544
Error rate	0.128	0.079	0.065	0.051	0.034	0.019
<i>Rhinolophus ferrumequinum</i>						
No. of bat passes	41	41	41	41	41	41
Occurrences	0.046	0.046	0.046	0.046	0.046	0.046
Error rate	0.000	0.000	0.000	0.000	0.000	0.000
<i>Rhinolophus hipposideros</i>						
No. of bat passes	128	117	116	116	116	113
Occurrences	0.113	0.107	0.104	0.104	0.104	0.104
Error rate	0.078	0.011	0.007	0.007	0.007	0.003

3. Results

Semi-automated acoustic identification on a subset

Over the 23 complete nights sampled, 212 347 bat passes were recorded with 167 504 (79%) assigned to *Pipistrellus pipistrellus* 28 589 (13%) to *Pipistrellus kuhlii*, 6 430 (3%) to *Myotis spp.* and 5 835 (3%) to *Barbastella barbastellus* (Table 1). A total of 1910 bat passes over all classes of confidence index were manually checked (Table 1). Error rates varied a lot between species, from 0.0% for *Rhinolophus ferrumequinum* to 69.4% for *N. noctula* (Table 1). The most errors detected in manual checks concerned *N. noctula* confused with social calls of *P. pipistrellus* and non-bat noises, and *Pipistrellus nathusii* confused with *P. kuhlii*, *P. pipistrellus* and non-bat noises (Table S2).

Error risk modelling from the semi-automated identification

Successes and fails in the automatic identification noted by manual checks were modelled in relation to the confidence indexes provided by the software, allowing to predict the needed confidence index to ensure a given maximum error rate tolerance (Fig. 2). Confidence indexes corresponding to the maximum error rate rates (i.e. 0.5, 0.4, 0.3, 0.2 and 0.1) did not vary much for some species such as *B. barbastellus* (0.12-0.20), *Eptesicus serotinus* (0.18-0.29) and *Rhinolophus hipposideros* (0.39-0.45), and more for others, e.g. *Nyctalus leislerii* (0.29-0.59), *P. kuhlii* (0.16-0.44) and *Plecotus ssp.* (0.18-0.36) (Table 2). In addition, the needed confidence indexes to limit error risks were overall low for *B. barbastellus* (0.12-20), *E. serotinus* (0.18-0.29), *P. kuhlii* (0.16-0.44), *Plecotus ssp.* (0.18-0.36), *Myotis spp.* (0.21-0.42), and higher for *P. nathusii* (0.67-0.77) and *N. noctula* (0.51-0.61) (Table 2).

A low maximum error rate tolerance allows to highly reduce the false positive rate (e.g. from 0.20 in raw data to 0.01 in data with a 0.1 maximum error rate for *Myotis spp.*), and even to fully remove false positives (e.g. for *E. serotinus* and *N. leislerii* starting from the 0.1 and 0.2 rates of maximum error rate, respectively) (Table 2; Fig. 2). However, reduce the maximum error rate tolerance can also generate moderate to high false negative rates, such as for *E. serotinus* (0.15), *Myotis spp.* (0.28), *N. leislerii* (0.79), *N. noctula* (0.51), *P. kuhlii* (0.38) or *Plecotus spp.* (0.27) (Table 2; Fig. 2).

For *P. pipistrellus* errors were too rare to get a prediction of the confidence index for a maximum error rate higher than 0.1. For *P. nathusii*, the number of passes in high confidence indexes did not allowed to get a prediction of the needed confidence index for the 0.1 maximum error rate, and there were no errors for *R. ferrumequinum* preventing the error risk modelling. For all other species, it was however possible to select the part of the dataset satisfying the lowest maximum error rate tolerance (0.1).

Total dataset sorting and environmental variables modelling at different error risk thresholds

Sort out data at high confidence indexes, corresponding to low maximum error rate tolerances, can led to important losses of bat passes contained in lower confidence indexes, as well as for occurrences (Table 3). Indeed, for a changeover from a maximum error rate of 0.5 to 0.1, this implies e.g. a loss in the number of passes of 27.8% and a loss in the occurrence of 6.7% for the *Myotis spp.* group, respectively 82.1% and 10.7% for *N. leislerii* (Table 3). For other species, the number of bat passes and occurrences can be more stable despite the sorting out of data at maximum error rate thresholds, such as *B. barbastellus*, *E. serotinus*, *P. kuhlii*, *Plecotus spp.* and *R. hipposideros* (Table 3).

The sort out of data according to the maximum error rate tolerances also affect the expected real error rate. Indeed, at the higher maximum error rate (0.5), the expected real error rate is high for 3 species, *N. leislerii* (0.31), *N. noctula* (0.21) and *P. nathusii* (0.44); low (<10%) for *Myotis spp.* (0.09) and *Plecotus spp.* (0.08); and very low (<5%) for *B. barbastellus* (<0.01), *E. serotinus* (0.02), *P. kuhlii* (0.03), *P. pipistrellus* (<0.01) *R. ferrumequinum* (0.00) and *R. hipposideros* (0.01) (Table 3). However, at the lower error risk (0.1), all species showed an error rate <0.05, except *N. leislerii* (0.08).

To study the influence of these changes in amount of data, occurrences and error rates according to the error risk thresholds for which data are selected, a modelling of the bat response to environmental variables was performed at all thresholds. Main changes in model outputs occurred from naive (i.e. raw data) to robust analyses (i.e. thresholds of error risk) with a loss or gain of significance, for the open areas vs. hedgerows variable for *N. leislerii*, the distance to forest for *Myotis spp.* and *N. leislerii*, the length of hedgerows for *N. leislerii* and the distance to urban for *N. noctula* (Table 4). In addition, an estimate inversion in cases of significance for the open areas vs. hedgerows variable occurred for *N. noctula* and *P. nathusii* (Table 4). In all other cases, no major changes were noted either for significant or no significant variables (Table 4).

Then, we did not detect major changes between the 0.5, 0.4, 0.3, 0.2 and 0.1 maximum error rates, with response estimates and standard errors highly stable (Table 4). In only two cases, we detected a loss of significance for *N. noctula* in lower maximum error rate than 0.2 and 0.3 for the distance to forests and the length of hedgerows variables, respectively (Table 4). However, concerning these species, the open areas vs. hedgerows variable remains significant and highly stable at all thresholds (Table 4).

Table 4. Species response to environmental variables (estimates, standard errors and p-values) according to the error risk tolerances (***) $P < 0.001$, (**) $P < 0.01$, (*) $P < 0.05$, (.) $P < 0.1$).

Species	Environmental variables	Maximum error rate tolerance					
		Raw data	0.5	0.4	0.3	0.2	0.1
<i>Barbastella barbastellus</i>	Open areas vs. hedgerows	-2.81±0.24 ***	-2.81±0.24 ***	-2.81±0.24 ***	-2.81±0.24 ***	-2.81±0.24 ***	-2.81±0.24 ***
	Dist. to forest	0.08±0.12	0.08±0.13	0.08±0.13	0.08±0.13	0.08±0.13	0.08±0.13
	Dist. to wetland	-0.03±0.12	-0.03±0.12	-0.03±0.12	-0.03±0.12	-0.03±0.12	-0.04±0.12
	Dist. to urban	0.01±0.1	0.01±0.1	0.01±0.1	0.01±0.1	0.01±0.1	0.02±0.1
	Length of hedgerows	0.17±0.12	0.17±0.12	0.17±0.12	0.17±0.12	0.17±0.12	0.17±0.12
<i>Eptesicus serotinus</i>	Open areas vs. hedgerows	-0.57±0.38	-0.43±0.4	-0.44±0.4	-0.45±0.41	-0.43±0.42	-0.35±0.42
	Dist. to forest	-0.07±0.23	-0.15±0.24	-0.15±0.25	-0.16±0.25	-0.15±0.25	-0.13±0.26
	Dist. to wetland	0.08±0.19	0.12±0.2	0.12±0.2	0.12±0.2	0.12±0.21	0.08±0.21
	Dist. to urban	-0.7±0.19 ***	-0.8±0.21 ***	-0.79±0.21 ***	-0.78±0.21 ***	-0.77±0.21 ***	-0.77±0.22 ***
<i>Myotis nattereri</i>	Open areas vs. hedgerows	-1.16±0.21 ***	-1.14±0.22 ***	-1.12±0.23 ***	-1.05±0.23 ***	-1.01±0.24 ***	-1.03±0.27 ***
	Dist. to forest	0.16±0.13	0.13±0.13	0.14±0.13	0.15±0.14	0.1±0.14	0.11±0.15
	Dist. to wetland	0.17±0.11	0.21±0.12 .	0.23±0.12 .	0.24±0.12 .	0.22±0.13 .	0.21±0.13
	Dist. to urban	0.07±0.1	0.08±0.11	0.09±0.11	0.11±0.12	0.11±0.12	0.13±0.13
	Length of hedgerows	0.18±0.12	0.22±0.13 .	0.24±0.13 .	0.27±0.14 .	0.32±0.14 *	0.3±0.16 .
<i>Myotis spp</i>	Open areas vs. hedgerows	-1.66±0.19 ***	-1.64±0.19 ***	-1.6±0.19 ***	-1.55±0.19 ***	-1.54±0.19 ***	-1.61±0.26 ***
	Dist. to forest	0.24±0.12 *	0.22±0.12 .	0.22±0.12 .	0.22±0.12 .	0.22±0.13 .	0.20±0.13
	Dist. to wetland	0.1±0.1	0.11±0.11	0.1±0.11	0.11±0.11	0.1±0.11	0.10±0.11
	Dist. to urban	-0.07±0.09	-0.08±0.09	-0.08±0.1	-0.06±0.1	-0.05±0.1	-0.03±0.1
	Length of hedgerows	0.13±0.12	0.15±0.12	0.15±0.12	0.17±0.12	0.18±0.12	0.21±0.13
<i>Nyctalus leislerii</i>	Open areas vs. hedgerows	-0.8±0.22 ***	-0.26±0.29	-0.23±0.35	0.43±0.4	0.69±0.45	1.1±0.64
	Dist. to forest	0.34±0.13 **	0.16±0.17	0.21±0.21	0.08±0.26	0.14±0.28	0.49±0.35
	Dist. to wetland	0.07±0.1	-0.09±0.15	-0.02±0.19	-0.12±0.26	-0.21±0.3	-0.17±0.42
	Dist. to urban	-0.1±0.1	-0.19±0.15	-0.01±0.18	0.08±0.23	0.23±0.26	0.43±0.35
	Length of hedgerows	0.35±0.12 **	0.23±0.16	0.23±0.21	0.27±0.25	0.28±0.29	0.22±0.41
<i>Nyctalus noctula</i>	Open areas vs. hedgerows	-1.19±0.17 ***	1.46±0.31 ***	1.7±0.36 ***	1.83±0.4 ***	1.37±0.44 **	1.28±0.49 *
	Dist. to forest	-0.55±0.11 ***	-0.68±0.23 **	-0.66±0.26 *	-0.7±0.29 *	-0.26±0.32	-0.12±0.35
	Dist. to wetland	-0.07±0.06	0.02±0.18	0.16±0.21	0.25±0.24	0.3±0.27	0.34±0.34
	Dist. to urban	0.25±0.07 ***	-0.07±0.18	-0.1±0.21	-0.12±0.23	-0.01±0.25	-0.04±0.29
	Length of hedgerows	0.34±0.08 ***	0.43±0.21 *	0.49±0.25 *	0.52±0.28 .	0.16±0.31	-0.03±0.36
<i>Pipistrellus kuhlii</i>	Open areas vs. Hedgerows	-1.98±0.26 ***	-1.98±0.26 ***	-1.98±0.27 ***	-1.98±0.27 ***	-1.98±0.27 ***	-1.98±0.27 ***
	Dist. to forest	0.09±0.13	0.09±0.13	0.09±0.13	0.09±0.14	0.09±0.14	0.1±0.14
	Dist. to wetland	0.25±0.13 *	0.25±0.13 *	0.26±0.13 *	0.25±0.13*	0.26±0.13*	0.26±0.13*
	Dist. to urban	0.07±0.13	0.07±0.13	0.07±0.13	0.08±0.13	0.08±0.13	0.08±0.13
	Length of hedgerows	0.07±0.15	0.06±0.15	0.06±0.15	0.06±0.15	0.06±0.15	0.06±0.15
<i>Pipistrellus nathusii</i>	Open areas vs. Hedgerows	-0.37±0.24	1.02±0.38 **	2.57±0.84 **	/	/	/
	Dist. to forest	0.1±0.16	0.28±0.23	0.81±0.46 .	/	/	/
	Dist. to wetland	0.06±0.13	0.02±0.2	0.53±0.42	/	/	/
	Dist. to urban	-0.05±0.13	0.09±0.21	0±0.44	/	/	/
	Length of hedgerows	0.11±0.16	0.42±0.24 .	0.88±0.54	/	/	/
<i>Pipistrellus pipistrellus</i>	Open areas vs. Hedgerows	-2.87±0.19 ***	-2.87±0.19 ***	-2.87±0.19 ***	-2.87±0.19 ***	-2.87±0.19 ***	-2.87±0.19 ***
	Dist. to forest	0.13±0.13	0.13±0.13	0.13±0.13	0.13±0.13	0.13±0.13	0.13±0.13
	Dist. to wetland	0.04±0.11	0.04±0.11	0.04±0.11	0.04±0.11	0.04±0.11	0.04±0.11
	Dist. to urban	-0.13±0.1	-0.13±0.1	-0.13±0.1	-0.13±0.1	-0.13±0.1	-0.13±0.1
	Length of hedgerows	0.35±0.12 **	0.35±0.12 **	0.35±0.12 **	0.35±0.12 **	0.35±0.12 **	0.35±0.12 **
<i>Plecotus spp.</i>	Open areas vs. Hedgerows	-0.91±0.19 ***	-0.85±0.19 ***	-0.87±0.19 ***	-0.87±0.19 ***	-0.85±0.19 ***	-0.79±0.2 ***
	Dist. to forest	0.08±0.12	0.1±0.12	0.11±0.12	0.1±0.12	0.09±0.12	0.08±0.13
	Dist. to wetland	-0.16±0.11	-0.14±0.11	-0.15±0.11	-0.15±0.11	-0.14±0.11	-0.17±0.12
	Dist. to urban	-0.25±0.1 **	-0.25±0.1 *	-0.26±0.1 **	-0.25±0.1 **	-0.25±0.1 *	-0.23±0.1 *
	Length of hedgerows	0.1±0.12	0.09±0.12	0.09±0.12	0.08±0.12	0.11±0.12	0.11±0.13
<i>Rhinolophus ferrumequinum</i>	Open areas vs. Hedgerows	0.26±0.39	0.26±0.39	0.26±0.39	0.26±0.39	0.26±0.39	0.26±0.39
	Dist. to forest	0.74±0.25 **	0.74±0.25 **	0.74±0.25 **	0.74±0.25 **	0.74±0.25 **	0.74±0.25 **
	Dist. to wetland	-1.2±0.29 ***	-1.2±0.29 ***	-1.2±0.29 ***	-1.2±0.29 ***	-1.2±0.29 ***	-1.2±0.29 ***
	Dist. to urban	-0.21±0.26	-0.21±0.26	-0.21±0.26	-0.21±0.26	-0.21±0.26	-0.21±0.26
	Length of hedgerows	0.83±0.29 **	0.83±0.29 **	0.83±0.29 **	0.83±0.29 **	0.83±0.29 **	0.83±0.29 **
<i>Rhinolophus hipposideros</i>	Open areas vs. Hedgerows	-3.08±0.74 ***	-2.92±0.73 ***	-2.92±0.74 ***	-2.92±0.74 ***	-2.92±0.74 ***	-2.89±0.73 ***
	Dist. to forest	0.09±0.3	-0.47±0.36	-0.5±0.37	-0.5±0.37	-0.5±0.37	-0.51±0.36
	Dist. to wetland	-0.33±0.26	-0.45±0.26 .	-0.49±0.27 .	-0.49±0.27 .	-0.49±0.27 .	-0.46±0.28 .
	Dist. to urban	-0.18±0.26	-0.17±0.26	-0.14±0.27	-0.14±0.27	-0.14±0.27	-0.15±0.27
	Length of hedgerows	0.03±0.3	0.06±0.3	0.07±0.3	0.07±0.3	0.07±0.3	0.08±0.3

All species had at least one significant habitat variable response over thresholds of maximum error rate tolerances, except *N. leislerii*. Hedgerows had significant higher number of bat passes than open areas for 7 species/groups (*B. barbastellus*, *Myotis nattereri*, *Myotis spp.*, *P. kuhlii*, *P. pipistrellus*, *Plecotus spp.* and *R. hipposideros*) and significant lower for 2 species/groups (*N. noctula* and *P. nathusii*) (Table 4). We also found significant negative relationship between the number of bat passes and the distance to urban for 2 species/groups (*E. serotinus* and *Plecotus spp.*; Table 4); a significant negative relationship with the distance to forest for 2 species (*N. noctula* and *R. ferrumequinum*; Table 4); a significant negative relationship with the distance to wetlands on *R. ferrumequinum* and the length of hedgerows on *N. noctula*, *P. pipistrellus*, *R. ferrumequinum* (Table 4); as well as a significant positive relationship with the distance to wetlands for *P. kuhlii* (Table 4).

4. Discussion

This study demonstrates that automatic acoustic identification of bats coupled to partial manual checking and error rate modelling (i.e. semi-automatic identification; Newson et al. 2015), is a key tool for knowledge improvements and the conservation of bats. Robust activity patterns could indeed be demonstrated even in cases where error rates were so far considered too high (Rydell et al. 2017). This new and robust framework takes advantage of confidence estimates provided by the automatic identification softwares, controlling error rate tolerance and checking for potential biases induced by identification errors.

Using confidence thresholds

To investigate the effect of the automatic identification errors on bat activity patterns, we studied the response of bat activity to several environmental variables known to impact bats. Most of the significant responses were, as expected, consistent with known patterns: open areas

vs. hedgerows (Verboom & Huitema 1997; Lacoëuilhe et al. 2016), forest (Boughey et al., 2011; Frey-Ehrenbold et al., 2013), urban (Mckinney, 2005; Jung & Threlfall, 2016) and wetlands (Santos et al., 2013; Sirami et al., 2013).

The comparison between the analyses conducted on raw data (i.e. no sort out of data) and based on maximum error rate tolerances (i.e. sort out of data to minimize the error rate) showed however some discrepancies, with sometimes opposed significant responses, such as the effect of open areas vs. hedgerows variable on *N. noctula* and *P. nathusii*. This demonstrates that analyses conducted on raw automatic identification of data could be severely biased. In this way sort out data with high error risks is essential, in accordance with concerns expressed by Russo & Voigt (2016), and thus it is indispensable to use a semi-automatic process (Newson et al. 2015).

Quite logically these biases due to false positives seem to impact mostly uncommon species which are acoustically close to commoner ones. Here the most impacted species is *P. nathusii* which suffer of a high false positive rate due to the local abundance of *P. kuhlii* and *P. pipistrellus*. Consequently, an analysis conducted on raw automatic identification data for this species seems to be completely driven by the response of the two other Pipistrelles.

However, we also shown that 15 of the 18 significant activity responses at the 0.5 maximum error rate tolerance were very consistent and highly stable while reducing the error risk tolerance to 0.1 (Table 4). Among the three exceptions, one response did not change much in magnitude but lost significance: the distance to forest for *N. noctula* (Table 4). Concerning the second exception, the magnitude of the response of *N. noctula* to the length of hedgerows did not change until the 0.3 error risk tolerance, but decrease then disappear at the 0.2 and 0.1 tolerances, respectively. Similarly, this response lost significance starting from the 0.3 error risk tolerance (Table 4). The response of these two exceptions were relatively weak compared to open vs. hedgerow responses, thus this discrepancy among error tolerance thresholds is more

likely due to a lack of statistical power in dataset sorted on low error tolerances than any source of bias in higher tolerances. Indeed, major changes in these two responses occurred at the 0.2 and 0.1 error risk tolerances for which the number of passes as well as the occurrences were very weak and divided by 2 compared to the 0.5 tolerance (Table 3). This shows that using a cautious threshold minimising false positive rates may prevent to detect subtle patterns. The last exception concern *P. nathusii* for which no analysis could be conducted for low error tolerances because all bat passes suffered of relatively high error risk due to commoner *Pipistrellus* species (see above). However, the fact that the positive response of *P. nathusii* to open areas vs. hedgerows was opposite to the two other species plead for a genuine pattern rather than a biased one, but this response should be more cautiously interpreted than other species response that were consistent with varying error risk tolerances.

Survey recommendations and limitations

This method propose a cautious method to account for identification errors in acoustic surveys, without fully check records, which aim to study the response bats in relation to environmental variables, anthropic pressures or temporal monitoring.

The maximum error rate tolerance of 0.5 is a threshold containing the minimum error rate, with an equilibrate balance between false negatives and false positives. However, false positives could more likely produce biases because their rate is strongly driven by the activity pattern of other species. In contrast, the maximum error rate tolerance of 0.1 minimise the false positive rate, but at the cost of discarding a lot of false negatives. Rather than looking for a possible optimal thresholds, our results suggest to systematically check the consistence of responses considering at least two thresholds (e.g. 0.5 and 0.1), in order to check the robustness of the obtained results and go to conclusive interpretation only when these are consistent.

A lack of consistency is particularly expected for rare species with very low abundances/occurrences (e.g. *Nyctalus spp.* in this study) and for uncommon species which are acoustically close to commoner ones such as *P. nathusii* here. For these species, either systematic manual checking or important improvement of automatic identification efficiency is needed to conduct robust analyses. However, our framework of error risk modelling is already sufficient to effectively identify these problematic species and should prevent automatic identification users to draw non robust conclusions.

This method can be applied to any ecological studies with standardized sampling but, of course, cannot help for surveys where no error could be tolerated, e.g. inventories, species distribution modelling or environmental impact assessment (Russo & Voigt 2016). However, in that case, the automatic identification indicate what bat passes to manually check in order to identify species presence at the site scale, selecting passes having best confidence indexes and thus saving time to the user.

Conclusions and perspectives

Despite concerns emitted by Rydell et al. (2017) about global error rates in automatic identification restricting their use, this study shows that it is possible to account for these errors by using the provided confidence index of identification reliability in order to model the error risk. This allowed to check consistence of responses at different maximum error rate tolerances involving a trade-off between quantity and quality of acoustic data.

This process, named semi-automatic identification (Newson et al. 2015), is a key tool for knowledge improvements and the conservation of bats. Such a method indeed allows to use bat acoustic data containing false positive passes, checking potential influence of error rates on the response of bat activity to various factors such as environmental variables, anthropic

pressures or temporal monitoring. A crucial advantage is that manually checking of a relatively small subset of bat passes (< 1 %) is sufficient to assess analysis robustness regarding error rates. This is especially true given that checking all data is very time-consuming and virtually impossible for such a large dataset.

Thus, this study provides new opportunities, starting with a time gain in manual checking in experimental studies. This also allows to widely generalize large-scale monitoring of bats improving knowledge on so far unknown ecological patterns (Newson et al. 2015). Current context with the recent development of citizen science programs is particularly favourable to the deployment of such large-scale acoustic monitoring, and could make it possible to study very important concerns such as population trends (Barlow et al., 2015; Jeliaskov et al., 2016), thus having an important implication for conservation of bats.

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ARTICLE 1

APPENDICES

Appendix 1

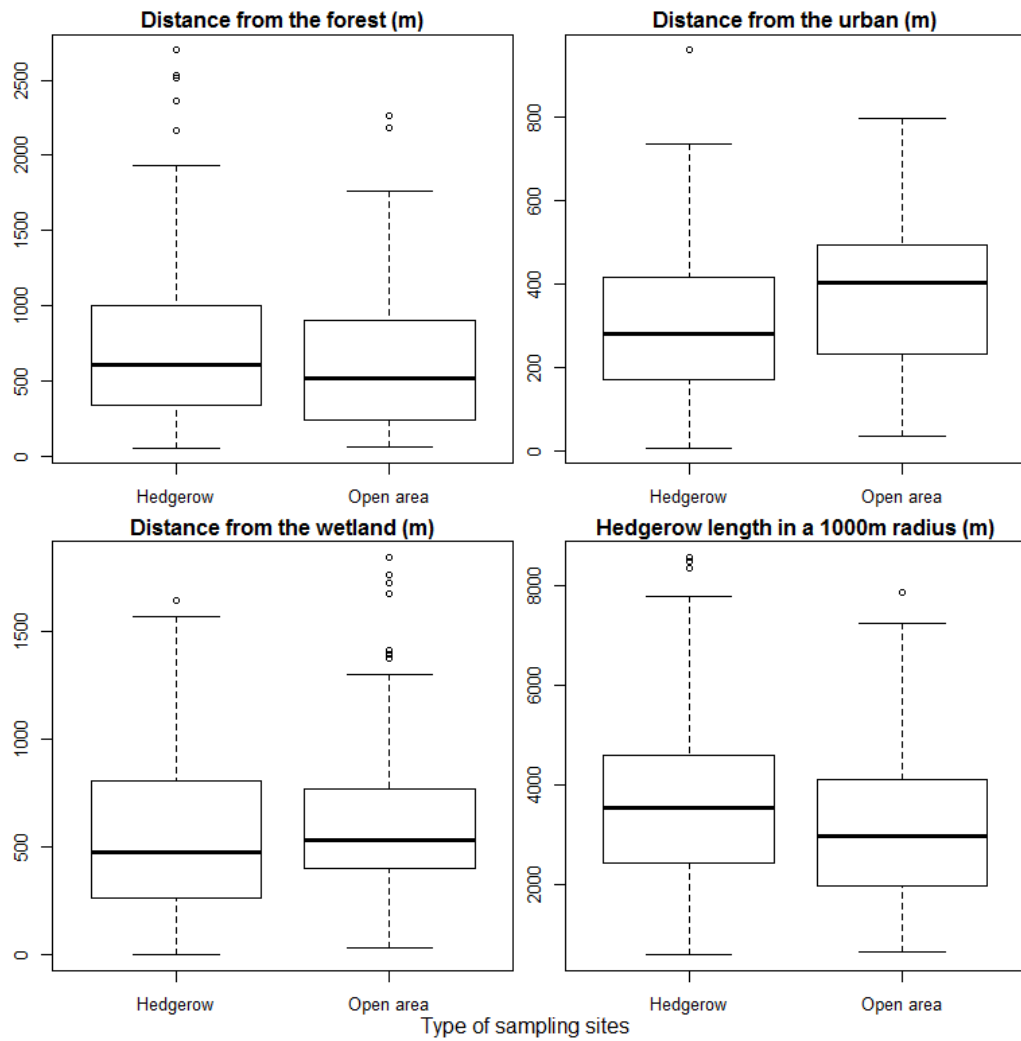


Fig. S1. Boxplots of the tested continuous variables according to the type of sampling sites (hedgerows or open areas).

Table S1. Estimates (β) and p-values (significant values are in bold) of the test of the dependence of the automatic identification efficiency (i.e. success/fail by manual checks) to the environmental variables, for species with an enough error rate (>10%; see Table 1).

Species	Environmental variables									
	Forest		Urban		Wetland		Hedgerows		Type of site	
	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value
<i>Eptesicus serotinus</i>	-0.561	0.513	-0.171	0.829	-0.499	0.664	0.202	0.834	3.929	0.442
<i>Myotis nattereri</i>	-0.312	0.785	0.767	0.636	0.162	0.890	0.192	0.872	1.322	0.721
<i>Myotis spp.</i>	-0.002	0.995	0.579	0.190	0.147	0.749	0.159	0.807	1.604	0.220
<i>Nyctalus leisleri</i>	-0.139	0.746	0.967	0.115	-0.059	0.901	0.103	0.815	3.102	0.059
<i>Nyctalus noctula</i>	0.859	0.507	0.290	0.714	-0.139	0.909	-0.335	0.766	18.167	0.000
<i>Pipistrellus kuhlii</i>	-0.595	0.412	0.101	0.909	0.486	0.565	0.721	0.442	0.033	0.987
<i>Pipistrellus nathusii</i>	0.351	0.413	0.005	0.987	-0.782	0.066	1.036	0.056	-0.464	0.582
<i>Plecotus spp.</i>	0.169	0.634	-0.055	0.858	0.262	0.372	-0.163	0.607	-0.211	0.789

Table S2. Species composition of detected errors in automatic identification from manual checking (Barbar: *Barbastella barbastellus*; Eptser: *Eptesicus serotinus*; Myosp: *Myotis spp.*; Nyclei: *Nyctalus leisleri*; Nycnoc: *Nyctalus noctula*; Pipkuh: *Pipistrellus kuhlii*; Pipnat: *Pipistrellus nathusii*; Pippip: *Pipistrellus pipistrellus*; Plesp: *Plecotus spp.*; Rhifer: *Rhinolophus ferrumequinum*; Rhihip: *Rhinolophus hipposideros*).

Automatically identified species	Species composition of detected errors in the automatic identification													Total
	Barbar	Eptser	Myonat	Myosp	Nyclei	Nycnoc	Pipkuh	Pipnat	Pippip	Plesp	Rhifer	Rhihip	Non-bat	
Barbar		0	0	1	0	0	0	0	0	0	0	0	8	9
Eptser	1		0	2	0	0	7	0	0	2	0	0	9	21
Myonat	2	1		/	0	0	3	0	1	0	0	0	10	17
Myosp	9	3	/		0	0	8	0	9	2	0	0	18	49
Nyclei	0	2	0	0		1	2	0	3	3	0	0	38	49
Nycnoc	0	0	0	0	1		0	0	54	0	0	0	47	102
Pipkuh	6	3	0	4	0	0		2	8	0	0	0	15	38
Pipnat	0	0	0	0	0	0	63		40	0	0	0	9	112
Pippip	0	0	0	1	0	0	0	1		0	0	0	4	6
Plesp	10	4	0	1	0	0	3	0	6		0	0	12	36
Rhifer	0	0	0	0	0	0	0	0	0	0		0	0	0
Rhihip	0	0	0	0	0	0	0	0	0	0	0		10	10

“Cities needlessly shine billions of dollars directly into the sky each year”

Smith 2009

CHAPTER 2

EVALUATING THE INFLUENCE OF LIGHT POLLUTION ON BAT ACTIVITY AT THE CITY SCALE

ARTICLE 2

Pauwels J., Le Viol I., Azam C., Valet N., Julien J.-F., Bas Y., Lemarchand C., Sánchez De Miguel A., Kerbiriou C. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. Accepted for publication in Landscape and Urban Planning. Accepted in Landscape and Urban Planning.

Introduction

Globally, urban areas cover only about 3% of the earth land surface (Millenium Ecosystem Assessment, 2005) yet the impact of urbanization has been global and it is regarded as a major threat to biodiversity (Grimm et al., 2008; Kowarik, 2011). Urban growth induce profound changes in the landscape not only in urban settlements but also beyond due to the important demands in resources to support urban populations (Grimm et al., 2008). Urban areas have effects on surrounding semi-natural and natural habitats and ecosystems (Savard, Clergeau, & Mennechez, 2000) and their negative impacts on species abundance, diversity and richness have been documented for numerous taxonomic groups (Devictor et al., 2007; Penone et al., 2013; Azam et al., 2016). However, urban areas can also be considered as a particular type of ecosystems which biodiversity is important to preserve as a contribution to the global conservation of biodiversity but also to enable the positive effects on human health and well-being brought by the exposure to natural systems (Kowarik, 2011). In addition, as a growing percentage of the population inhabits urban areas, people are becoming less likely to have direct contact with nature in their everyday life which is worrying as it may lead to a disaffection toward nature (Soga & Gaston, 2016) and ultimately reduce people's willingness to conserve biodiversity (Keniger et al., 2013; Soga et al., 2016). Thus, to increase daily interaction with nature and favor positive emotions and behavior toward the environment, it is important to preserve biodiversity within urban areas.

Urban areas are often highly fragmented with only few small remnants of vegetation scattered within an impervious matrix (Savard et al., 2000). This fragmentation of urban landscapes induces a decrease in the landscape functional connectivity, i.e. it negatively affects species ability to move across the landscape. Urban ecosystems also tend to have a dense distribution of light sources and high levels of light emissions which result in a significant

degree of light pollution. ALAN can have a large variety of impacts on species, affecting their physiology, behavior, movement and interactions (Gaston et al., 2012). Light can also decrease habitat quality and for the most sensitive species can result in a loss of habitat. Thus light pollution can be another factor leading to landscape fragmentation and have a cumulative effect with the important expansion of soil sealing in urban areas. Green infrastructures policies aim at tackling this issue by identifying and restoring ecological corridors therefore improving landscape connectivity. Although this is a valuable strategy to promote biodiversity, often the design of corridors is only based on cartographic elements hence not accounting for species behavior and does not account for light pollution (Billon et al., 2017). Both these limits may have important impacts on ecological networks design in this way. To conceive urban planning which limits the impact of urbanization on both diurnal and nocturnal biodiversity, land managers need spatially explicit information on the areas where actions should be prioritize and how action could be taken. Scientific studies may help answering both biological and societal issues by evaluating spatial patterns at a scale that is coherent with ecological processes but also with management scale.

Most studies on the impact of light pollution focus on fine scale effects, i.e. at the scale of a light source (e.g., Lewanzik & Voigt, 2017), and a few investigate large scale (Bennie et al., 2015; Azam et al., 2016). However, intermediate scales of only tens of kilometer square remain unstudied possibly due to the difficulty to access data with a fine enough resolution for such spatial extent (Hale et al., 2013). Nonetheless this scale which corresponds to the size of cities or municipalities is highly relevant for both species movements and lighting planning. Indeed, public outdoor lighting, which is the most pervasive, aggregated and permanent source of lighting in urban areas (Gaston et al., 2012) and represents 30 to 50% of the light sources (Aubé et al., 2018), is managed at this scale.

Aims of the chapter

In this chapter, I investigated the impact of light pollution on spatial patterns of activity of a bat species at the city scale testing several possible source of information on light emissions. I evaluated the relevance of a ground-based source of data, the location of streetlights, and a remote sensing source of data, pictures taken by astronauts from the international space station (ISS). These two sources of information can be accessed online and thus the study performed in this study may be reproduced by land managers in other areas. It is important to note that both types of data on light emissions do not contain the same information. Indeed, streetlights location data only give information on the position of public light sources and thus do neither inform on the quantity and spectral composition of light nor on the emissions produce by private lighting. ISS pictures have a less precise resolution but they include information on the quantity and spectral distribution of light for both public and private lighting.

This study focuses on evaluating the pattern of response of a common bat species, *Pipistrellus pipistrellus*, at the city-scale using data from a national citizen science bat monitoring program. This bat species is often the most abundant within highly urbanized areas and is qualified as light-tolerant as it opportunistically forage for insects flying around light sources (Rydell, 1992). However national scale studies showed that the activity of species locally feeding on light attracted insects could be negatively impacted by light (Azam et al., 2016). These contradictory findings highlight the importance to evaluate species responses to a pressure at different spatial scales. Fine scale studies may give insight on specific behavior in a local context such as the foraging behavior of *P. pipistrellus* at streetlights whereas large scale studies allow to investigate population dynamics thus including the diverse effect of a pressure on individuals' behavior. Compared to local scale studies, large scale ones account for species response to the landscape composition which is of particular importance for landscape management. The study presented aim at investigating the spatial distribution of bat activity at

an intermediate scale which is closer to this species home range size and thus participates to the assessment of scale effects on bat activity patterns which is particularly useful to evaluate the impact of landscape fragmentation (Donovan & Lamberson, 2009). Thus, in the study presented in this chapter, I intended to **compare the potential of ground based and remote sensing nighttime light data to characterize the effect of light pollution on *P. pipistrellus* at the city-scale**. I used citizen science data sampled in three large cities of France (Paris, Lille, and Montpellier) as part of the national bat monitoring program (Vigie-chiro). With these data, I modelled bat activity in regard to environmental variables including light pollution variables.

In this chapter, I also discuss part of the results arising from another study (Laforge et al., *in prep*, Article 3 in chapter 3) which use a similar methodology to the one presented previously. This study evaluate the impact of light pollution at the scale of a conurbation (almost 300 km²) in the North of France. Within the study areas, a diversity of land covers can be encountered such as densely built urban cores, suburban landscapes and agricultural lands within which semi-natural tree vegetation and wetlands. The effect of light is evaluated for three bat species, *Pipistrellus nathusii*, *Eptesicus serotinus* and *Myotis daubentonii*, which have different behavioral ecology and have distinct responses to light pollution. Indeed, at the local scale, both *P. nathusii* and *E. serotinus* activity increase with light level (Lacoeuilhe et al., 2014) but another study showed that *E. serotinus* activity was negatively affected at 25 to 50 m of a streetlight (Azam et al., 2018). In addition, *E. serotinus* is negatively affected by ALAN at large scale (Azam et al., 2016). *Myotis* species are known to be negatively impacted by light even at low levels (Stone, Jones, & Harris, 2012; Lacoeuilhe et al., 2014) and possibly at tens of meters away from streetlights (Azam et al., 2018). **This study intents to evaluate how *P. nathusii*, *E. serotinus* and *M. daubentonii* respond to light level at the scale of a conurbation**. The methodology employed was similar to the one used in the first study

presented in this chapter although the measure of light pollution was given by a satellite image (VIIRS DNB) with a 250 m resolution.

Principal results & discussion

The first study revealed that, regardless of the type of data on light, *P. pipistrellus* is **negatively affected by artificial light at the city scale**. This result is coherent with a national scale study which showed that four common bat species activity decreases with increasing radiance level (Azam et al., 2016). This further demonstrates that although *P. pipistrellus* can forage at streetlights, when accounting for different behaviors through larger scale studies, it is globally negatively impacted by ALAN. *P. pipistrellus* was the only species which was abundant enough in all three cities to carry out the analysis however it would be interesting to repeat it for other cities where other species are present in relatively high numbers. The presence of *P. pipistrellus* in highly urbanized areas attests of its adaptability and resilience however, this is not the case for other bat species which may in addition be very sensitive to light such as *Rhinolophus* species (Stone, Jones, & Harris, 2009). The sensitivity to light of such species has been demonstrated at small spatial scales (Stone et al., 2012; Azam et al., 2018) but never at intermediate or large scale possibly due to insufficient data. The impact of ALAN on their spatial distribution may be much more important and should be a focus in future studies.

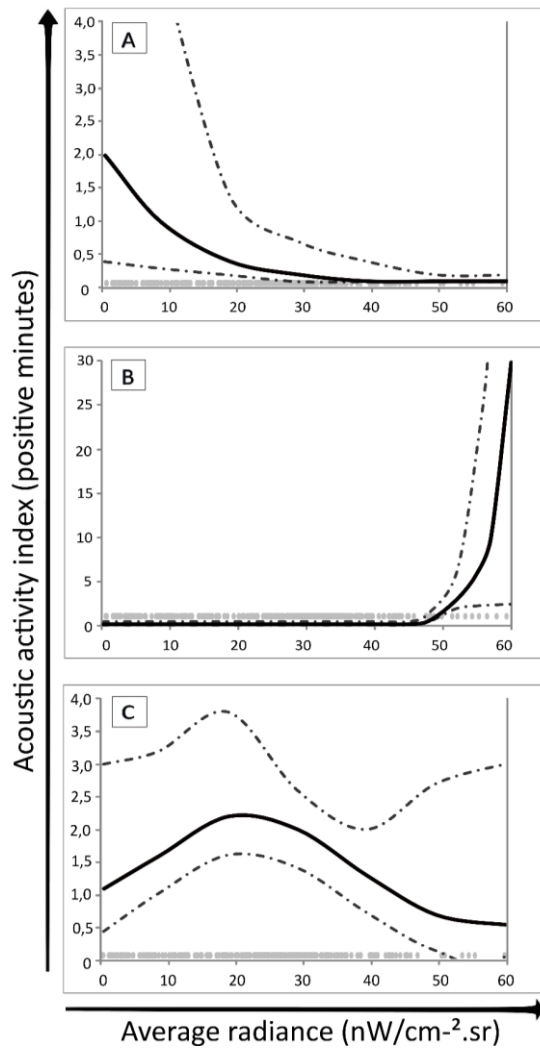


Fig. 21. Representative GAM response curves showing the predicted activity of a species at a location along the average radiance gradient. **A** is the response of *M. daubentonii* at 100 m scale, **B** is the response of *E. serotinus* at 500 m scale and **C** is the response of *P. nathusii* at 800 m scale (extracted from Laforge et al.).

The study by Laforge et al. showed **different responses to light of the three species at the conurbation scale**. Similarly to results found at local scales (Stone et al., 2012; Lacoeuilhe et al., 2014; Azam et al., 2018), *M. daubentonii* exhibited a negative response to light with its activity decreasing with increasing radiance (Fig. 21) On the opposite, *E. serotinus* activity increased with the radiance level. This result is not consistent with Azam et al. (2016) who found a negative effect of light on this species at the national scale. Finally, *P. nathusii* had a contrasted response to light, being positively affected by low levels of light and negatively affected by high levels of light. This may reflect a tradeoff between the use of streetlight as foraging grounds detected at the local scale (Azam et al., 2018) and the perceived increase predation risk under high light levels (Rydell,

1992). Such differing behaviors and differences with studies at other scales highlight the complex relationship of individuals with light depending both on the scale and the species considered.

The comparison of the two source of data on light emissions in the first study showed that **ISS pictures were more suitable than streetlight location to measure the impact of**

ALAN on bat activity. This may be due to the fact that remote sensing data encompass all sources of lighting and include an information on the quantity of light (radiance level). However, ISS pictures reflect the upward light emissions measured from a far distance above ground and may be quite different from the perception bats have at their flight level. Indeed, a study found that vertical measures of the quantity of light (illuminance level) better explained bats response to light than the same measure taken at horizontal (Azam et al., 2018). The reconstitution in three dimensions of the distribution of light may be a better predictor of bats spatial patterns however, it requires extensive data on lighting sources and on the presence of obstacles (e.g., buildings, vegetation) and such models have only been created for small spatial scales (Bennie et al., 2014). In addition, ISS picture have a fine resolution but not to the point that individual light sources can be identified thus its use to determine points of conflict with nocturnal biodiversity is limited to the designation of fairly large areas in terms of light management (in this particular case at least 3600m² areas). One issue I discussed with people in charge of the street lighting in Paris is that the public outdoor lighting is more and more regulated but although regulations for private lighting also exist, they are not enforced and there are no controls. Thus, for example, currently, the brightest source of lighting in Paris comes from the upward directed spots of a private hotel on the Champs Élysées. As 30 to 50% of city lighting are due to streetlights (Aubé et al., 2018), a fairly important part of light sources are privately owned and to not follow any regulations possibly emitting important quantity of light above the horizon and thus contributing to light pollution and skyglow effect. Therefore, the regulation of public lighting does not suffice and there is an urgent need to control private light sources. Nevertheless, remote sensing data allow to account for all types of lighting and are getting increasingly available with fine resolution hence representing a powerful tool for future studies on landscape effects of light on biodiversity and ecosystems.

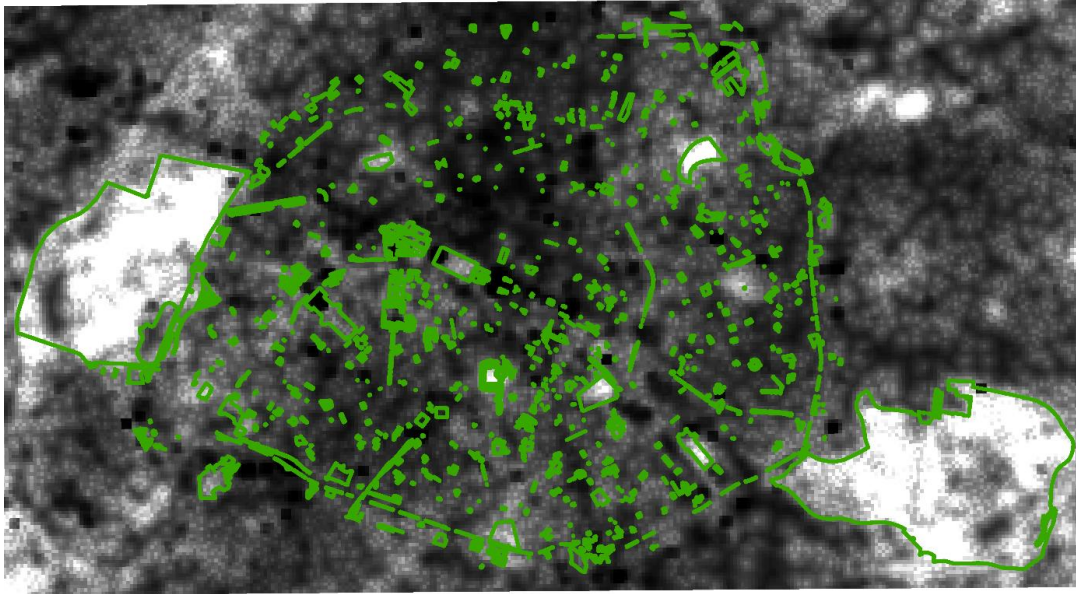


Fig. 22. Prediction of *P. pipistrellus* activity in Paris made with the best model. The activity is represented in grey scale from low (black) to high (white). Vegetation areas are bordered in green.

Perspectives

In this study, we used environmental data that are fairly accessible and thus a similar methodology could be applied to other cities. The model built can be used to produce predictive maps of bat activity and visualize areas of high and low activity (Fig. 22.). Spatially explicit representations are important to communicate scientific findings to land managers and determine locations where preservation or restoration of dark areas should be prioritized. Such maps could be useful for landscape planning as they allow land manager to visualize areas predicted to have important bat activity. Our result show that bat activity is often concentrated in urban parks where the proportion of vegetation is high and the lighting generally low (Fig. 2). This information could raise the awareness of municipalities on their responsibility regarding biodiversity. Although urban parks are mostly planned for recreational purposes, they also participate in the sustenance of urban biodiversity and appropriate management may improve their potential to be a habitat for various species. Moreover the interaction between the proportion of tree cover and the radiance showed that, when considering the most common

environmental situation within the cities, increasing proportion of tree cover limits the negative effects of radiance. Therefore, this study shows for the first time that tree vegetation may be a tool to mitigate the effect of artificial light on bat activity at the city scale. This effects may be due to the capacity of trees to block the light and thus provide dark refuges where the perceived risk of predation may be lower. Yet, although it may be sufficient for city-dweller bat species, it is not so for more light sensitive species. Indeed a study showed that *Rhinolophus hipposideros* bats activity along a hedge is highly reduced by the presence of light and that only very few bats use the unlit side of the hedge (Stone et al., 2009, 2012). High vegetation only partly blocks the light and the level of light on the unlit side may be sufficient for urban adapted bats but not for bats species very sensitive to light. Nonetheless, the use of vegetation to shield light and create dark refuges may be of great interest in urban context where the species present are more resilient.

In this study, I evaluate this importance of two aspects of urbanization on bat activity, soil sealing (through the measure of remnant vegetation areas) and light pollution due to outdoor lighting. However another important factor due to urbanization that may affect bat activity is road traffic. Passing vehicles can cause disturbance through noise (Bonsen, Law, & Ramp, 2015) and light (Bennett & Zurcher, 2013). Although the light emitted by cars headlights might have an overall low contribution to light pollution (Bará et al., 2017), no studies have investigated how such intermittent high levels of light (Fig. 23) could influence bat's behavior. The expansion of

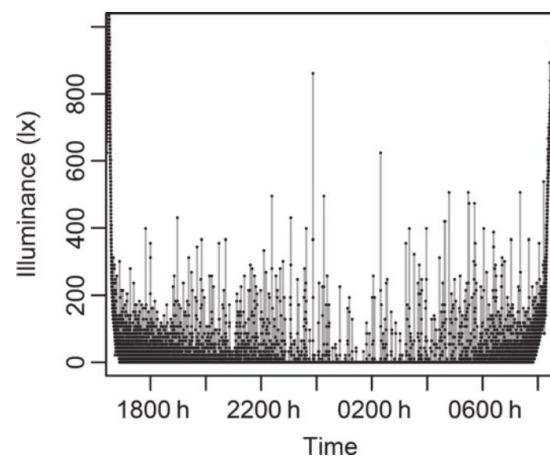


Fig. 23. Variation in illuminance measured in roadside vegetation between sunset and sunrise on a rural main road with no fixed lighting. Peaks represent pulses of light from passing vehicles. Typically, light from these sources has a high degree of variability, but can reach much higher magnitudes than those under street lights (extracted from Bennie et al., 2016).

urban areas is accompanied by the development of transport infrastructures (Dulac, 2013) and roadsides can represent an important proportion of land surface that may constantly (e.g., streetlights) or intermittently (e.g., cars headlights) be lit. The expansion of road networks represent a major threat to biodiversity (Maxwell et al., 2016) and although a few species may benefit from roads, the majority of species suffer negative effects through mortality by vehicle collisions, habitat destruction or degradation, barrier effect and fragmentation (Trombulak & Frissell, 2000; van der Ree, Smith, & Grilo, 2015). During my PhD, I contributed to a study on the effects of roads on the level of bat activity in the surrounding landscape (Claireau et al., *unpublished*, see Appendix). This work is based on over 300 full-night recordings sampled in three 100 km² study sites centered on major roads. The results show that amongst the 13 bat taxa present in the study area, 5 bat taxa are negatively affected by major roads up to 5 km away from the road with their activity increasing with the distance to the road. This negative effect might be explained by the perception of a risk as indeed, three out of the five impacted taxa are considered to be the most prone to collide with vehicles due to their low flying altitude (Fensome & Mathews, 2016). Another non-exclusive hypothesis is that bats may be avoiding the noise and light associated with the traffic. Indeed, coincidentally, the bat taxa that are the most affected by roads are also bat species known to be particularly sensitive to light at the local scale (Stone et al., 2009; Azam et al., 2018). It would be interesting specifically to test for the effect of vehicles headlights on bat activity. If the negative effect of road is partly due to light, the implantation of tree hedges along the road may help mitigate this effect and reduce the distance of impact of the road. Still, roads represent a barrier to bats movement as they constitute a rupture in the structural elements of the landscape they follow while flying (Pinaud et al., 2018) and the disturbance linked to traffic (noise and light) may increase this barrier effect. Cities and roads are often considered only as areas of sealed soil however, they are associated with increased levels of light and noise which may lead to cumulated effects.

ARTICLE 2

ACCOUNTING FOR ARTIFICIAL LIGHT IMPACT ON BAT ACTIVITY FOR A BIODIVERSITY- FRIENDLY URBAN PLANNING

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Abstract

Light pollution constitutes a major threat to biodiversity by decreasing habitat quality and landscape connectivity for nocturnal species. While there is an increasing consideration of biodiversity in urban management policies, the impact of artificial light is poorly accounted for. This is in a large part due to the lack of quantitative information and relevant guidelines to limit its negative effects. Here we compared the potential of two sources of information on light pollution, remote sensing (nocturnal picture taken from the International Space Station ISS) and ground-based (location of streetlights) data, to measure its impact on bats. Our aims were to (i) evaluate how light pollution affected *Pipistrellus pipistrellus* activity at the city scale, (ii) determine which source of information was the most relevant to measure light pollution's effect and (iii) define a reproducible methodology applicable in land management to account for biodiversity in lighting planning. We used citizen science data to model the activity of *P. pipistrellus*, a species considered light tolerant, within three cities of France while accounting for artificial light through a variable based on either source of information. We showed that at the city scale, *P. pipistrellus* activity is negatively impacted by light pollution irrespective of the light variable used. This detrimental effect was better described by variables based on ISS pictures than on streetlights location. Our methodology can be easily reproduced and used in urban planning to help take the impact of light pollution into consideration and promote a biodiversity-friendly management of artificial light

1. Introduction

Urbanization is characterized by an increase of impervious surfaces (McKinney, 2002) but also by the emission of environmental stressors such as chemical, noise, and light pollution (Isaksson, 2015). Amongst these pollutants the least understood, in terms of impacts on species and ecosystems, is light pollution (Gaston, Visser, & Holker, 2015; Hölker, Moss, Griefahn, & Kloas, 2010), i.e. the emission of artificial light that alter the natural patterns of light and dark in ecosystems (Longcore & Rich, 2004). The modification of the natural day/night rhythm can have considerable impacts on ecosystems (Navara & Nelson, 2007) especially as nocturnal species represent 30% of vertebrates and more than 60% of invertebrates (Hölker, Wolter, Perkin, & Tockner, 2010). In recent decades, light emissions increased globally at an average rate of 6% per year (Hölker, Moss, et al., 2010) and currently, 88% of Europe experience light-polluted nights (Falchi et al., 2016). Moreover, there is a shift in lighting technologies from yellow light sources (e.g., high- and low-pressure sodium vapor lamps) to broader-spectrum white light sources with a higher proportion of blue wavelength (e.g., metal halide and light emitting diodes) that have a higher energy efficiency (Gaston, Visser, & Holker, 2015). This change will most likely result in a global increase in short wavelength (i.e. blue light) emission (Falchi, Cinzano, Elvidge, Keith, & Haim, 2011) and might have major impacts on nocturnal biodiversity.

A green infrastructure policy was adopted by the European Union to preserve and promote ecological corridors and landscape connectivity. However the green infrastructure policy does not account for the impact of artificial light. Thus the corridors designed following this policy might be ineffective for nocturnal species. Taking into account light pollution's effects on nocturnal species is crucial to design biodiversity-friendly urban lighting plans. Recommendations to mitigate the negative impacts of artificial lighting on biodiversity are

scarce with only few studies proposing possible local measures (e.g., Azam et al., 2018; Rydell, Eklöf, & Sánchez-Navarro, 2017). More quantitative information on the impact of artificial light is needed to be able to design a city's lighting plan preserving some dark areas that can be used as habitats and corridors for nocturnal biodiversity.

Due to their nocturnal lifestyle, bats are good model species to study the impact of artificial light. European bats are long-lived insectivorous species that have great potential as bio-indicators partly because their population trends tend to reflect those of lower trophic levels species such as arthropods (Jones, Jacobs, Kunz, Willig, & Racey, 2009; Stahlschmidt & Brühl, 2012). Some bat species can live in urban areas and are hence directly confronted to light pollution. For instance, species such as *Pipistrellus spp.*, *Plecotus spp.*, *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis daubentonii*, and *Myotis myotis* often use man-made structures as breeding roosts and can live in built areas (Marnell & Presetnik, 2010; Simon, Hüttenbügel, & Smit-Viergutz, 2004). In addition, since all bat species are protected at the EU level (Council Directive 92/43/EEC, 1992), they represent one of the few cases of protected species living within urban environments.

Light-sensitive species such as *Rhinolophus* and *Myotis* species are negatively impacted by artificial lighting through a decrease of their fitness (Boldogh, Dobrosi, & Samu, 2007) and a loss and fragmentation of their habitat (Stone, Jones, & Harris, 2009, 2012). Yet species such as *P. pipistrellus*, *P. kuhlii*, and *Nyctalus leisleri* forage in urbanized and illuminated areas (Bartonicka & Zúkal, 2003; Gaisler, Zúkal, Rehak, & Homolka, 1998; Rainho, 2007). These three species are qualified as light tolerant because they prey on insects that are attracted and trapped within the halo of streetlights (Eisenbeis, 2006; van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011). But although the short-term installation of streetlights on a previously dark flying route did not change *Pipistrellus* species activity level (Stone et al., 2012), a study showed that the activity of *P. pipistrellus* was similar or lower in lit areas

compared to dark areas in environments with scattered vegetation (Mathews et al., 2015) and another that, *P. pipistrellus* will not cross brightly lit gaps while flying along a hedgerow (Hale, Fairbrass, Matthews, Davies, & Sadler, 2015). While considering a large scale dataset, collected at a national scale across 8 years and mostly looking at permanent street lighting, Azam et al. (2016) showed that bat activity was negatively affected by artificial light even for species described as light tolerant. Hence, overall it would seem that the global effect of light pollution might actually be deleterious even to light tolerant species.

Assessing the impact of light pollution on biodiversity first requires the ability to measure it. This is not straightforward as artificial light is composed of several measurable characteristics such as intensity, spectral composition, or flux directionality. As street lighting is the most persistent, aggregated, and intense source of lighting in urban areas (Gaston, Davies, Bennie, & Hopkins, 2012), the location of streetlights can be a relevant source of information. Streetlight location data exist for most large cities and are easy to understand, however they do not contain information on the light characteristics or on private lighting which could have a substantial role in light pollution (Gaston et al., 2012). Remote sensing data, such as aerial or satellite pictures are another information source and include all types of lighting (public and private) and also the skyglow (Kyba & Hölker, 2013). Aerial pictures can have a spatial resolution up to 1 m (Hale et al., 2013; Kuechly et al., 2012), but are seldom available as they are very expensive to produce. DMSP OLS and VIIRS Day-Night Band are grey-scale satellite images of the surface of the Earth at night (<https://www.ngdc.noaa.gov/eog/>) but due to their coarse resolution they cannot be used for city-scale land management studies (Fig. 1). Another remote sensing information source are the pictures taken from the International Space Station (ISS ; <https://eol.jsc.nasa.gov>) that have started to be geo-referenced by the citizen science program Cities at Night (<http://citiesatnight.org> – Sánchez De Miguel et al., 2014). ISS pictures can reach a spatial resolution of 10 m, contain four spectral bands in the visible range (one red,

two green, one blue), and each pixel's intensity is proportional to the emitted light (Fig. 1). There are a variety of sources of information on artificial light with different spatial resolution, extent, and information on light characteristics. Ground-based and remote sensing data sources both have advantages and drawbacks (presented in Table 1) and represent an opportunity to better understand the impact of artificial light on biodiversity as well as a challenge for their application to an ecological and land management context (Kyba et al., 2014).

This study investigated the impact of light pollution on bat activity at the city scale comparing two sources of information on artificial light: the location of streetlights and ISS

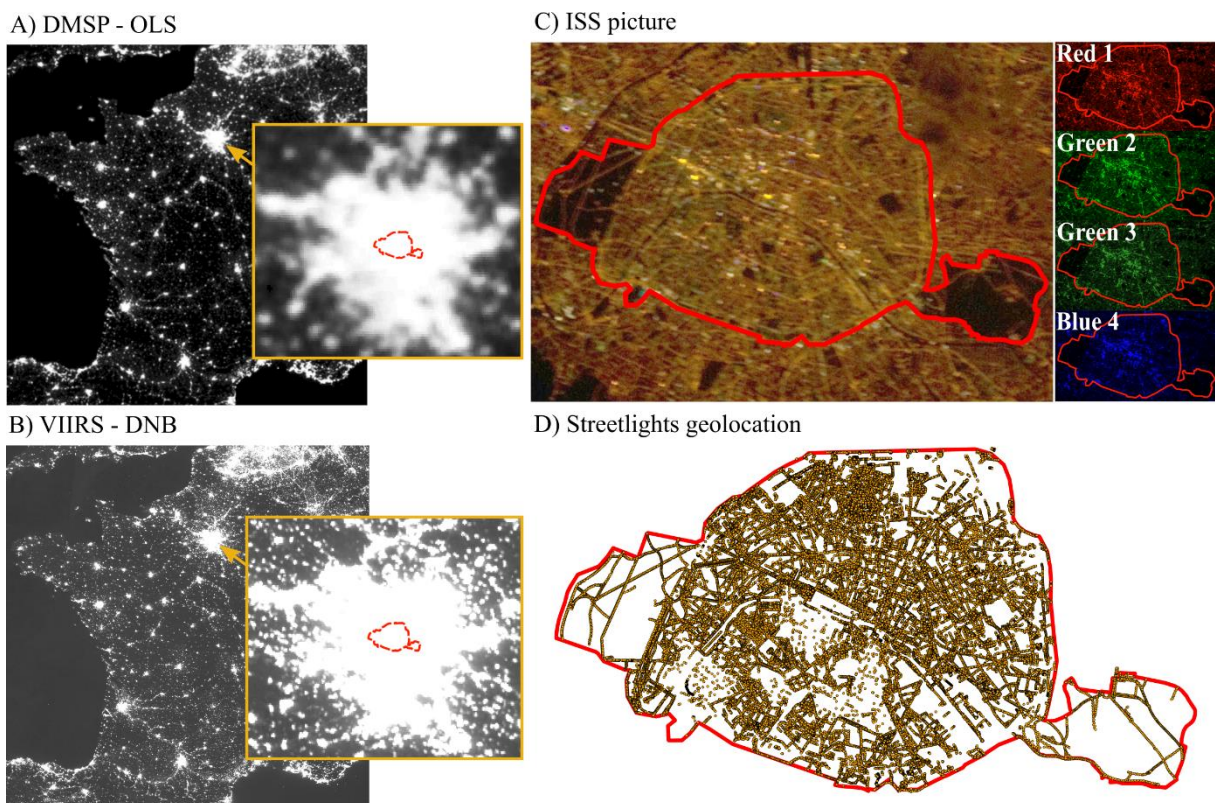


Fig. 1. Different possible sources of information on light pollution. DMSP – OLS (A) and VIIRS –DNB (B) satellite images of France with a zoom on Paris and its surrounding. The resolution of the images is too low (930 m for DMSP – OLS and 460 m for VIIRS – DNB) to see the difference of radiance emitted in Paris. The better resolution (60m) of this ISS picture of Paris (C) allows to distinguish areas with low and high radiance at a fine scale. Also, this picture is composed by 4 color bands (2 green, 1 blue, and 1 red) which represent the radiance emitted in each spectral band. Another source of information on light pollution is the location of streetlights (D). Each orange dot represent a streetlight (over 51 000 in Paris).

nocturnal pictures. We chose these two sources of information because their resolution was coherent with the scale of our study, they were easily accessible, and their comparison may bring insights on which source of information is the most adapted to measure the impact of light pollution on bats. Our aims were (i) to evaluate how light pollution affected *P. pipistrellus* activity at the city scale, (ii) to determine which source of information on artificial light was the most relevant to measure the effect of light pollution and (iii) to define a reproducible methodology that could be used in land management to make recommendations for a biodiversity-friendly lighting planning and hence we kept low data requirements. To achieve these goals, we examined how *P. pipistrellus* activity was affected by artificial light within three large cities of using a panel of light variables based on either source of information. Although *P. pipistrellus* is considered a light tolerant species, we expected a negative impact of light pollution on its activity as at the national scale the average radiance had a negative effect (Azam et al., 2016).

Table 1 Comparison of the advantages and drawbacks of two sources of information on artificial light: ground-based data (GB; e.g., streetlights location) and remote sensing data (RS, e.g., ISS pictures).

	Ground-based data (GB)	Remote sensing data (RS)	Comparison
Precision	+	-	GB data give the precise location of light sources whereas RS data give a global radiance value for a pixel
Height perspective relative to bat flight height	+	-	Streetlight heights (GB data) are closer to bats flight height whereas RS data give a radiance value as perceived from space
Exhaustiveness	-	+	RS data include all types of lighting whereas GB data only include public lighting
Light characteristics	-	+	RS data give information on the quantity and the spectrum of the light whereas GB data do not always include information on the light sources characteristics

2. Methods

2.1 Study sites

To address our main research questions we based the analysis on bat activity and environmental data from three large and highly urbanized cities of France: Paris, Lille, and Montpellier (Fig. 2). These three cities are amongst the most light-polluted areas of France with nights 20 to 40 times brighter than natural illumination in Lille and Montpellier and over 40 times brighter in Paris (Falchi et al., 2016). Paris is the largest of the three cities with 105 km² (Fig. 2.A). There are few green areas in Paris' center but there are two large parks on the outskirts (Vincennes on the East side and Boulogne on the West side) which represent 17 km² in total. Tree cover represented 21% of Paris' surface however, when not including the two large parks, it only represented 12%. Montpellier and Lille have a smaller surface than Paris (respectively, 57 and 40 km² – Fig 2.B and 2.C). Only 14% of the surface of Lille corresponded to vegetation whereas Montpellier was the greenest of the tree cities with 21% of vegetation distributed in small patches across the city. The three cities had a similar overall density of streetlights per square kilometer (549 SL/km²).

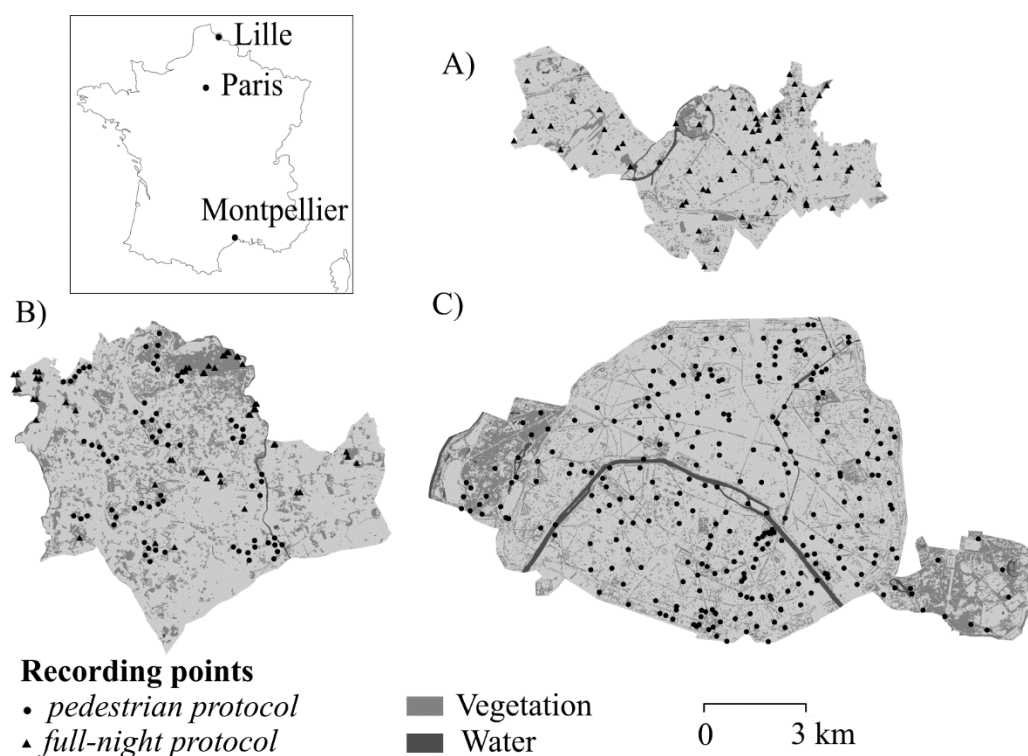


Fig. 2 Study sites: Lille (A), Paris (B), and Montpellier (C). Triangles represent points of full-night recordings and dots represent points of pedestrian recordings.

2.2 Bat monitoring

Bat activity recordings were taken following the recommendations of the French national bat-monitoring scheme ‘Vigie-Chiro’ (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science program running since 2006 and coordinated by the National Museum of Natural History of Paris (France). All recordings occurred between June and October, the seasonal peak in bat activity. Recordings were only carried out when weather conditions were favorable (i.e. no rain, wind speed below 7 m/s, temperature at sunset above 12°C).

The data for Paris and Montpellier were provided by the French bat-monitoring scheme (<http://vigienature.mnhn.fr/page/vigie-chiro/page/protocoles>) following two different protocols. The first was the pedestrian protocol for which volunteer surveyors recorded bat activity for 6 minutes at 10 selected locations within a 4 km² area. The volunteers began their

sampling 30 minutes after sunset. In Paris, volunteers used a time expansion detector (Tranquility Transect Bat detector, Courtpan Design Ltd, UK) and in Montpellier, they used a SM2BAT detector (Wildlife Acoustics Inc). The second protocol was the full-night protocol for which volunteers placed a SM2BAT detector at a given location 30 minutes before sunset and let it until the morning (30 minutes after sunrise) to record bat activity all night. Data for Lille were recorded by authors following the full-night protocol and using SM2BAT detectors. In Paris, 923 recordings lasting 6 minutes were taken at 282 different points following the pedestrian protocol between 2008 and 2013. In Lille, each of the 73 points was sampled once in 2015 using the full-night protocol. In Montpellier, 82 points were sampled with the full-night protocol and 71 points sampled with the pedestrian protocol (2011 and 2012). To have a similar data sampling unit among cities, we only took into account recordings of the full-night protocol occurring during the first two hours of the night (beginning 30 minutes after sunset) and split the recordings into 6 minutes time slots. Then, to avoid pseudo-replication, we calculated the mean activity per point. When considering entire nights of recordings, bat activity was fairly stable throughout the night, slightly decreasing toward the end of the night (see Appendix A – Fig. A.1).

2.3 Bat acoustic data analysis

All bat calls recorded in Paris were identified by volunteers and then validated by experts using Syrinx software version 2.6 (Burt, 2006). For data recorded in Lille and Montpellier, we used the software SonoChiro (Bas et al. 2013) to automatically classify the echolocation calls to the most accurate taxonomic level possible. All ambiguous calls were then checked manually using Syrinx software. As it is impossible to identify individual bats from their echolocation calls, we calculated bat activity as the number of bat passes per species. A bat pass is defined as the occurrence of a single or several echolocation calls of the same bat

species during a 5-second interval (Millon, Julien, Julliard, & Kerbiriou, 2015). We believe that this duration is a good compromise between multiple counts of the same individual and the risk of missing other individuals' passage. Indeed 5 seconds is the mean duration of sequences of calls recorded (Kerbiriou, Parisot-Laprun, & Julien, 2018; Millon et al., 2015). In addition, we think that multiple detection of the same individuals have a biological meaning since they reveal foraging intensity. Indeed, our aim was to have a bat activity measure that reflected the suitability of the habitat in terms of food resource. *P. pipistrellus* and *P. nathusii* were the only bat species detected in the three cities (Appendix A - Table A.1). However the number of bat passes of *P. nathusii* was very low in Paris and Lille (respectively 6 and 37 bat passes) hence we only performed the analysis on *P. pipistrellus*.

2.4 Light pollution variables

We used two sources of information for light pollution. Firstly, we used the location of streetlights. Data for Montpellier were accessible for free at <http://data.montpellier3m.fr/> and data for Paris and Lille were provided by the private companies managing the cities' public lights (Engie Ineo for Lille and Evesa for Paris). Secondly, we used nighttime ISS pictures from the Cities at Night program. The images were corrected for linearity of the sensor, vignetting, and calibrated absolutely using reference stars on other lenses and relatively to the VIIRS image of May 2014 using synthetic photometry (Sánchez De Miguel, 2016). There was no atmospheric correction. The value of each pixel corresponded to the radiance which is the radiant flux reflected or emitted by a given surface (units $\text{nW/cm}^2/\text{sr/A}$).

A study investigating the impact of light pollution on bat at different scales showed that the best spatial scale to study the impact of artificial light on *P. pipistrellus* was 200 m (the smaller spatial scale tested; Azam et al., 2016). Thus we defined our light variables within a 200 m buffer but also within a 100 m buffer to explore if a smaller spatial scale could bring

further insights. We calculated several light variables based on either source using QGIS 2.8.3 (QGIS Development Team, 2017). Using the streetlight location, we calculated the distance to the closest streetlight from each recording point, the number of streetlights within a 100 m and a 200 m buffer around each recording point, and the weighted density of streetlights within the same buffers (the sum of the multiplicative inverse of the distance to streetlights within the 100 m and 200 m buffers). For several species, the impact of a streetlight seems to be detectable within a 25 m distance (Azam et al., 2018) so we built two more variables based on this information: the presence of a streetlight within 25 m of the recording point (binary variable) and the proportion of surface impacted by artificial light within a 100 m and a 200 m buffer. As Azam et al. (2018) found that light had an effect up to 25 m away from a streetlight, we considered that all surface within 25 m of a streetlight was impacted by light pollution. We used the four color bands (one red, one blue, and two green bands) that compose the ISS pictures separately and calculated two variables for each color band: the pixel value at each recording point and the mean pixel value within a 100 m and a 200 m buffer around the recording point. Hence in total there were 8 variables based on the location of streetlights and 12 based on the ISS pictures (Table 2). All variables were calculated using the same 60 m x 60 m grid in order to have the same resolution. For the analysis, we removed recordings taken at four points considered as outliers because of their very high radiance value due to a singular urban context (e.g., Eiffel Tower illuminations ; n=12; 1% of the dataset). Note that similar results were obtained when including these recordings in the analysis (see Appendix B).

Table 2 Variables used as explanatory variables to model bat activity. Each light variables were used in a separate full model and all environmental variables, meteorological variables and covariables were included in all full models. Variables based on the ISS pictures are defined for each color band, the red (Red 1), the two green (Green 2 and Green 3), and the blue (Blue 4).

Variable	Description and units	Reference
LIGHT VARIABLES		
SL distance	Distance to the closest streetlight	
SL density - 100 ; SL density - 200	Number of streetlights within a given radius (100 m or 200 m) (units: m)	
SL weighted density - 100 ; SL weighted density - 200	Sum of the multiplicative inverse of the distance to streetlights within a given radius (100 m or 200 m) (units: m ⁻¹)	
SL presence	Presence/absence of a streetlight within 25 m	
Impacted surf. - 100 ; Impacted surf. - 200	Proportion of surface within 25 m of streetlight in a given radius (100 m or 200 m) (units: %)	
Red 1 - pixel ; Green 2 - pixel ; Green 3 - pixel ; Blue 4 - pixel	Pixel value of the ISS picture (units: nW/cm ² /sr/A)	
Red 1 - 100 ; Green 2 - 100 ; Green 3 - 100 ; Blue 4 - 100 ; Red 1 - 200 ; Green 2 - 200 ; Green 3 - 200 ; Blue 4 - 200	Mean pixel value in a given radius (100 m or 200 m) (units: nW/cm ² /sr/A)	
ENVIRONMENTAL VARIABLES		
Dist. to water	Distance to the closest water surface (units: m)	Kañuch et al., 2008; Rainho & Palmeirim, 2011; Russo & Jones, 2003
Dist. to tree cover	Distance to the closest tree cover (units: m)	Boughey et al., 2011
Prop. of tree cover	Proportion of tree cover within 200 m (units: %)	Boughey et al., 2011
METEOROLOGICAL VARIABLES		
Temperature	Temperature at sunset (units: °C)	O'Donnell 2000; Ciechanowski et al., 2008
Humidity	Humidity at sunset (units: %)	O'Donnell 2000; Ciechanowski et al., 2008
Wind speed	Wind speed at sunset (units: km/h)	O'Donnell 2000; Ciechanowski et al., 2008
COVARIABLES		
Year	Year of recording	Kerbirou et al., 2018
Julian Day	Julian day of recording	Kerbirou et al., 2018; Newson et al., 2015
City	City where the recording took place	
Recording point	Identification of the recording point	
Method	Recording method: fullnight or pedestrian protocol	

2.5 Environmental and meteorological variables

Bat activity is influenced by environmental conditions both at a fine (i.e. flight path) and intermediate (i.e. home range) scale hence we included several variables to account for their effect using BD TOPO data (IGN; Table 2). Several studies identified aquatic habitat as a favorable habitat for bats (Kaňuch et al., 2008; Rainho & Palmeirim, 2011; Russo & Jones, 2003) thus we calculated the distance to the closest water source (in meters). In addition, as the distance and the extent of wooded areas are positively correlated with bat presence (Boughey, Lake, Haysom, & Dolman, 2011), we calculated the distance to the nearest tree cover (in meters), and the proportion (%) of tree cover within a 200 m buffer. A set of complementary variables were used as fixed effects to control for specific recording conditions (Table 2): the method (pedestrian or full-night protocol), the year (Kerbiriou, Azam, et al., 2018), the Julian day and its associated quadratic term as bat activity is expected not to be linear across the study period and include a peak when young start to fly (Kerbiriou, Azam, et al., 2018; Newson, Evans, & Gillings, 2015), and meteorological conditions at sunset (temperature C°, wind speed m/s, and humidity %; Ciechanowski, Zając, Biłas, & Dunajski, 2008; O'Donnell, 2000).

2.6 Bat activity modeling

We built statistical models to test the effect of light pollution on *P. pipistrellus* activity (response variable) while accounting for environmental and meteorological parameters. To outline a general pattern and build robust models, data from the three cities were analyzed as a single dataset. Several light variables were correlated with one another (Spearman's $|r| > 0.7$; Dormann et al., 2013; see Appendix C) thus we built a separate full model for each light variable (i.e. 20 models). We ensured that all the variables used within the same model had a Spearman's rho between -0.7 and 0.7. As all variables showed a VIF value < 3 (Heiberger & Holland, 2004)

and as the mean of VIF values < 2 (Chatterjee & Bose, 2000) there was no obvious sign of multicollinearity.

We performed Generalized Linear Mixed Models (GLMM ; glmmTMB 0.2.0 ; Brooks et al., 2017) using bat activity as the response variable and a light variable, environmental variables and, meteorological variables as fixed effects. According to the nature of the response variable (i.e. count data with over-dispersion) we used a negative binomial error distribution with a log link (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; See Appendix A – Fig A.2). Recording points were distributed within the three cities and sometimes replicated hence we included the city as a fixed effect and a random effect on the recording point. Explanatory variables were standardized to facilitate comparisons between estimates. We added an interaction between the light variable and the proportion of vegetation as a study found a difference in the responses of *P. pipistrellus* activity to the presence of streetlights depending on the local tree cover (Mathews et al., 2015). The full models were written as follow:

*Bat activity ~ light variable*proportion of vegetation+distance to vegetation+distance to water+Julian day+(Julian day)^2+Year+temperature+humidity+wind speed+recording protocol+city+ (1|recording point)*

where light variable was one of the 20 light variables listed in Table 2. Hence we had 20 full models. For each full model, we ran all possible combinations (subsets) of fixed effects (MuMIn 1.15.6 ; Barton, 2013). Among each ensemble of candidate models (one full model and its subset models), we selected the best model using Akaike's Information criterion (AIC; Burnham & Anderson, 2002). However, the AIC tends to overestimate the number of parameters in a model by adding uninformative variables that do not improve fit (Guthery, Brennan, Peterson, & Lusk, 2005) hence, amongst the best models (i.e. within a Δ AIC of two of the minimum AIC), we selected the simplest model that had significant parameters. Thus, at the end of the selection process, we had 20 best models, one per light variable. We compared

these 20 models using the AIC. To explore the possible nonlinear effect of the light variable, we tested a GAMM (mgcv 1.8-16 ; Wood, 2011) model with the same structure as the overall best model (lowest AIC) with a smoothing effect on the light variable. The degree of smoothness is left to be estimated as part of the fitting. All analyses were conducted using R 3.3.3 (R Core Team, 2017).

3. Results

3.1 Bat acoustic data analysis

A total of 20,599 bat passes of *P. pipistrellus* were recorded at the 508 recording points (1,205 in Paris, 7,035 in Montpellier, and 12,359 in Lille; see Appendix A – Table A.1 for details on all the species recorded). *P. pipistrellus* represented 47% of the overall bat passes recorded (86% in Paris, 24% in Montpellier, and 98% in Lille) and was detected in 48% of the recordings (27% in Paris, 40% in Montpellier, and 98% in Lille).

3.2 Bat activity modeling

We selected one best model for each light variable (Table 3). After model selection on the full models, for five models, the light variable was not retained and the best model was the one without light variable. Three of the light variables not retained were based on streetlight location (streetlight distance, streetlight presence and streetlight density in a 100 m radius) and two on ISS pictures (pixel value for the Red 1 and Green 3 color band). In all models with a light variable, *P. pipistrellus* activity was negatively affected by light. Seven out of the eight models containing a light variable based on streetlight location did not perform better than the model containing no light variable. The three models that performed the best ($\Delta AIC < 2$) were based on mean values of the ISS picture in a 100 m or 200 m radius. Globally, among the 15

models where a light variable was retained, all the models containing a light variable based on the ISS pictures performed better than models containing a light variable based on the streetlight location. For six models, the interaction between the light variable and the proportion of tree cover was retained. Within these six models, five had a light variable based on one of the green color band of the ISS picture and one on the red color band. The interaction showed that for low proportions of tree cover, the radiance level had a negative effect on bat activity whereas for high proportions of tree cover, the radiance level is expected to have a positive effect on bat activity (Fig. 3). Note, however that no recording were taken at points combining very high proportion of tree cover and very high level of radiance because such situation is particularly rare. The GAMM model built with the same structure as the best overall model with a smooth function on the light variable (mean pixel value of the blue color band in a 100 m radius) showed that there was no nonlinear effect of the light variable.

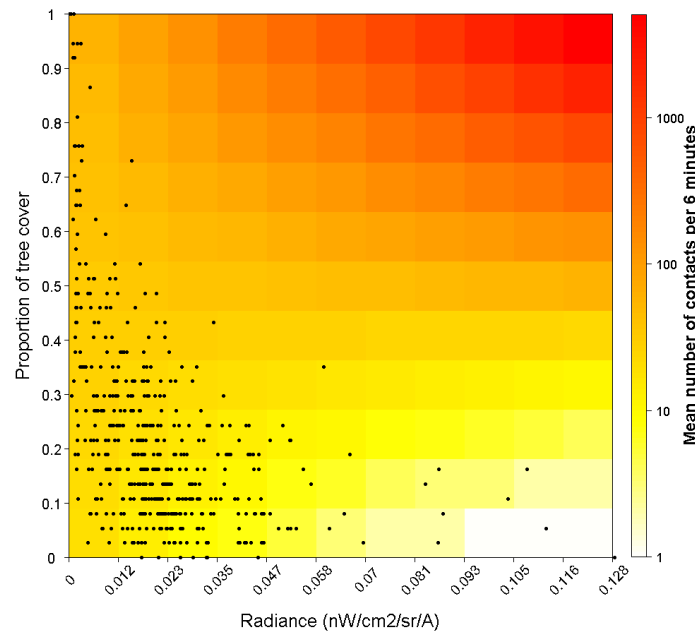


Fig. 3 Interaction between the light variable (mean value of radiance within a 100 m radius for the Green 2 color band of the ISS picture) and the proportion of tree cover. The color scale represent the predicted mean number of bat passes per six minutes (log scale). Black dots represent combination of light variable values and tree cover proportion sampled in the data. Data were back transformed to be presented with their original units.

After model selection, all the best models contained the same environmental and meteorological variables except for the distance to tree cover that was not retained in six models. The distance to water and to tree cover negatively impacted the activity of *P. pipistrellus* and the proportion of tree cover had a positive effect on *P. pipistrellus* activity (Appendix D – Table D.1) as expected. The Julian day and its quadratic term were retained, reflecting the fluctuations of bat activity along the seasons (see Appendix D – Fig. D.1). The wind speed had a positive effect on *P. pipistrellus* activity. Wind speed usually has a negative effect on bat activity when considering high wind speed. Here wind speed were always low with 91% of data taken for wind speed below 5.5 m/s.

Table 3 Selection of best models to explain bat activity using a light variable and best model without light variable. Estimates of the light variable and the interaction between the light variable and the proportion of tree cover (when retained in the model selection). After model selection on the 20 full models, for five models, the light variable was not retained (*not selected*) and the best model was the one without light variable. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates		AIC	Δ AIC	Weights	Marginal R2	Conditional R2
	Light variable	Light variable * Tree cover					
Blue 4 - 100	-0.34 **		3331.3	0.0	0.26	0.33	0.62
Green 2 - 100	-0.21	0.25 .	3332.0	0.7	0.18	0.34	0.63
Red 1 - 200	-0.16	0.27 *	3333.1	1.8	0.11	0.33	0.63
Green 2 - pixel	-0.13	0.31 *	3333.6	2.3	0.08	0.33	0.63
Green 2 - 200	-0.15	0.24 *	3333.9	2.6	0.07	0.33	0.63
Blue 4 - pixel	-0.26 *		3334.4	3.1	0.06	0.32	0.62
Red 1 - 100	-0.31 *		3334.5	3.2	0.05	0.33	0.62
Blue 4 - 200	-0.26 *		3334.8	3.5	0.05	0.32	0.62
Green 3 - 200	-0.10	0.27 *	3335.2	3.9	0.04	0.32	0.63
Green 3 - 100	-0.06	0.28 *	3336.3	5.0	0.02	0.32	0.62
SL density - 200	-0.19 *		3336.6	5.3	0.02	0.31	0.62
Impacted surf. - 200	-0.20 *		3336.8	5.5	0.02	0.31	0.62
Impacted surf. - 100	-0.19 .		3337.0	5.7	0.02	0.31	0.62
SL density - 100	-0.17 .		3337.2	5.9	0.01	0.31	0.63
SL weighted density - 200	-0.15		3337.7				
None			3338.7	7.4	0.01	0.30	0.62
SL distance	Not selected						

<i>SL weighted density - 100</i>	<i>Not selected</i>
<i>SL presence</i>	<i>Not selected</i>
<i>Red 1 - pixel</i>	<i>Not selected</i>
<i>Green 3 - pixel</i>	<i>Not selected</i>

4. Discussion

We found that, whatever the light variables tested, *P. pipistrellus* activity was negatively affected by artificial light at the city scale. This result is coherent with large scale studies (Azam et al., 2016; Mathews et al., 2015) although numerous small scale studies showed a local positive effect of artificial light on light tolerant bat species (e.g., Azam et al., 2018; Rydell, 1992). The models containing ISS picture based variables were better in terms of AIC than the models with streetlight location based variables showing that ISS pictures better explain the effect of light than streetlight location for bats. The methodology we used to measure the impact of artificial light on bats had low data requirements and could be reproduced elsewhere as these data are available for most cities. Prediction derived from our models could be used to produce maps to identify favorable areas for bats that should be preserved and to work on landscape connectivity.

The negative effect of light pollution on *P. pipistrellus* at the city scale suggests that the local foraging advantage streetlights can represent (Rydell, 1992) is outweighed by the global negative impact of artificial light. Moths preyed on by bats are attracted to short wavelengths (blue) (Koh, 2008; van Langevelde et al., 2011) thus we could have expected areas with high values of radiance of the blue color band to be areas of high concentration of prey and consequently areas of high bat activity. But on the contrary, our results showed that high radiance values affected negatively the activity of *P. pipistrellus* irrespective of the color band used. The underlying mechanisms that drive the negative response of bats to artificial light are not clear. Rydell (1992) suggested that bats might avoid lit areas due to an intrinsic perception

of increased predation risk. However the interaction between the proportion of tree cover and the radiance level showed that the effect of light on bat activity could be positive in areas with important tree cover although this combination was not present in our study areas. Similarly, Mathews et al (2015) found that *P. pipistrellus* activity was higher in lit than dark environments when there was an important tree cover although in open areas, light had a negative effect on this species' activity. Hence it is possible that the tree cover reduces the risk of predation linked to lit areas but also that streetlights close to wooded areas attract more insects and therefore are particularly advantageous foraging grounds. The negative effect of artificial light might partially explain (Azam et al., 2016) why although *P. pipistrellus* is still present in urbanized and strongly illuminated areas, it is less abundant than in more favorable landscape (e.g., aquatic areas) (Kerbirou, Parisot-Laprun, et al., 2018). This species is more resilient to anthropogenic pressures than other species that are seldom found in urban landscapes. Hence species that are more sensitive to light pollution might experience an even more detrimental impact highlighting the importance of including biodiversity in artificial lighting planning schemes.

Surprisingly, the two sources of data on artificial light were weakly correlated (Spearman's $|r| = 0.13 \pm 0.06$, Appendix C). This absence of clear relationship between the two types of data is most likely due to the absence of information on private lighting such as monuments, university or shop lights in the streetlight location data although they can be a major source of illumination within cities. Moreover, location data do not inform on light characteristics (e.g., height, type, intensity) which determine the repartition and brightness of the light. Conversely, ISS pictures include both public and private lighting and are a measure of the radiance due to direct and reflected light emissions, including skyglow. The ISS pictures encompass the global level of radiance and hence might be a closer representation of what bats experience than streetlight location. Nevertheless, the streetlight density in a 200 m radius was informative and had a similar effect as ISS picture based variables. Hence ideally, using the

mean pixel value of an ISS picture within a 100 radius would be best but if there is no picture available, streetlight location data can be useful. Moreover, if information on streetlight characteristics are available, this could further increase the explicative power of the ground-based data.

We deliberately kept a low data requirement to allow our model to be reproducible although complex models using streetlights characteristics and light dispersion models have been developed to map cities nighttime light emissions (Bennie, Davies, Inger, & Gaston, 2014). Our goal was to construct a methodology using fairly simple variables and analysis to be applied to other cities as a management tool. Our model can be used to produce predictive maps of bat activity and to visualize areas where light pollution should be reduced. Furthermore, in addition to preserving dark areas, it is crucial to also consider the landscape scale through which this species move. Favorable habitat patches need to be connected to one another by corridors to sustain populations and allow for daily movement (e.g., foraging), seasonal movement (e.g., migration), and dispersion (i.e. gene flow). As artificial light can have a barrier effect on bats (Hale et al., 2015), it is important to evaluate its impact on landscape connectivity and our methodology could help map potential ecological corridors for bats at the city scale. Then, to adapt lighting at a fine scale, the information brought by studies on light types (Lewanzik & Voigt, 2017; Rowse, Harris, & Jones, 2016; Stone, Wakefield, Harris, & Jones, 2015) and spectrum (Spoelstra et al., 2017) could help target light sources that might have important impacts on bats. We found a linear negative effect of artificial light on bat activity, whereby increasing radiance was associated with a proportional decrease in bat activity. This relationship suggests that reducing lighting pollution will have a positive effect on bats. Moreover it was shown that even a slight decrease in artificial light intensity could greatly enhance the number of dark patches necessary to nocturnal species (Marcantonio et al., 2015). With the development of adaptable lighting technologies in terms of flux directionality and light

intensity, it seems feasible to decrease light intensity and limit trespass while still complying with socio-economic and security constraints (Gaston et al., 2012).

Remote sensing data offer promising opportunities to account for artificial light impact in urban planning and their availability increases greatly with citizen-science initiatives such as Cities At Night (<http://citiesatnight.org> – Sánchez De Miguel et al., 2014). Although some technical difficulties remain (need for location, calibration, and correction of the images) the technological advances in nocturnal remote sensing represent an opportunity to have a direct representation of the global artificial light emissions at fine resolutions. Thus citizen science programs of biodiversity monitoring and remote sensing imaging and interdisciplinary collaboration between ecologists and astrophysicists will undoubtedly help increase our understanding of light pollution and its impact on the environment.

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ARTICLE 2

APPENDICES

Appendix A. Bat activity data

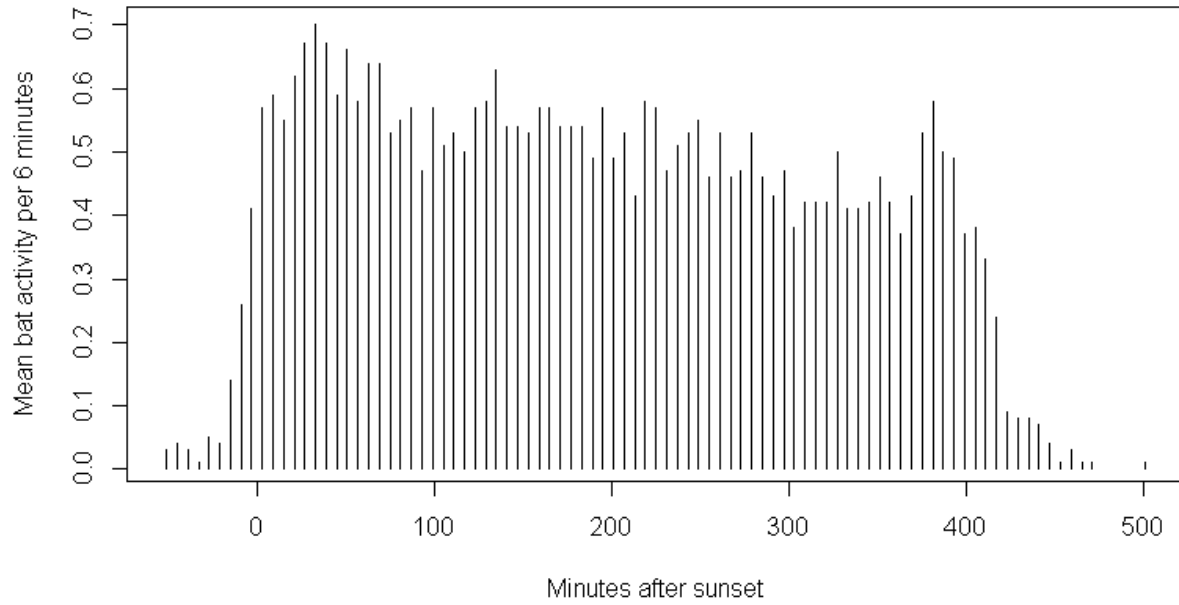


Fig. A.1. Mean activity of *P. pipistrellus* per 6 minutes throughout the night for the full night recordings in Lille.

Table A.1. Number of bat passes during the two first hours of the night per species for each city and occurrence within the recording points of each city.

	Paris		Lille		Montpellier	
	Bat passes	Occ.	Bat passes	Occ.	Bat passes	Occ.
Species						
<i>Pipistrellus pipistrellus</i>	1,205	27%	12,359	99%	7,035	61%
<i>Pipistrellus pygmaeus</i>	1	0%			13,367	73%
<i>Pipistrellus kuhlii</i>	122	3%			6,581	66%
<i>Pipistrellus nathusii</i>	6	0%	37	1%	723	9%
<i>Nyctalus noctula</i>	45	1%				
<i>Nyctalus leisleri</i>			8	0%	1,032	14%
<i>Eptesicus serotinus</i>			246	5%	150	2%
<i>Myotis daubentonii</i>	22	1%			753	6%
<i>Myotis emarginatus</i>					3	0%
<i>Myotis nattereri</i>					9	0%
<i>Miniopterus schreibersii</i>					2	0%
<i>Plecotus austriacus</i>					45	1%
<i>Tadarida teniotis</i>					3	0%
<i>Hypsugo savii</i>					14	0%
Single-genus group						
<i>P. nathusii</i> / <i>P. kuhlii</i>			5	0%		
<i>Myotis spp.</i>	1	0%			1	0%
<i>Plecotus spp.</i>					2	0%
Multi-genus group						
<i>Nyctalus</i> / <i>Eptesicus</i>			4	0%		

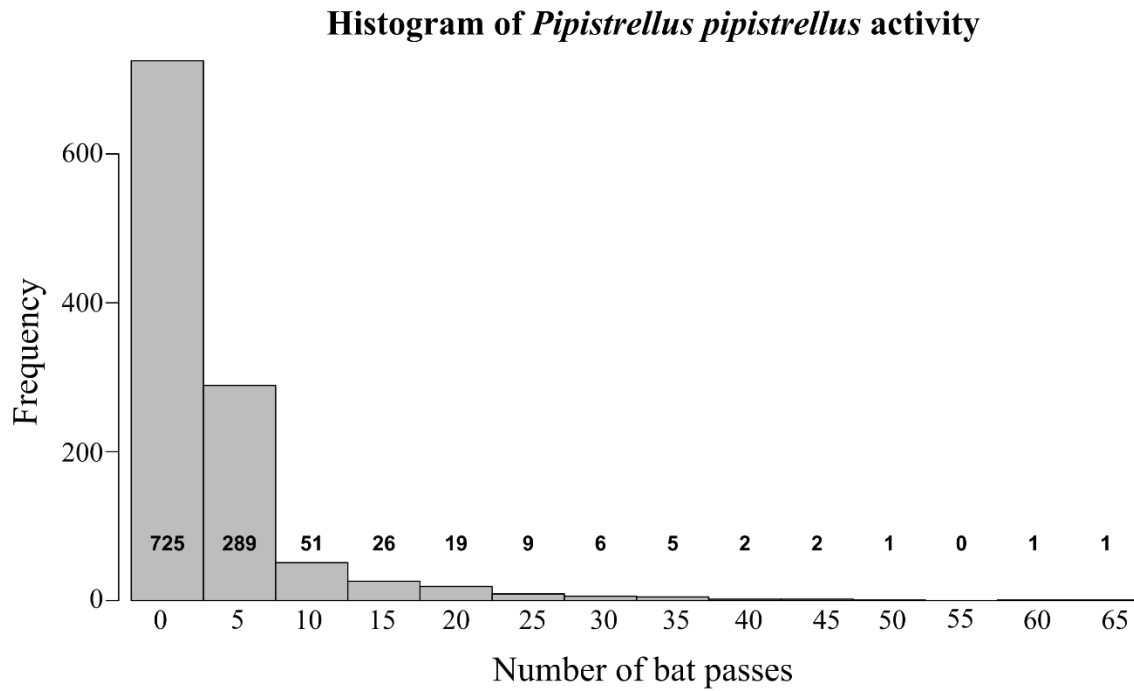


Fig. A.2. Number of *P. pipistrellus* passes in 6 minutes of recording. For *full-night* recordings, we only considered the two first hours of the night and the activity of the night was the average number of bat passes per 6 minutes time slots. The number of occurrence of each number of bat passes is given in bold above the x-axis.

Appendix B. Definition of the outliers and results when including them in the dataset

We considered four recording points to be outliers because of their particularly high radiance value on the ISS picture (Fig. B.1.). Three recording points with the highest values of radiance are located next to the Eiffel Tower and the fourth one is on the Esplanade Charles de Gaulle, in Montpellier city center. We carried the same analysis as in the core paper and found similar results when including the 4 outlier points (Table B.1.).

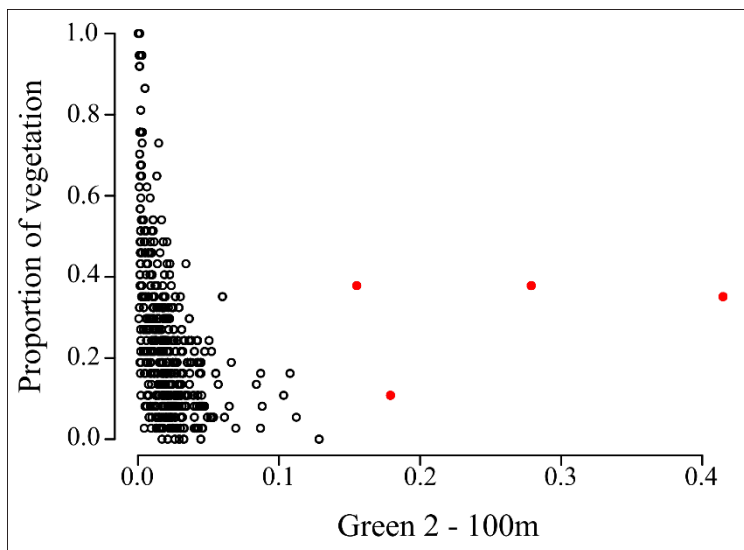


Fig. B.1. The four sites considered as outliers for their particularly high radiance value are represented in red.

Table B.1. Selection of best models to explain bat activity using a light variable and best model without light variable. After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. The reference level for the factor variable “city” is the city of Lille. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates										Marginal		Conditional			
	Intercept	City - Paris	City - Montpellier	Julian Day	(Julian day) ²	Wind speed	Dist. to water	Dist. to tree cover	Prop. of tree cover	Light variable *	Light variable	AIC	ΔAIC	Weights	R ²	R ²
Green 2 - 100	2.94 ***	-3.13 ***	-2.60 ***	0.33 ***	-0.28 **	0.16 ·	-0.27 **	0.61 ***	-0.35 **	0.50 ***	3365.2	0.0	0.32	0.34	0.63	
Blue 4 - 100	2.92 ***	-3.12 ***	-2.62 ***	0.32 ***	-0.28 **	0.16 ·	-0.27 **	0.55 ***	-0.30 **	0.38 **	3365.0	1.8	0.13	0.34	0.63	
Red 1 - 200	2.95 ***	-3.14 ***	-2.61 ***	0.34 ***	-0.29 **	0.15 ·	-0.26 **	0.65 ***	-0.45 **	0.60 ***	3365.4	2.2	0.11	0.33	0.63	
Green 2 - pixel	3.00 ***	-3.20 ***	-2.63 ***	0.33 ***	-0.28 **	0.16 ·	-0.28 **	0.58 ***	-0.19 ·	0.36 **	3365.4	2.2	0.11	0.33	0.62	
Green 2 - 200	2.94 ***	-3.13 ***	-2.60 ***	0.34 ***	-0.30 **	0.16 ·	-0.26 **	0.63 ***	-0.38 **	0.52 ***	3366.0	2.8	0.08	0.33	0.62	
Blue 4 - pixel	3.02 ***	-3.22 ***	-2.67 ***	0.34 ***	-0.30 **	0.14 ·	-0.26 **	0.43 ***	-0.22 *	0.25 *	3366.1	2.9	0.08	0.33	0.62	
Red 1 - 100	2.89 ***	-3.10 ***	-2.56 ***	0.32 ***	-0.28 **	0.17 ·	-0.27 **	0.56 ***	-0.27 *	0.37 **	3367.7	4.5	0.03	0.33	0.63	
Green 3 - 200	3.01 ***	-3.23 ***	-2.68 ***	0.34 ***	-0.29 **	0.16 ·	-0.27 **	0.61 ***	-0.42 **	0.55 **	3367.8	4.6	0.03	0.32	0.62	
Green 3 - 100	2.92 ***	-3.15 ***	-2.60 ***	0.32 ***	-0.28 **	0.16 ·	-0.27 **	0.56 ***	-0.40 **	0.50 **	3368.3	5.1	0.03	0.32	0.62	
Blue 4 - 200	3.04 ***	-3.26 ***	-2.72 ***	0.34 ***	-0.29 **	0.16 ·	-0.26 **	0.56 ***	-0.25 *	0.34 **	3368.8	5.6	0.02	0.32	0.62	
SL density - 200	3.04 ***	-3.33 ***	-2.67 ***	0.34 ***	-0.29 **	0.14 ·	-0.20 *	0.27 *	-0.20 *		3369.1	5.9	0.02	0.31	0.62	
SL density - 100	3.00 ***	-3.28 ***	-2.66 ***	0.33 ***	-0.29 **	0.15 ·	-0.20 *	0.29 **	-0.18 *		3369.8	6.6	0.01	0.31	0.62	
Impacted surf. - 200	2.99 ***	-3.27 ***	-2.63 ***	0.33 ***	-0.29 **	0.16 ·	-0.19 ·	0.27 *	-0.20 ·		3369.9	6.7	0.01	0.31	0.62	
Impacted surf. - 100	2.93 ***	-3.21 ***	-2.61 ***	0.33 ***	-0.29 **	0.16 ·	-0.19 *	0.28 **	-0.18 ·		3370.1	6.9	0.01	0.31	0.62	
SL weighted density - 200	3.05 ***	-3.34 ***	-2.70 ***	0.34 ***	-0.29 **	0.15 ·	-0.21 *	0.29 **	-0.16 ·		3370.3	7.1	0.01	0.31	0.62	
None	###	###	-2.58 ***	###	###	###	###	0.35 ***			###	8.5	0.01	0.30	0.62	
SL distance	Not selected															
SL weighted density - Not selected	Not selected															
SL presence	Not selected															
Red 1 - pixel	Not selected															
Green 3 - pixel	Not selected															

Appendix D. Model results

Table D.1. Selection of best models to explain bat activity using a light variable and best model without light variable. After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. The reference level for the factor variable “city” is the city of Lille. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates										AIC	ΔAIC	Weights	Marginal Conditional	
	Intercept	City - Paris	City - Montpellier	Julian Day	(Julian day) ²	Wind speed	Dist. to water	Dist to tree cover	Prop. of tree cover	Light variable *				Tree cover	R ²
Blue 4 - 100	2.77 ***	-3.05 ***	-2.59 ***	0.32 ***	-0.28 **	0.18 .	-0.24 **	-0.21 .	0.25 *	-0.34 **	3331.3	0.0	0.26	0.33	0.62
Green 2 - 100	2.92 ***	-3.11 ***	-2.58 ***	0.32 ***	-0.27 **	0.17 .	-0.27 **	0.55 ***	-0.21	0.25 .	3332.0	0.7	0.18	0.34	0.63
Red 1 - 200	2.98 ***	-3.15 ***	-2.59 ***	0.33 ***	-0.28 **	0.16 .	-0.27 **	0.63 ***	-0.16	0.27 *	3333.1	1.8	0.11	0.33	0.63
Green 2 - pixel	3.00 ***	-3.19 ***	-2.61 ***	0.32 ***	-0.27 **	0.16 .	-0.28 **	0.57 ***	-0.13	0.31 *	3333.6	2.3	0.08	0.33	0.63
Green 2 - 200	3.05 ***	-3.23 ***	-2.67 ***	0.34 ***	-0.28 **	0.16 .	-0.27 **	0.60 ***	-0.15	0.24 *	3333.9	2.6	0.07	0.33	0.63
Blue 4 - pixel	2.86 ***	-3.14 ***	-2.61 ***	0.32 ***	-0.28 **	0.17 .	-0.24 **	-0.24 *	0.28 **	-0.26 *	3334.4	3.1	0.06	0.32	0.62
Red 1 - 100	2.74 ***	-3.02 ***	-2.55 ***	0.31 ***	-0.27 **	0.17 *	-0.24 **	-0.21 .	0.26 *	-0.31 *	3334.5	3.2	0.05	0.33	0.62
Blue 4 - 200	2.88 ***	-3.16 ***	-2.67 ***	0.33 ***	-0.28 **	0.16 .	-0.24 **	-0.23 *	0.26 *	-0.26 *	3334.8	3.5	0.05	0.32	0.62
Green 3 - 200	3.07 ***	-3.25 ***	-2.65 ***	0.34 ***	-0.28 **	0.16 .	-0.27 **	0.64 ***	-0.10	0.27 *	3335.2	3.9	0.04	0.32	0.63
Green 3 - 100	3.00 ***	-3.19 ***	-2.57 ***	0.32 ***	-0.27 **	0.16 .	-0.27 **	0.61 ***	-0.06	0.28 *	3336.3	5.0	0.02	0.32	0.62
SL density - 200	3.00 ***	-3.31 ***	-2.64 ***	0.33 ***	-0.28 **	0.15 .	-0.20 *	-0.27 *	0.27 *	-0.19 *	3336.6	5.3	0.02	0.31	0.62
Impacted surf. - 200	2.96 ***	-3.26 ***	-2.61 ***	0.33 ***	-0.28 **	0.16 .	-0.18 .	-0.26 *	0.26 *	-0.20 *	3336.8	5.5	0.02	0.31	0.62
Impacted surf. - 100	2.89 ***	-3.20 ***	-2.58 ***	0.33 ***	-0.27 **	0.17 .	-0.19 *	-0.26 *	0.27 *	-0.19 .	3337.0	5.7	0.02	0.31	0.62
SL density - 100	2.96 ***	-3.27 ***	-2.63 ***	0.33 ***	-0.28 **	0.16 .	-0.20 *	-0.27 *	0.28 **	-0.17 .	3337.2	5.9	0.01	0.31	0.63
SL weighted density - 200	3.01 ***	-3.32 ***	-2.67 ***	0.33 ***	-0.28 **	0.15 .	-0.21 *	-0.27 *	0.28 **	-0.15 .	3337.7	6.4	0.01	0.31	0.62
None	2.85 ***	-3.17 ***	-2.56 ***	0.32 ***	-0.27 **	0.17 .	-0.23 *	-0.25 *	0.34 ***		3338.7	7.4	0.01	0.30	0.62

The Julian day and its quadratic term were retained in all models as they reflect the fluctuations of bat activity along the seasons. A GAMM model with a smoothed term on the Julian day variable showed a significant nonlinear effect (edf = 4.4, p-value = 0.0006) (Fig. C.1.)

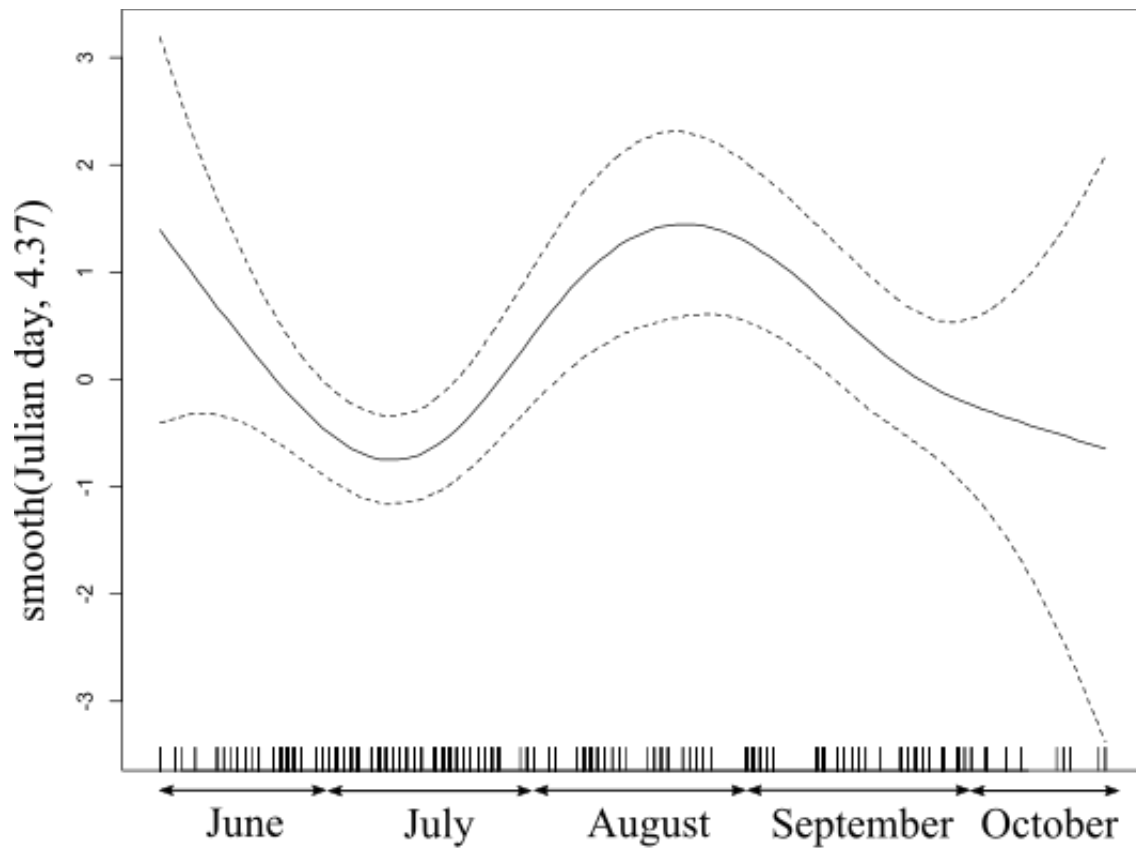


Fig D.1. Representation of the non-linear effect of the date on *P. pipistrellus* activity.

“Those who would destroy the last remnants of natural connectivity should bear the burden of proving that corridor destruction will not harm target populations.”

Beier 1998

CHAPTER 3

IMPACT OF ARTIFICIAL LIGHT ON LANDSCAPE CONNECTIVITY: CURRENT STATE & SCENARIOS OF OUTDOOR LIGHTING

ARTICLE 3

Laforge A., Pauwels J., Faure B., Bas Y., Kerbiriou C., Fonderflick J., Besnard A. Light reduction improves connectivity for bats in an urban landscape. *In prep.*

ARTICLE 4

Pauwels J., Laforge A., Valet N., Bas Y., Fonderflick J., Besnard A., Le Viol I., Kerbiriou C. Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas. *In prep.*

Introduction

Almost all organisms have to move during their live either in response to short-term goals such as reproduction and feeding or for long-term fitness implications such as dispersal and the avoidance of inbreeding (Holyoak et al., 2008). Movement is a fundamental characteristic of life driven by processes across multiple spatial and temporal scales (Nathan et al., 2008). It has a major role in the survival of individuals, the transfer of genes and ultimately affects population dynamics, the distribution of species and ecosystem functioning (Nathan et al., 2008). Due to the central place of movement in animal behavior, understanding the factors that affect movement is crucial to develop effective landscape-level conservation planning and particularly in landscapes undergoing rapid environmental change (Rayfield, Fortin, & Fall, 2011; Zeller, McGarigal, & Whiteley, 2012).

Promoting landscape connectivity, i.e. the degree to which a landscape facilitates the movement of organisms (Taylor et al., 1993), has become a global conservation priority to mitigate widespread landscape modifications and their impact on biodiversity (Crooks & Sanjayan, 2006). In this context, the landscape is generally described by dividing it in two types of elements, the habitat patches and the matrix. The definition of what is considered a habitat is not often stated and may vary. Broadly, habitat can be defined as “the range of environments suitable for a given species” (Fischer & Lindenmayer, 2007). Depending on the scale at which the landscape connectivity is considered, habitat may refer to areas suitable to support a species population durably or areas that may be used by individuals to fulfill a daily need (e.g., foraging). The matrix is then defined as all the landscape that is not a habitat (Kindlmann & Burel, 2008). Its composition can influence movement behavior and habitat patches reachability thus affecting landscape connectivity (Kindlmann & Burel, 2008). Land conversion leads to habitat loss and therefore to an increased proportion of matrix in the landscape which in turn

tends to decrease the size of habitat patches and increase the distance between them (Kindlmann & Burel, 2008). This process leads to an increased landscape fragmentation and is considered as a key driver of global species loss (Fischer & Lindenmayer, 2007).

Since the formalization of the landscape connectivity concept in landscape ecology (Taylor et al., 1993), its meaning has been interpreted and used in different ways. Thus, two types of connectivity have been distinguished, the structural connectivity which is entirely based on the landscape structure and the functional connectivity which considers both the landscape structure and organism's behavioral responses to landscape elements (Kindlmann & Burel, 2008). Structural connectivity is easier to measure and is independent of species behavior however it ignores the complexity of how organisms interact with spatial heterogeneity and which may affect species ability to move (Taylor, Fahrig, & With, 2006). For example, species with low dispersal abilities may be sensitive to low degrees of landscape fragmentation while highly mobile species may perceive landscapes as functionally connected across a greater range of fragmentation severity although they are not structurally connected (With & Crist, 1995). Thereafter in this chapter we will only consider functional connectivity.

The vast majority of connectivity studies evaluated the impact of land cover types and land uses on the species ability to cross the matrix to join habitat patches but only very few account for diffuse anthropogenic pollutions (LaPoint et al., 2015). Inclusion of anthropogenic pollutions was achieved through the use of data on road traffic (Joly, Morand, & Cohas, 2003; Magle, Theobald, & Crooks, 2009) which is a proxy for both light and noise disturbance induced by roadside lighting and vehicles noise and headlights. However, there are limitations to this proxy as not all roads are lit and all lit places are not roads (and similarly for noise). Nonetheless, no studies have specifically focused on the effect of light pollution on landscape connectivity in spite of its potential to modify individual's behavioral response to landscape elements and its wide spatial extent. Indeed, as light may attract some species (Eisenbeis, 2006),

be avoided by others (Wise, 2007) or act as a barrier (Stone, Jones, & Harris, 2009), it may have important implications in the perception of landscape connectivity. For example, hedges are known to be important linear feature for bat species movements and they may serve as commuting routes (Verboom & Huitema, 1997). However, hedges roles as movement corridors for bats may be greatly altered by light (Stone et al., 2009) and the gap-crossing ability of bats may be reduced by the presence of light within gaps (Hale et al., 2012). In this case, considering the network of hedgerows as elements facilitating movement without accounting for the potential negative effect of light may lead to erroneous conclusions on landscape connectivity. The impact of ALAN on a landscape is complex to asses as light is diffuse and thus not easily delineated. Indeed, it is estimated that the skyglow effect propagates light tens or hundreds of kilometers away from their light sources (Kyba et al., 2015). Moreover, it is possible that ALAN's effects on species movement behavior is dependent on the land cover type, the landscape element considered and the global environmental context and landscape composition.

The second chapter of this PhD thesis revealed the potential of fine resolution remote sensing data on light pollution to measure the impact of ALAN on bat activity. Furthermore, the model developed allowed to produce predictive map of the distribution of bat activity with may be used by land manager to locate habitat areas where it would be beneficial to limit light emissions. However these maps do not include information on bats movement between suitable areas and as such their use for conservation purposes may lead to inefficient or even damaging landscape planning (Taylor et al., 1993). Locally enhancing a habitat patch that is poorly connected will have a lesser contribution to the global population than a possibly lower quality patch that is well connected to a network of patches (Taylor et al., 1993). Therefore, in addition to information on habitat patches, it is crucial to consider the connectivity between these patches to produce the most relevant and fruitful landscape planning recommendations.

Aims of the chapter

The present chapter hence draws on the precedent one (Fig. 24), using bats response curves to ALAN to intent to **model the functional landscape connectivity for bats in urban environments while accounting for light pollution**. The chapter is based on two studies evaluating the impact of light on connectivity at two intermediate scales, the city-scale (Article 4) and the conurbation-scale (Article 3), and investigating the potential effects of changes in lighting planning on landscape connectivity. These studies are the first to investigate the effect of light pollution on functional connectivity.

In the first study (Laforge et.al, *in prep*; Article 3), we assessed the contribution of ALAN to landscape fragmentation for two species of bats in a large conurbation (almost 300 km²) in the North of France. As bat activity had a low variability for the two species, the connectivity analysis were carried out on bat presence response curves. In addition to evaluating the current state of the functional landscape connectivity for bats, Laforge et.al **investigate the potential of lighting schemes to improve it through scenarios of light extinction**. Scenarios ranges from the extinction of small areas considered as potential bat habitats such as wetlands and urban parks to the extinction of wide urban areas. This study is based on bat data collected

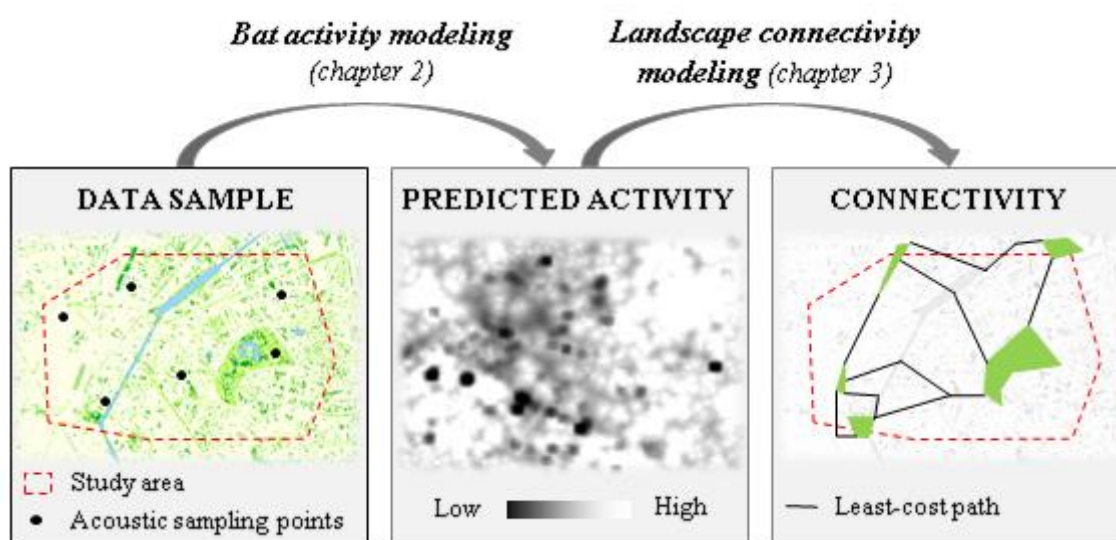


Fig. 24. Modeling steps to evaluate the landscape connectivity for bat species

throughout the conurbation following a random stratified sampling and a satellite picture of nighttime lighting from the VIIRS DNB (250m resolution). These data were used to predict bat activity and probability of presence throughout the study area and then the landscape connectivity was measured using least-cost path modeling.

The second study presented in this chapter (Pauwels et al., *in prep*; Article 4) is based on the best model defined in the second chapter to predict *P. pipistrellus* activity across three cities. I carried out this analysis on several study areas in order to evaluate the role of the spatial arrangement of land cover types and the distribution of light on the landscape connectivity. In addition, similarly to Laforge et al., I tested the impact of different lighting scenarios on the landscape connectivity. Outdoor lighting technologies are undergoing a technological change toward energy efficient LED lights. This type of lamps emit light across a broader spectrum than current lamp types and include an important proportion of short (blue) wavelengths. Therefore, the shift toward LED lamps is predicted to drastically increase the emissions of blue light with potentially large impacts on biodiversity. Here **I tested how a global change of outdoor lighting toward LEDs would impact landscape connectivity for *P. pipistrellus***. The study was based on the same biological data as in the first chapter and followed a similar methodology as in Laforge et al.

Principal results & discussion

In the first study, the **scenarios of extinction were applied to *M. daubentonii* and *P. nathusii* and showed the potential of localized extinctions to promote landscape connectivity** in the conurbation (Fig. 25). For both species, scenarios of extinction of urban parks (3) and wetlands (5) significantly improved the functional connectivity. Such extinction schemes seem both feasible as most urban parks are closed at night and desirable to enhance

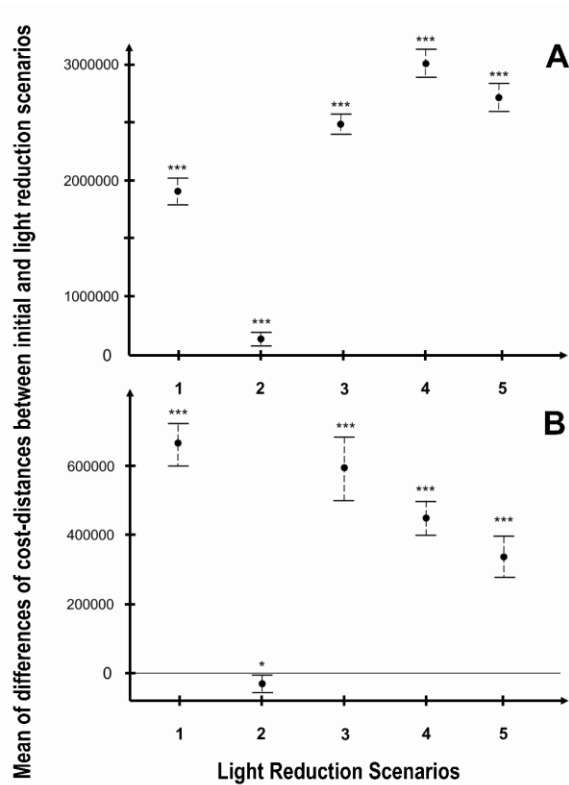


Fig. 25. Means of differences of paired cost-distances between initial LCP and LCP after each light reduction scenarios. **A:** *M. daubentonii*; **B:** *P. nathusii*. Light reduction scenarios on: (1) urban areas of municipalities of more than 10 000 inhabitants; (2) urban areas of municipalities of less than 10 000 inhabitants; (3) urban parks; (4) main roads; (5) wetlands.(extracted from Laforge et al.).

connectivity for urban bats. However due to the absence of available fine scale remote sensing data, this work was carried out using a satellite picture (VIIRS) with a 250 m resolution.

The second study (Pauwels et al., *in prep*; Article 4) revealed **that the effect of light pollution was negative for *P. pipistrellus* landscape connectivity but in highly differing extent depending on the study area** (Fig. 26). Indeed the scenario in

which all lights were turned off induced much higher changes in the overall connectivity in Lille (+210%) than in Montpellier (+18%). This result stresses the context-dependence of the impact of light on species perception of landscape

fragmentation. Moreover, the model species used in this study can forage in the vicinity of streetlights (Rydell, 1992; Azam et al., 2018) and may thus be less impacted by light pollution than other species that avoid light even at low levels (Lacoeuilhe et al., 2014; Azam et al., 2018). Therefore, the landscape connectivity perceived by light sensitive species may be affected by ALAN in even more important proportions.

Scenarios simulating a change in lighting technology toward the generalized use of LEDs showed that the modification in light emissions in the blue spectrum differ between cities increasing more in Paris and Lille than in Montpellier. This may be linked to the differences in the current lighting technologies used in the three study areas. Nevertheless, **our results demonstrate that changing all light sources to LEDs while keeping the same**

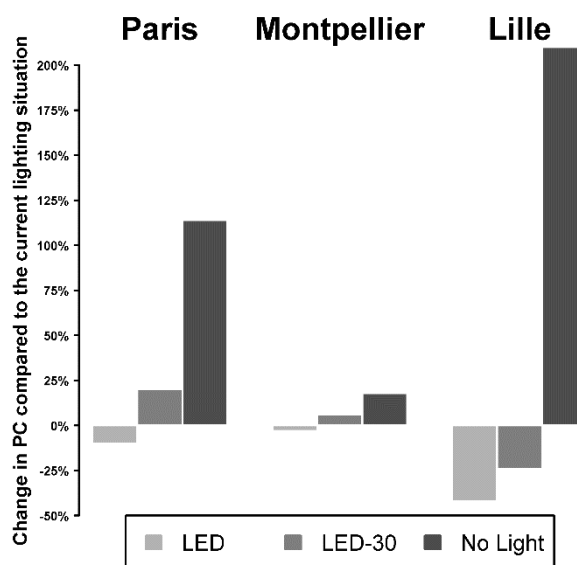


Fig. 26. Change in overall landscape connectivity for the lighting scenarios compared to the current situation (extracted from Pauwels et al.).

overall radiance will negatively affect landscape connectivity for *P. pipistrellus*. An adaptation of lighting fixtures concomitantly to the change to LED lighting may reduce upward emitted light thus decreasing the radiance measured through ISS pictures (60 m resolution). Such a scenario would reduce the negative impact of a change toward LEDs and potentially increase connectivity depending on the landscape context. Indeed, for the city of Lille, the decrease in radiance mostly took place in the city center which is densely built and is thus not suitable for bats. These results showed that although there is a similar general pattern in the landscape connectivity variations for the three cities, it is not straightforward to estimate the influence of a change in lighting technology as it depends on the landscape context in terms of land use and current lighting distribution. Moreover, our study highlights the importance to take several parameters into account to prioritize areas where the reduction of light would most benefit bats as some light changes may have more or less impact on the landscape connectivity.

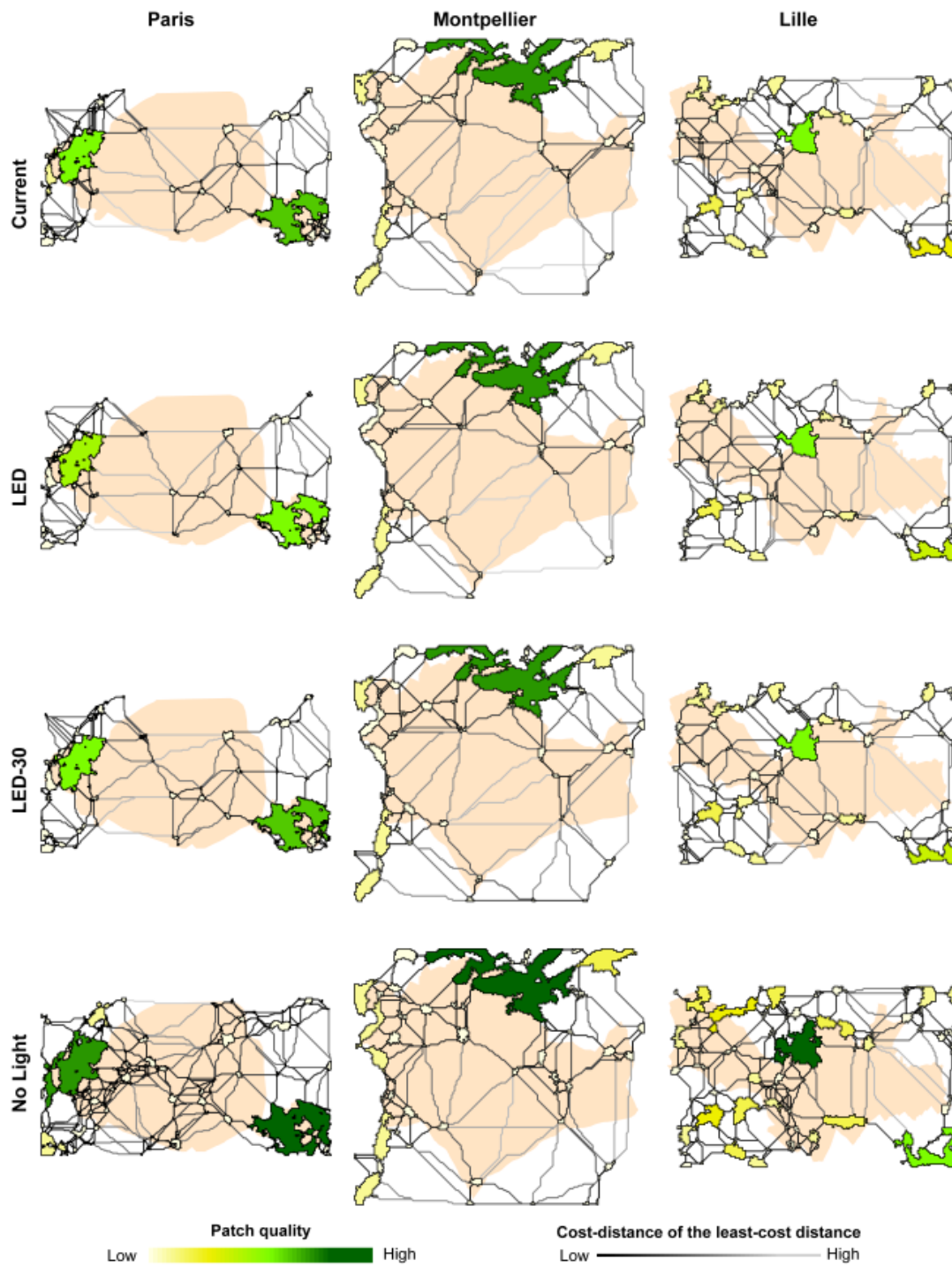


Fig. 27. Spatial representation of habitat patches and least-cost paths for each study area and each scenario. The light orange shape represent the area of the cities.

Perspectives

The two studies demonstrate the importance to target specific areas for the implementation of mitigation measures to help reduce the impact of ALAN. Both studies provide methodological basis to identify connectivity corridors for nocturnal species which implies to account for the necessity to have suitable habitat but also to promote landscape connectivity. Moreover, the scenarios tested, can give global insight as to where it would be most efficient to preserve darkness. Nonetheless, the applied use of such scenarios may be limited for several reasons. First, the scenarios that can be built from the satellite pictures only allow to modify the spectrum and radiance of the current lighting situation. It would be much more complicated to mimic the implementation of new lighting in a currently dark area. Secondly, satellite pictures do not have a fine enough resolution to identify specific light sources and thus we are not able to indicate if the radiance emitted comes from public or private lighting which may limit the application for public outdoor lighting planning. Thirdly, it is not yet feasible to build scenarios that would reflect the change of specific light points and thus predict how a specific change in lighting may impact connectivity. This is both due to the relative coarseness of the picture and to the fact that we are not able to translate illuminance measures from a light source to the radiance as measured from remote-sensing. In addition, this would require to model how halos of different light points may superpose or how built structure may limit trespass. Nevertheless, the global evaluation of connectivity and the comparison with scenarios may give global insight and allow to delineate global directives.

The analysis carried out in this chapter used fairly accessible environmental and light data in order to be replicated in other areas and potentially used in landscape management. In the framework of knowledge transfer from the result arising from this PhD's work to the environmental engineering company associated to it, such a replication of the methodology is currently ongoing in Douai, a small municipality in the North of France (17 km² whereas the

smaller city studied in this chapter was 35 km²). As fine-resolution ISS pictures are currently mostly available for large cities because they are easier to georeference than smaller localities, we used a coarser picture from the VIIRS DNB (250m resolution). The methodology used is the same as developed in Pauwels et al. (Article 4). Preliminary results showed no significant effect on *P. pipistrellus* and *E. serotinus*. This result differs from the ones arising from both studies presented in this chapter however this might be linked to the use of low resolution light pollution data on a small study area. Indeed, *P. pipistrellus* and *E. serotinus* may have a relatively fine perception of the distribution of light and thus may be able to navigate in a mosaic of lit and dark areas. Therefore the radiance at a 250m scale might not be an accurate representation of their perception. They may be able to move across pixel with a high radiance at the scale of the VIIRS image as it can contain local low light level areas. This differing results emphasize the necessity to evaluate the impact of data resolution on the response measured. Future research should investigate the sensitivity of the analysis carried out in this chapter to the resolution and type of light data. For example, for a same study area, it would be interesting to evaluate the response of bat to light as measured by VIIRS images and ISS pictures and/or ISS pictures resolution could be degraded to various degrees. The study carried out in Douai also showed a negative effect of the radiance level on *Nyctalus noctula* activity. *N. noctula* has been documented to forage at streetlights (Rydell, 1992) and its activity increases with illuminance at the local scale (Lacoeuilhe et al., 2014; Azam et al., 2018) however at the scale of this small municipality, the effect seems to be negative. This finding is similar to the scale-dependence of *P. pipistrellus* activity response to ALAN. Yet hypothesis concerning *N. noctula* response to light should be considered carefully as this species spends an important proportion of its time at high altitudes (Roemer et al., 2017) which may limit its detection by recorders placed at ground level and therefore bias the understanding of its behavior. Due to the relatively large size of *N. noctula*, it can be tracked using GPS devices. This technology could be used to

explore *N. noctula* behavior in regard to light pollution. It may be possible that individuals' response to light vary depending on the altitude at which they fly or that they avoid light while commuting by gaining altitude.

ARTICLE 3

LIGHT REDUCTION IMPROVES CONNECTIVITY FOR BATS IN AN URBAN LANDSCAPE

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Abstract

Light pollution can alter animal movements and landscape connectivity. This is particularly true in urban landscapes where a need to incorporate conservation issues in urban planning is urgent. In the present study we investigated how potential light-reduction scenarios at a conurbation scale can improve landscape connectivity for bats. Through random stratified sampling and species distribution modelling, we assessed the relative importance of light pollution on presence probability and activity of bats. We recorded bats during entire nights on 305 sampling points in 2015. In 2016, we surveyed 94 supplementary points to evaluate our models performance. We used our spatial predictions to characterize landscape resistance to bat movements. Then we applied a least-cost modelling approach to identify nocturnal corridors and estimated the impact of five light-reduction scenarios on landscape connectivity of two light non-tolerant bat species. We found that light pollution had a major influence on bat presence and activity up to 700 m. Our results exhibited three contrasting responses to light intensity: *M. daubentonii* responded negatively, *P. nathusii* had a positive response for low values then a negative response after a threshold radiance value of $20 \text{ W}\cdot\text{m}^{-2}\cdot\text{sr}^{-1}$ and *E. serotinus* responded positively. Five and four light-reduction scenarios significantly improved landscape connectivity for *M. daubentonii* and *P. nathusii* respectively. Light-reduction measures should be urgently included in urban planning to provide sustainable conditions for bats in cities. Finally, we advocate for the use of our new methodological approach to further studies to find the best trade-off between conservation needs and social acceptability.

1. Introduction

Movements of individuals between habitats or between (sub)populations are crucial for population viability and thus biodiversity conservation (Zeller, McGarigal, & Whiteley, 2012). Such movements require the landscape matrix to be pervious (Tischendorf & Fahrig, 2000). This permeability is usually referred to landscape connectivity, i.e. the degree to which a landscape facilitates or impedes the movement of individuals (Tischendorf & Fahrig, 2000). Identifying landscape and restoring conditions, structures and processes that facilitate animals movements, have thus become a global conservation priority to mitigate widespread anthropogenic landscape modifications and their impacts on biodiversity (LaPoint, Balkenhol, Hale, Sadler, & van der Ree, 2015). The first approach to identify and maintain ecological corridors in the landscape relied on structural connectivity through the use of landscape configuration metrics such as habitat patch size or tree linear length that are thought to act as conduits or barriers to movements (Taylor, Fahrig, & With, 2006). This approach often ignored non-structural landscape factors that could influence landscape connectivity (LaPoint et al., 2015) such as Artificial Light At Night (ALAN).

ALAN may have negative impacts on ecosystems (Gaston, Visser, & Hölker, 2015) but our knowledge on the extent of effect on landscape connectivity is weak (Azam, Le Viol, Julien, Bas, & Kerbiriou, 2016; Hale et al., 2015; Hölker, Wolter, Perkin, & Tockner, 2010). ALAN has increased worldwide in extent (2,2 % per year) and radiance (1.8% per year) between 2012 to 2016 (Kyba et al. 2017), threatening a substantial proportion of global biodiversity as 30% of all vertebrates and more than 60% of all invertebrates are nocturnal (Hölker et al., 2010). The widespread use of ALAN has major impacts on animal movements and species distribution at multiple spatial scales for a large variety of species and taxa such as birds, butterflies, eels, turtles, zooplanktons and bats (Gaston, Duffy, Gaston, Bennie, & Davies, 2014; Hölker et al.,

2010). Hence, it is of major importance to characterize the relative contribution of ALAN to landscape fragmentation to propose sustainable land-use planning strategies (Azam et al., 2016; Gaston et al., 2014; Grimm et al., 2008). Furthermore, ALAN is especially present in urban areas with an annual growth rate of 6% per year (Hölker et al., 2010) and with the strongest current issues of public lighting renewal (Tsao et al. 2010). In the same time, many bat species are adapted to live in built areas (Dietz, von Helversen, Nill, Dubourg-Savage, & Jourde, 2009) and can thus be directly confronted to light pollution. Bats represent a rare case of species protected at the European level within urban environments (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora).

In order to investigate the effect of ALAN on landscape connectivity, we used insectivorous bats as they are nocturnal and very sensitive to habitat loss and fragmentation (Frey-Ehrenbold, Bontadina, Arlettaz, & Obrist, 2013; Mickleburgh, Hutson, & Racey, 2002). Bats activity and occurrence are negatively or positively affected by ALAN depending on their foraging strategies, their flight abilities and on the considered landscape-scale (Azam et al., 2016; Hale, Fairbrass, Matthews, & Sadler, 2012). At a local scale, the illumination of hedges or rivers near colonies of slow-flying gleaner species such as *Rhinolophus* spp. and *Myotis* spp. had for instance a negative impact on bat activity and altered individual's movement behavior as they sought to avoid the newly illuminated areas (Kuijper et al., 2008; Stone, Jones, & Harris, 2009). In contrast, fast-flying species hunting insects at dusk in the open air such as *Pipistrellus* spp. and *Nyctalus* spp. can benefit at a local scale from new spatially foraging areas provided by ALAN (Azam et al., 2015; Lacoëuilhe, Machon, Bocq, & Kerbirou, 2014). In the other hand, ALAN has been shown to decrease landscape connectivity by altering movements and gap-crossing behaviors of *Pipistrellus pipistrellus* (Schreber 1774) individuals in an urban matrix (Hale et al., 2015). Those findings suggest that ALAN can act as a barrier for bats and thus further increase the landscape fragmentation. All of this highlight the importance of

integrating ALAN in sustainable urban-planning schemes to allow the persistence of biodiversity in urban landscapes through darker environments (Gaston et al., 2015). Currently, the knowledge on response of urban bat communities along urbanization and ALAN gradients is insufficient to identify, preserve and develop efficient nocturnal corridors (Hale et al., 2012; Mathews et al., 2015; McDonnell & Hahs, 2008). This is notably due to the fact that sampling bats in cities is challenging hence highly urbanized areas are often under-sampled leading to a lack of data for this type of landscapes (LaPoint et al. 2015).

Here, we aimed at: (i) assess the contribution of ALAN to landscape fragmentation for bats, (ii) provide methodological basis to identify nocturnal corridors and (iii) predict the effect of different light reduction scenarios on landscape connectivity for bats in order to improve ALAN management. To achieve these goals, we used species distribution modeling based on standardized empirical data from a random stratified sampling to (1) predict bat species' use of urban landscape and characterize the landscape-resistance to bat movements (Stevenson-Holt, Watts, Bellamy, Nevin, & Ramsey, 2014) and (2) identify the most suitable habitat patches to connect. We then used least-cost path modeling to identify nocturnal corridors and assess effects of light reduction scenarios on landscape connectivity.

2. Materials and methods

The whole methodological procedure is given in the Figure 1.

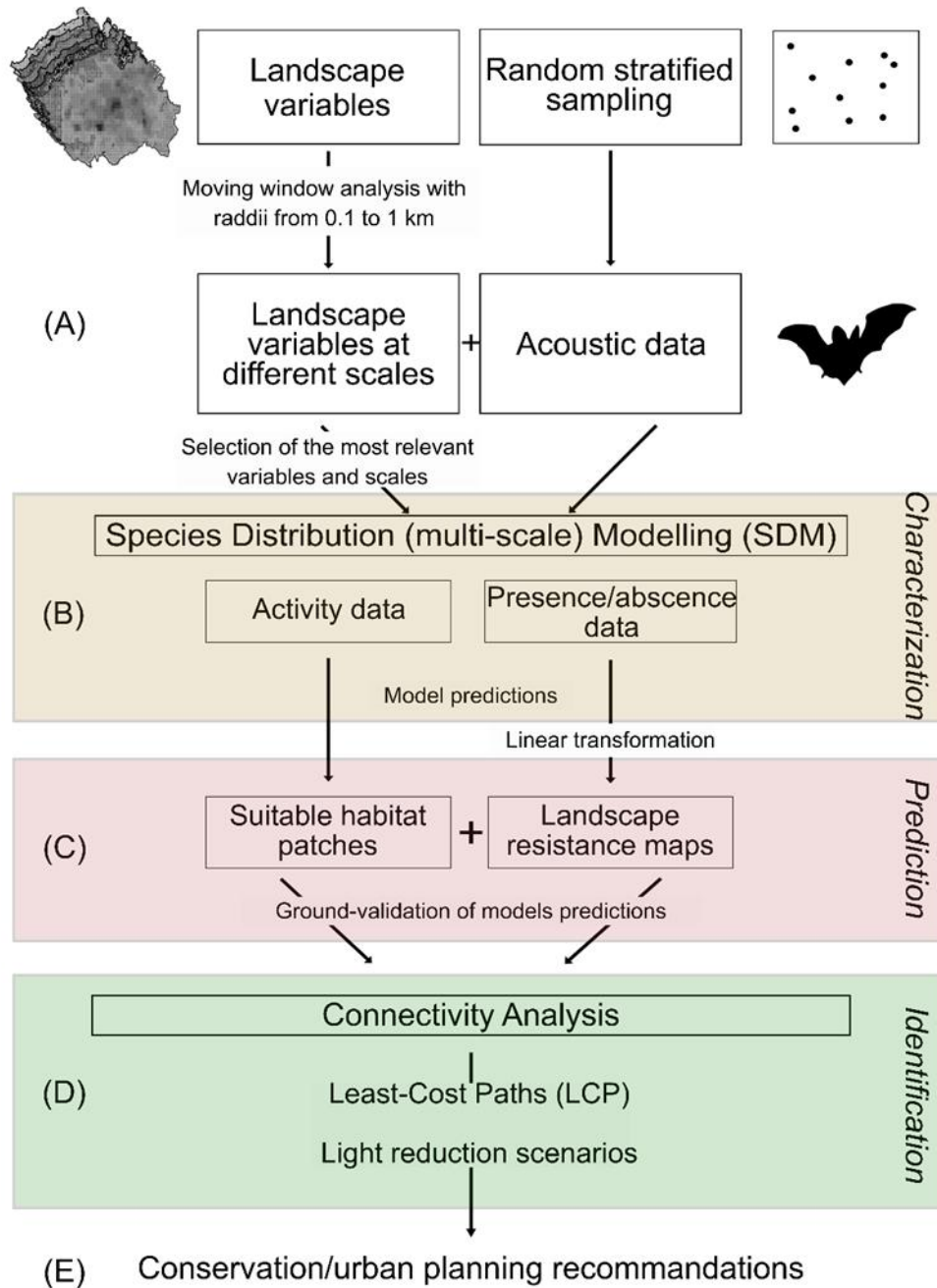


Fig. 1. Global methodological procedure followed to assess the effects of light-reduction scenarios on landscape connectivity for bats.

2.1. Study area

The study was carried out in the Métropole Européenne de Lille in Northern France. It is the second most important French conurbation with more than 1.1 million inhabitants (Fig. 2). The selected study area covers 27 307 hectares and 41 municipalities (50.6294 N, 3.0571 E; Fig. 2). The temperate oceanic climate dominates with mild average daily temperatures (1-10°C in winter, 11-23°C in summer) and a constant rainfall level throughout the year (743 mm.year⁻¹ on average). The study area is dominated by dense urbanization and intensive agricultural landscapes (respectively 65% and 23% of the total study area cover). Forests and natural areas

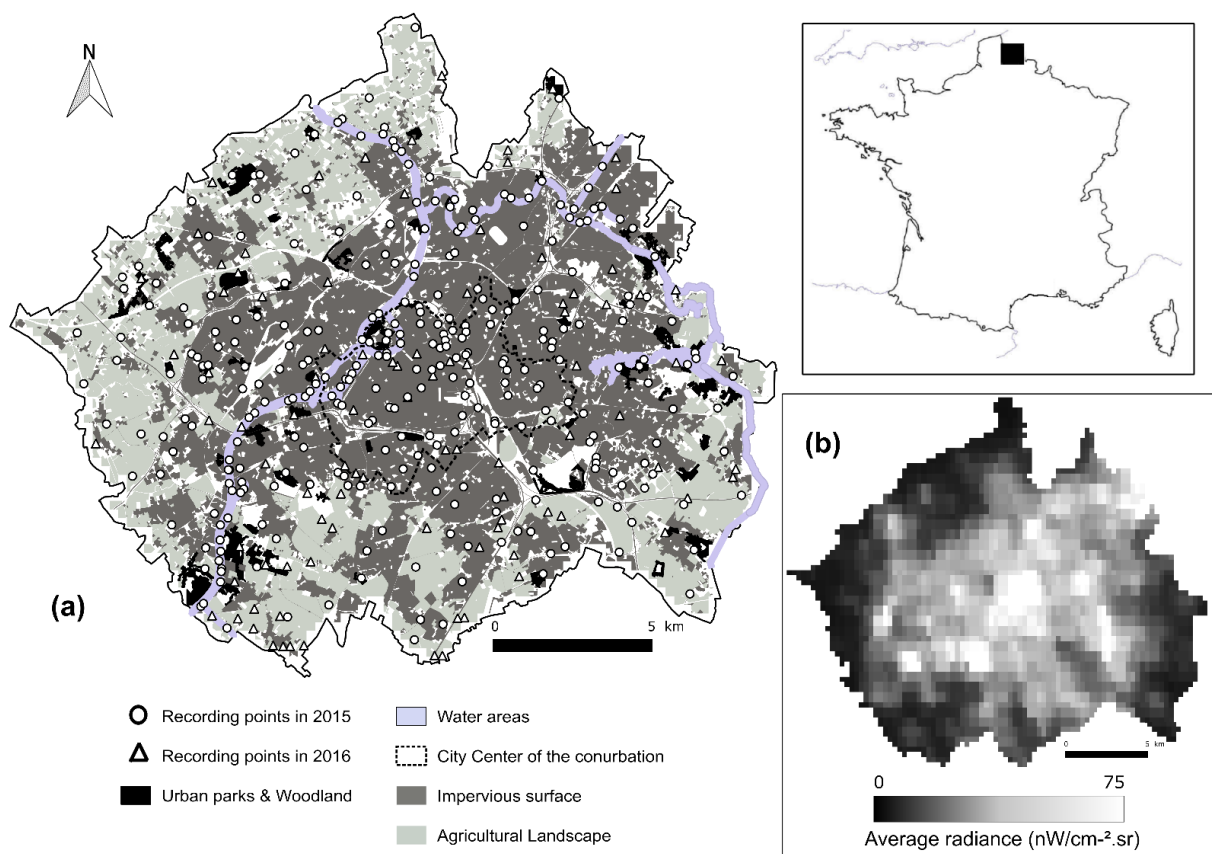


Fig. 2. (a) Map of the study area presenting the spatial sampling effort carried out in 2015 and 2016 as well as the main landscape components of the conurbation of Lille. (b) Spatial gradient of average radiance on the study area obtained from the Earth Observation Group, NOAA National Geophysical Data Centre (http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html).

are restricted to relatively small patches which are mainly urban parks on rivers' and ponds' banks (Fig. 2).

2.2. Sampling design

A crucial assumption to use SDM to define landscape resistance values is that all the habitats of the landscape studied have been randomly sampled with the same effort (Beier et al. 2008). Thus we defined a random stratified sampling to record bat calls in every landscape context existing on the study area in terms of three covariates: impervious surface proportion (including buildings and pavements such as roads, sidewalks, driveways and parking lots), tree-cover proportion and ALAN (Fig. 2). The selection of these variables was based on two criteria: (i) they influence bat presence and activity (Azam et al., 2016; Fonderflick, Azam, Brochier, Cosson, & Quékenborn, 2015; Hale et al., 2015) and (ii) their variations in the study area are large enough to yield important gradients. The importance of these corridors for bat movements seems to be greater in lit and urbanized areas (Hale et al., 2012). In order to obtain the most representative sampling of the three landscape gradients, we developed an algorithm to randomly select at most two cells in all the combinations of these three covariates. We made this sampling procedure two times: one among exclusively non-aquatic cells and another among cells covering, even partially, wetlands (watercourses and ponds). Indeed we know that wetlands in urban context is an important habitats for bats and hence a strong predictor for both occurrence and activity (Straka, Lentini, Lumsden, Wintle, & van der Ree, 2016).

ALAN data were obtained from VIIRS nighttime imagery (2012) which is a 2-months composite raster of radiance data (in nW/cm².sr) collected by the Suomi NPP-VIIRS Day/Night Band during 2 time-periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh, Hsu, Elvidge, & Zhizhin, 2013) and produced by the Earth Observation Group, NOAA National Geophysical Data Centre (<http://www.ngdc>.

noaa.gov/eog/viirs/download_monthly.html). The land cover variables are provided by the French National Institute for Geographic and Forestry Information (<http://www.ign.fr/>). The landscape variables were built using a grid at a resolution of a 250 m x 250 m with the software QGIS 2.14 (QGIS development team, 2016). This resolution corresponds to the precision of the satellite picture (Fig. 2). For each cell, we calculated the values of the three variables and grouped them into five classes of equal size (0-20%, 20-40%, 40-60%, 60-80%, 80-100% for impervious surface and tree cover proportions and 2.6-17, 17-31.4, 31.4-45.8, 45.8-60.2, 60.2-74.6 nW/cm².sr for ALAN) to define the combinations of the three covariates. This procedure allowed us to randomly select 305 cells.

2.3. Bat surveys

We used acoustic surveys to gather bat presence/absence and activity data transformed here as activity index (AI) which is the number of minutes where at least one call of bat has been recorded (Haquart, 2013; Miller, 2001). We recorded all bat calls during one full night (30 minutes before dusk to 30 minutes after dawn) at all locations. We used stationary automated ultrasound detectors (Song Meter SM2BAT, Wildlife Acoustics, USA) fitted with multidirectional microphones (SMX-US weatherproof ultrasonic microphone, Wildlife Acoustics, USA). The position of the detectors in the cells has not been controlled because of the strong constraints to hide it in an urban landscape. The sampling was carried out between the 1st June and the 31st August in 2015, which corresponded to the seasonal peak of activity of bat species, as recommended by the French national bat-monitoring program ‘Vigie-Chiro’ (<http://www.vigienature.mnhn.fr/>). Recordings were only carried out when there was no rain, when the wind was below 30 km/h and the ambient temperature above 12°C. We used the software SonoChiro© (Bas et al., 2013) to automatically classify the echolocation calls to the most accurate taxonomic level possible. We then checked the software classification by

screening all ambiguous calls with Syrinx software version 2.6 (Burt, 2006) and the support of existing identification keys (Barataud, Tupinier, Limpens, & Cockle-Betian, 2015). Identification was possible to the species level for the most part of our acoustic data due to low bat species diversity in the study area which allowed to avoid the problematic acoustic overlaps between some species pairs such as *Pipistrellus nathusii*/*Pipistrellus kuhlii*, *Myotis daubentonii*/*Myotis mystacinus*/*Myotis bechsteinii* and *Eptesicus serotinus*/*Nyctalus leisleri*. Indeed, *P. kuhlii*, *M. mystacinus*, *M. bechsteinii* and *N. leisleri* are very rare in the study area according to regional atlas data (Dutilleul, 2009). Nevertheless, to reduce false absences, the recording points where a studied species was not identified for sure, but where we were just able to identify a group of species which include the studied species, were excluded from the analysis of that species (Boughey, Lake, Haysom, & Dolman, 2011).

2.4. Species distribution modelling (SDM)

When SDM is used to calculate landscape resistance we often make the underlying assumption that habitat selected by species to forage are also those that facilitate their movements (LaRue & Nielsen, 2008). However, this assumption has so far been rarely tested and Roever et al. (2012) pointed out that it is unlikely that the same landscape variables will determine both habitat selection and movement of animals. Thus, we used presence-absence data to define landscape resistance as we considered that the resistance was not linked with the level of activity but only to the probability that a bat would move through the landscape. We defined habitat patches using bat activity as a high level of activity can denote a foraging area or a roosting site. Furthermore, the selection of suitable habitat patches is often carried out on the basis of expert opinion and each landscape feature is given a constant resistance value (FitzGibbon, Putland, & Goldizen, 2007). We assumed that our methodological procedure, by providing predictions at each location rather than constant levels of resistance for a particular

land cover type, are likely to provide more accurate models to describe ecological patterns (Beier et al. 2008).

2.4.1. Response variables

We modelled the presence probability and the activity of bat species using Generalized Additive Models (GAM; Hastie & Tibshirani 1990). GAMs provide useful flexibility for fitting ecologically realistic relationships in SDMs and bring benefit to fit complex nonlinear relationships between predictors and the response variable (Elith et al., 2006; Elith & Leathwick, 2009). Presence probability of species were modelled with presence/absence data using a binomial error distribution and a logit link function. AI were modelled using a negative binomial error distribution and a log link function to take into account the over-dispersion of our data (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

For details on the methods for multiscale and multivariate model selection, multicollinearity and spatial autocorrelation evaluations, see Appendix A1. For details on the methods to evaluate the models performances see Appendix A2. We made our statistical analysis in R 3.2.5 (package “Raster”, “ROCR”, “GAM”).

2.5. Connectivity analysis

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

2.5.1 Selection and localization of suitable habitat patches

In a first step we identified the most suitable habitat patches, which will be used as nodes to connect through corridors, using predictive bat activity maps. Patches were defined as areas where predicted activity values are in the category "High" of the French bat activity framework (Haquart, 2013) i.e. > 12 positive minutes per night for *M. daubentonii*; > 50 for *E. serotinus*; > 33 for *P. nathusii*. We then arbitrarily kept only the suitable habitat patches with surface area up to 25 000 m² (i.e. 10 aggregated cells).

2.5.2 Landscape resistance maps

Presence probability maps obtained with the SDM can be interpreted as the landscape resistance level to bats movements between habitat patches: the lower the presence probability value, the more the landscape is resistant to bats movement (Guisan & Thuiller, 2005). To transform SDM maps previously obtained into resistance surfaces, we inverted the maps by calculating for each cells the landscape resistance values in the following way:

$$R_i = P_{\max} - P_i$$

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

2.5.3. Least-Cost Paths (LCP)

We modelled the corridor network using the LCP modelling technique (Watts et al., 2010), a graph theory-derived method (Urban & Keitt, 2010). The LCP modelling was performed with Linkage Mapper toolbox (for more information on the technique see McRae &

Kavanagh 2011) using ArcGis 10 (ESRI, Redlands, CA). All pairs of habitat suitable patches have been connected by a LCP.

2.5.4. *Light reduction scenarios*

We tested five light-reduction scenarios: (1) on urban areas of municipalities of more than 10 000 inhabitants, (2) on urban areas of municipalities of less than 10 000 inhabitants, (3) on urban parks, (4) on main roads, (5) on wetlands (spatial distribution of those areas are shown in Fig. B1 and means and standard deviations of initial radiance values before light reduction can be found with total unlit area for each scenario in table B1). For light reduction scenarios (1) and (2), we choose not to change light intensity on areas globally lighted by private ALAN (see Appendix B2). This choice has been made to provide realistic recommendations for policy makers and city managers who only work on public ALAN. For each pixel of the NOAA satellite picture we reduced the initial radiance value proportionally to the surface within the pixel corresponding to areas where light is turned off in the scenario considered. We used paired-Student's t-test to test whether LCP's cost-distances were significantly lower with the scenarios than with predictions using non-modified light radiance data. In using presence probability to define landscape resistance driven by ALAN, we made the hypothesis that presence probability is negatively impacted by ALAN. Hence, we applied scenarios only on light non-tolerant bat species as it is unlikely that reducing ALAN would deteriorate landscape connectivity for light tolerant species.

3. Results

In 2015 we recorded 235 793 bat calls at 305 locations over 164 700 recording hours. In 2016, we recorded 40 553 bat calls at 94 locations over 50 760 recording hours. Within all the bat calls recorded, 264 667 (95.7%) were identified as *P. pipistrellus*. Because *P. pipistrellus*

was present at all sampling locations we couldn't model its presence probability depending on covariates so we did not include this species for further analysis. We registered 6971 bat calls (2.5%) identified as *Pipistrellus nathusii*, 2161 bat calls (0.8%) as *Myotis daubentonii* and 1250 bat calls (0.4%) as *Eptesicus serotinus*. From the procedure to avoid false absences (see methods), we made our analysis from 297 points for *E. serotinus*, 282 points for *M. daubentonii* and 291 for *P. nathusii*.

3.1. Most relevant variables

While the percentage of impervious surface was not identified as a variable having a significant effect on the presence probability or activity of bats (except on the activity of *M. daubentonii*), the average radiance had significant effects on the presence probability and the activity of the three species (except on the activity of *P. nathusii*). For all models, the average radiance was the second or third most important variable. Our results showed contrasting trends: the effect of the average radiance is positive on *E. serotinus* whereas it is negative on *M. daubentonii* (Fig. 3 & 4). In the case of *P. nathusii*, the average radiance had a positive effect for low values then a negative effect after a threshold radiance value of 20 W.m⁻².sr⁻¹ (Fig. 3.C & 4.C). For the three studied species, the response curves of activity and presence probability to average radiance were similar (Fig.3 & 4). Average radiance showed significant effects at scales from 100 to 700 m (Table 1). Distance to water represented the best predictor and the most important landscape factor (always significant) to explain the distribution of the three species in terms of both presence probability and activity (Table 1). We never found the same groups of selected variables between activity models and presence probability models (Table 1). The number of tree patches and the distance to vegetation had significant effects only on bats' activity and not on their presence probability. On the contrary, the percentage of water surfaces only had a significant effect on presence probability and not on activity (Table 1).

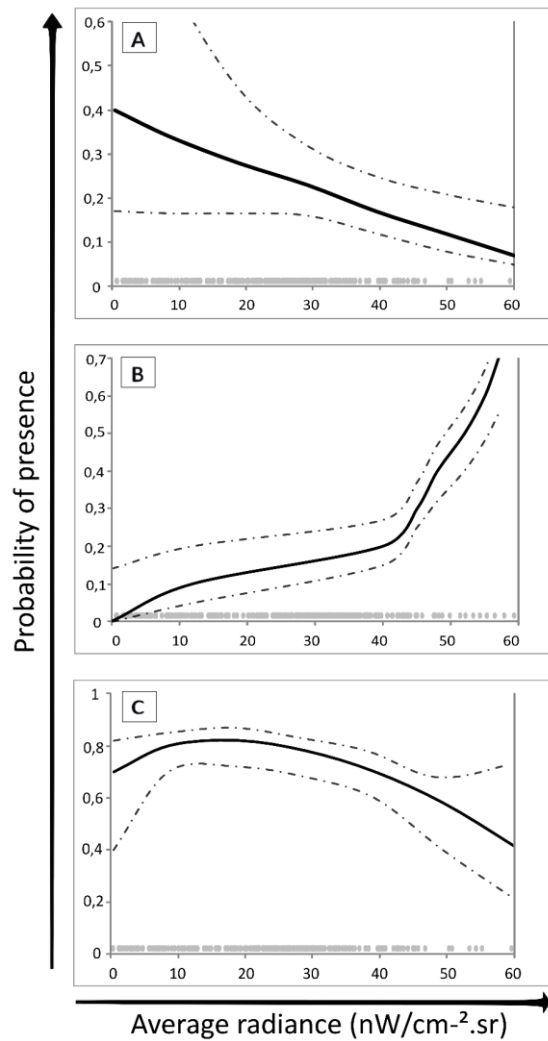


Fig. 3. Representative GAM response curves showing the probability of a species' presence at a location along the average radiance gradient. **A** is the response of *M. daubentonii* at 300m scale, **B** is the response of *E. serotinus* at 700 m scale and **C** is the response of *P. nathusii* at 100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

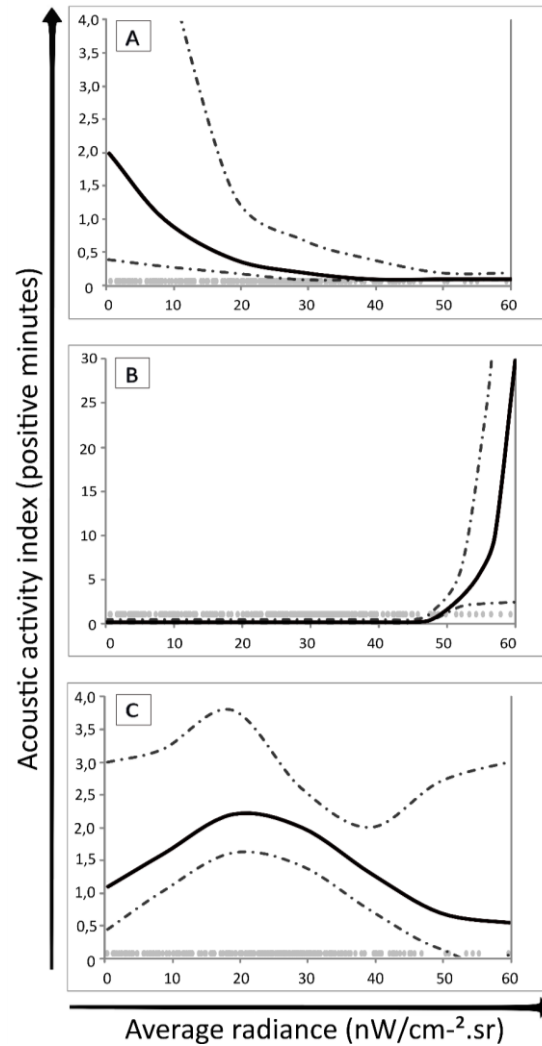


Fig. 4. Representative GAM response curves showing the predicted activity of a species at a location along the average radiance gradient. **A** is the response of *M. daubentonii* at 100 m scale, **B** is the response of *E. serotinus* at 500 m scale and **C** is the response of *P. nathusii* at 800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

Table 1. Summary of the best fit multi-scale models to predict probability of presence and activity of bats and their evaluations scores

Species	Landscape variables and spatial scales (m)					Deviance explained	AIC	AUC	COR	Sensitivity	Specificity	NRMSE		
	100	200	300	500	700								800	
	Probability of presence													
Pipnat	<i>light</i> ₃ * <i>road</i> ₄ *							<i>water</i> ₂ ** <i>distwat</i> ₁ **	24.40%	319.5	0.73 ***	0.87 ****	77.78	48.98
Epteser					<i>light</i> ₃ ** <i>distwater</i> ₁ *		<i>water</i> ₂ *	13.90%	251.1	0.72 *	0.65	20	96.43	
Myodau		<i>water</i> ₄ <i>road</i> ₅ ** <i>distwater</i> ₁ **		<i>light</i> ₃ *			<i>veget</i> ₂ *	27.30%	214.5	0.75 ***	0.68 *	25	96.15	
	Activity													
Pipnat	<i>urban</i> ₃					<i>light</i> ₄ <i>nTP</i> ₂ ***	39.30%	1348.2	0.3 **				0.22	
Epteser				<i>light</i> ₂ ***	<i>distwater</i> ₁ ***	<i>distveget</i> ₃ *	35.20%	506.8	-0.03				0.17	
Myodau	<i>light</i> ₃ ** <i>road</i> ₂ *** <i>urban</i> ₅ ** <i>distveget</i> ₄ *					<i>distwater</i> ₁ *** <i>veget</i> ₆	62%	554.7	0.5 ***				0.15	

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. The index numbers of the variables indicate the rank of importance (eg "*distwater*₂" = *distwater* is the second most important variable in the model). *Pipnat* indicates *Pipistrellus nathusii*, *Pippip* *Pipistrellus pipistrellus*, *Epteser* *Eptesicus serotinus*, *Myodau* *Myotis daubentonii*; "*Light*" indicates ALAN, "*road*": total length of roads, "*water*": proportion of water surface, "*distwater*": mean distance to water, "*veget*": proportion of tree-cover, "*urban*": proportion of impervious surface, "*nTP*": mean number of tree patches, "*distveget*": mean distance to tree patches

3.2. Model evaluation

The AUC values showed that the predictive performance of the presence probability model are at the same quality level for three studied species (Table 1). For *E. serotinus* and *M. daubentonii*, specificity values showed that absences were better predicted than presences with 96% of absences of 2016 correctly predicted by 2015's modelling being confirmed as real absences by 2016's models. In contrast, presences of *P. nathusii* were better predicted than absences (see Table 1). In terms of correlation coefficient (COR), the model for *P. nathusii* had the best predictive performance for presence probability (COR = 0.87). In comparison, the predictive performances of the activity models were poorer with COR values ranged from -0.03 to 0.5 (Table 1).

3.3. Predicted distributions

E. serotinus and *M. daubentonii* presence probabilities were concentrated on water areas. In contrast, *P. nathusii* had a more homogeneous spatial distribution (Fig. 5.1). The most urbanized and illuminated section of the major canal of the conurbation is the least suitable section for *M. daubentonii* and *P. nathusii* whereas it's the most conducive section for *E. serotinus* (Fig. 5.1). Our results also highlight that the city center is globally a barrier to bat movements although *E. serotinus* was the only species having two suitable patches predicted in the center of city which are urban parks (Fig. 5.1).

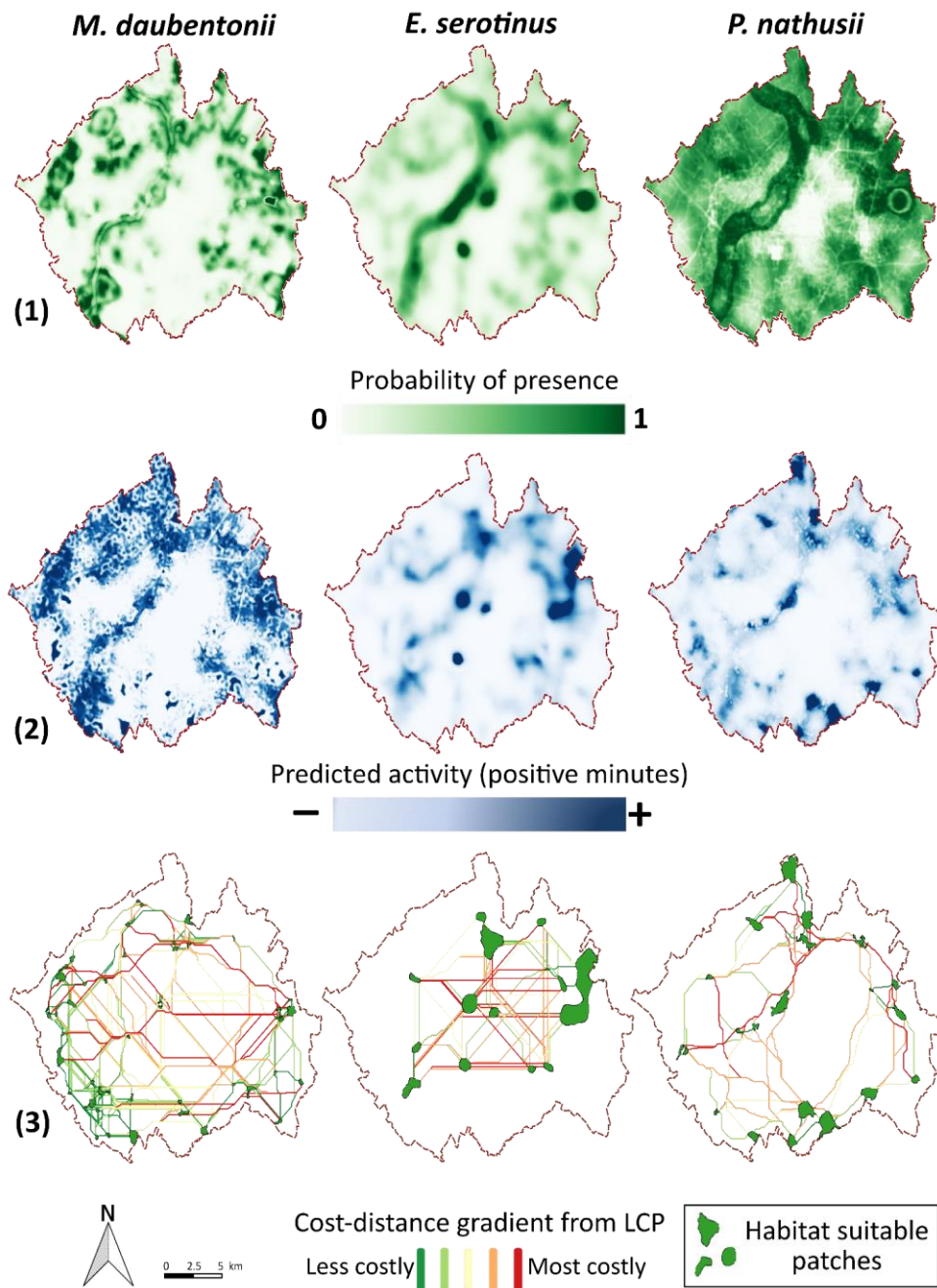


Fig. 5. Predicted distribution of probability of presence (1) and activity (2) of the three studied species. (3) represents the Least-Cost Paths identified on the study area. Activity gradient (positive minutes) has values bounded between 0 and 114 for *E. serotinus*, 0 and 326 for *P. nathusii*, 0 and 540 for *M. daubentonii*.

The activity-based modelling underlined the importance of parks for bat foraging in urban areas (Fig. 5.2). Indeed, the only habitat patches in the city center predicted as very suitable for all species were the most important urban parks of the city, located on the canal's

banks in the middle of the most illuminated section of the watercourse. *M. daubentonii*'s activity was much higher on the canals out of the city on the northern and southern sections than on the central section in the city of Lille except in the urban parks. *E. serotinus* was predicted as very active in urban parks and forest patches of the study area. *P. nathusii* had a wider distribution on the study area but was predicted as not very abundant. Its highest activity was concentrated on urban parks near the canals and on the suburban areas at confluence areas between agricultural landscapes, suburban areas and forests (Fig. 5.2). Based on the predictive activity maps and a French bat activity framework (Haquart, 2013) we identified 14 suitable habitat patches for *E. serotinus*, 47 for *M. daubentonii* and 22 for *P. nathusii* (Fig. 5.3).

3.4. LCP and light reduction scenarios

We assessed all the 91, 1081, 231 LCP connecting each pair of suitable habitat patches respectively for *E. serotinus*, *M. daubentonii* and *P. nathusii* (Fig. 5.3). We didn't apply scenarios on *E. serotinus*' LCP because of its positive response to light. For *M. daubentonii* all scenarios improved the connectivity by significantly reducing the cost-distance values of LCP (Fig. 6). For *P. nathusii* all scenarios improved the connectivity on the study area except the scenario (2) where the cost-distance values of LCP significantly increased. Scenarios ranged from more to less efficient in this order: (4)>(5)>(3)>(1)>(2) for *M. daubentonii* and (1)>(3)>(4)>(5) for *P. nathusii* (Fig. 6).

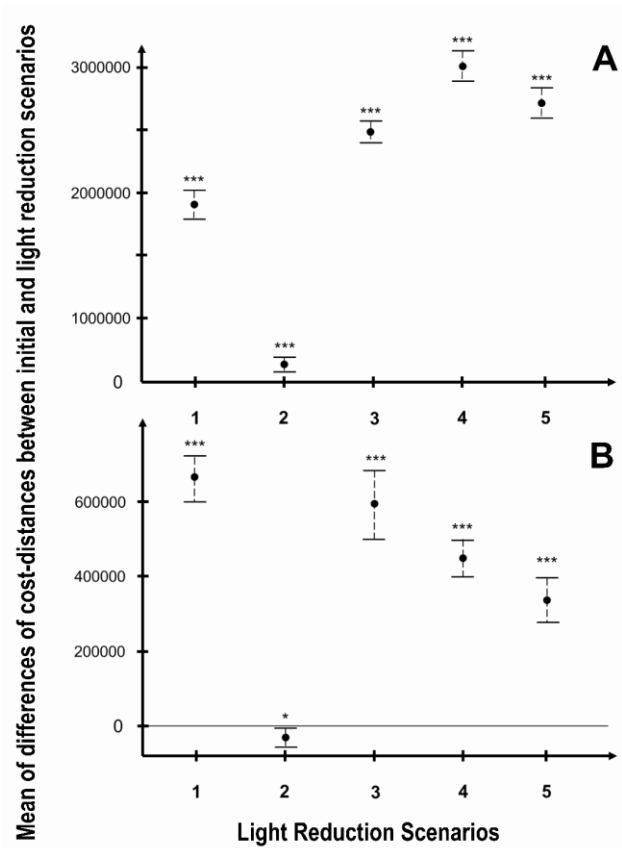


Fig. 6. Means of differences of paired cost-distances between initial LCP and LCP after each light reduction scenarios from Student's *t*-test with their 95% confidence intervals. **A:** *M. daubentonii*; **B:** *P. nathusii*. Light reduction scenarios on: (1) urban areas of municipalities of more than 10 000 inhabitants; (2) urban areas of municipalities of less than 10 000 inhabitants; (3) urban parks; (4) main roads; (5) wetlands. * = $P < 0.05$; *** = $P < 0.001$.

4. Discussion

We showed that the average radiance is an important predictor of activity and occurrence of bats even in a highly-urbanized context. Furthermore, this study demonstrated the efficiency of light reduction to improve connectivity for bats in an urban landscape. Hence it is urgent to take into account light pollution in addition to structural landscape criteria in biodiversity conservation strategies such as the restoration of ecological networks in urban planning (Azam et al., 2016; Grimm et al., 2008).

4.1. Model evaluation

While the predictions of presence probability models were relatively good, the model evaluation of activity models were not (Table 1). We think that these bad predictions are due to the fact that we measured activity very locally while activity is very sensitive to spatial and temporal variations of prey resources. Furthermore, predicting activity levels with only landscape variables is very difficult as spatial variation in the abundance of species can be driven by other factors such as the complex interaction between stochastic temporal variations in species' abundance and dispersal of species in space (Ives & Klopper, 1997). We observed a non-negligible difference between precipitation levels between 2015 (Mean rainfall/day = 1.6 mm \pm 3.1) and 2016 (Mean rainfall/day = 7.4 mm \pm 11.2) at the same sampling period (June/July) and Erickson & West (2002) found that average summer precipitation can explain the largest portion of the variance of bat activity levels. Hence it could be a factor limiting models prediction performance. Yet the weak prediction performances were not a problem because we only used activity levels to identify the most suitable habitat patches. We kept the same patches in the different light reduction scenarios so their comparison is relevant irrespective of the quality of the predictions.

4.2. ALAN: a major impact of urbanization on bats

Our results showed that the average radiance is a more important landscape parameter to model bats distribution than the proportion of impervious surface in highly urbanized area like Azam et al. (2016) found at a country scale (Table 1). Hence we confirm the predictions of some studies that predicted that the effect of ALAN on the movement of bats are expected to be much more pronounced in urban context (Hale et al., 2015, 2012; Russo & Ancillotto, 2015). Therefore we emphasize that ALAN, as a consequence of urbanization, should be taken into account in ecological corridor modeling to maintain functional connectivity of bat populations

in urban areas. Our study is the first to describe precisely the effect of ALAN on the presence probability and activity of *P. nathusii* and *M. daubentonii* (Fig. 3 & 4). The negative response of *M. daubentonii* to the average radiance is consistent with previous works which studied *Myotis spp.* group response (Stone, Jones, & Harris, 2012). Indeed *Myotis* species are light-sensitive species. As they have a slow flight, they systematically seek to avoid the potentially increased predation risk in illuminated zones (Rydell, 1991). *P. nathusii* had an intermediate response with a light tolerance threshold ($\approx 20 \text{ W.m}^2.\text{sr}^{-1}$) (Fig. 3.C & 4.C). We believe that this response pattern is driven by a trade-off between benefits of the concentration of insects at low intensities and disadvantages at high intensities from increased predation risk. *E. serotinus* had a positive response to the average radiance due to its ecological plasticity and fast flight capacity allowing them to exploit the illuminated foraging areas rich in insects (Fig. 3.B & 4.B). This positive response at scales of 500 m (activity) and 700 m (probability of presence) (table 1) is not consistent with results of Azam et al. (2016) that found that the average radiance had a negative effect on the probability of presence of this species at any considered landscape scales (200, 500, 700 or 1000 m). We hypothesize that in a highly urbanized landscape, *E. serotinus* is more light-tolerant than in a more natural landscape in a way that streetlights become sub-optimal foraging areas because there's no or few optimal foraging areas for the species in the study area (Stone, Harris, & Jones, 2015). Such contradictory results point out that the relationship between bat activity/presence and ALAN is complex as it might be species, context and scale dependent (Azam et al., 2016; Hale et al., 2012; Mathews et al., 2015).

4.3. Importance of some landscape variables on bats in urban context

Distance to water represents our best predictor of presence probability and activity. Hence bat distributions are mainly concentrated on wetlands in our study area. Aquatic habitats such as canals and ponds are known as one of the main driver and a key factor of bat activity

and distribution in urban areas (Straka et al., 2016). This fact is particularly true for *M. daubentonii* and *P. nathusii* which are species adapted to aquatic habitats and that forage on aquatic insects such as Diptera, Trichoptera and Ephemeroptera (Dietz, Encarnação, & Kalko, 2006; Krüger, Clare, Symondson, Keišs, & Pētersons, 2014). While *E. serotinus* has a more generalist diet and foraging habits, the close relationship between water areas and its distribution/activity described in our study may result from the fact that the aquatic insects are more available than terrestrial insects especially in urban area (Akasaka, Nakano, & Nakamura, 2009).

Wooded vegetation associated variables also have positive significant effects on the activity of the three studied species (Table 1). In the literature, it is widely documented that wooded vegetation such as riparian vegetation, forest patches or hedges are key habitats and have an essential ecological and functional importance for bats as commuting route between roosts and foraging habitats, landmarks for orientation, a protection against predators and wind, roosting sites and support higher density of insects densities on water areas (Bougey et al., 2011; Fonderflick et al., 2015).

The city center of our study area is globally an avoided area by our studied species which is consistent with previous studies (Gaisler, Zukal, Rehak, & Homolka, 1998; Russo & Ancillotto, 2015). Indeed dense urbanization inevitably reduces favorable habitats and wooded vegetation that impacts the richness and abundance of bats community (Hale et al., 2012). *P. nathusii* activity is higher in suburban areas than in the city center which is also congruent with some previous studies (Coleman & Barclay, 2012; Luck, Smallbone, Threlfall, & Law, 2013). This result might be explained by the intermediate disturbance hypothesis (Connell, 2013). Hence the suburban conditions, halfway along a gradient from natural to urban habitat, would produce “optimal” intermediate levels of disturbance intensity and frequency for a large number of species such as *P. nathusii* (Russo & Ancillotto, 2015). *E. serotinus* is considered to be one

of the most urban-tolerant species in Europe (Arthur & Lemaire, 2009) which is congruent with the fact that is the only species of this study having two suitable habitat patches in the city center (except banks of watercourse) (Fig. 5).

We found that groups of variables with significant effects on bats differs between probability of presence and activity (table 1). This result suggests different functional and ecological relationships between the landscape with movement and foraging behavior of bats and confirm the relevant of our methodology.

4.4. Light reduction scenarios improve urban landscape connectivity

The efficiency of light reduction scenarios in improving landscape connectivity for each species depended on (1) the spatial distribution of unlit areas (i.e. where we apply light reduction, Fig. B1), (2) the initial values of radiance on those areas before light reduction (Table B1), (3) the response curves of species presence probability to the average radiance (Fig.3) and (4) the predicted spatial distribution of bat species depending on their response to landscape variables (Fig. 5).

The predicted spatial distribution of *P. nathusii* is the widest (Fig. 5). Hence the strength of light reduction scenarios effects is less depending on spatial distribution of unlighted areas than on the initial values of radiance and on the response curves of the species to average radiance (Fig. 3). Indeed, the higher the initial radiance value landscape element and the stronger is the effect of light reduction scenario on this element in improving landscape connectivity for this species (Fig. 6 and table B1). The four scenarios improving significantly landscape connectivity for *P. nathusii* have initial radiance in the range of values where the species response is negative (Fig. 3). It is consistent that reducing ALAN in those areas will improve landscape connectivity. It is also consistent that reducing ALAN on municipalities of

less than 10 000 inhabitants will decrease landscape connectivity because initial mean radiance values on those areas is $10.2 \text{ W}\cdot\text{m}^{-2}\cdot\text{sr}^{-1}$, which is in the range of values where *P. nathusii* responded positively to radiance (Fig.3, Table B1). It is congruent that every scenarios improve significantly landscape connectivity for *M. daubentonii* because of its general negative response to radiance (Fig. 6). *M. daubentonii* is a specialist gleaner bat species mostly present in wetlands and flying at low altitude also depending on vegetation to commute. Hence light reduction scenarios on urban areas (scenario 1 & 2) are the least effective to improve connectivity for *M. daubentonii* because those areas are not used by this species. Reducing ALAN in urban parks and wetlands were respectively the third and second most effective scenarios to improve connectivity for this species. Surprisingly light reduction on main roads was the most effective scenario to increase landscape connectivity for *M. daubentonii*. We argue that this result is mostly due to the spatial distribution of main roads in our study area (Fig. B1). Main roads are crossing or are close to wetlands (ponds and canals) and urban parks. Reducing ALAN on main roads potentially improved the quality of wetlands and urban parks habitats to a greater extent than light reduction separately on either just wetlands or just urban parks. But this result seems to be very context dependent and should be tested in other cities.

Light reduction scenarios are powerful tool to assess the efficiency of potential future urban landscape planning and to guide political decision. Artificial light planning should be driven by a trade-off between biodiversity conservation measures and social/political acceptability (esthetic, security, outdoor activities). For instance, light reduction measures should be easier to accept by policies and inhabitants on small areas of wetlands than on large areas in city centers. Our findings showed that light reduction scenarios on largest concerned areas are not necessary the most efficient to improve connectivity for bats and that the best landscape element to apply light reduction are not always the same depending on the given species. Hence, further analysis should urgently use light reduction/extinction scenarios to

clarify what is the best factors combination between the total surface area, the spatial distribution (few large areas or many small areas), the prioritize habitats and the intensity of reduction to optimize the efficiency of conservation measure and the social/political acceptability in urban landscapes.

4.5. Methodological perspectives

To our knowledge, this study is the first to carry out such a random stratified design with 399 full-nights recordings points in a highly-urbanized context. We advocate for the use of this methodology for future studies aiming at identifying landscape corridors. It is important to remind that our data are not movement data per se. Yet as we recorded individuals in movement we assumed that LCP modelling approach remained relevant for our case. Our results, though, would benefit from confrontation with movement data through radio-telemetry or miniaturized global positioning system (GPS) tags (LaPoint et al., 2015; Stevenson-Holt et al., 2014), recently adapted for micro-chiropteran species (Weller et al., 2016).

We have modeled the functional connectivity of bats between the most important foraging sites (in regard to activity levels). Functional connectivity between foraging sites is relevant for conservation issues because it is well-known that bats use several foraging sites per night (Arthur & Lemaire, 2009; Dietz et al., 2009). Nonetheless, it would be very important, in the cities where the knowledge of roost locations is sufficient, to use our methodology to model the connectivity between roosts and foraging areas, this latter being critical to ensuring the survival of populations (Fischer & Lindenmayer, 2007).

5. Conclusion

This study showed that ALAN has preponderant impact on some bats species in an urban landscape. Our findings provide important recommendations to plan future urban conservation strategies: light-reduction improve landscape connectivity for bats in a highly urbanized landscape from semi-natural habitats such as urban parks or wetlands to city centers. The efficiency of each scenario varied between species and seems to depend on the ecological plasticity and requirements of each species. Furthermore light reduction would not be totally efficient without the presence of important landscape elements for bats such as wetlands and wooded vegetation, no matter the surface area or the initial light pollution intensity. Because studied species responded significantly to ALAN at different scales and at least at 700 m, we highlight the great importance to build large nocturnal corridors in order to optimize the efficiency of light reductions.

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ARTICLE 3

APPENDICES

Appendix A. Method details

A.1. Multi-scaled landscape variables and statistical analysis

For statistical analysis, we created eight gridded landscape variables at a 50 m resolution (Bellamy, Scott, & Altringham, 2013): the proportion of impervious surface and the total length of roads, considered as potential confounding factor of the average radiance (Azam et al., 2016), the average radiance, the proportion of tree-cover, the proportion of water surface, the mean number of tree patches, the mean distance of the cell centroid to water and the mean distance of the cell centroid to tree patches as they were known to influence bat activity and bat movements at a landscape scale (Boughey et al., 2011; Fonderflick et al., 2015; Frey-Ehrenbold et al., 2013). Hale et al. (2012) found that the influence of a variable on the presence probability or activity of bats may vary according to the considered spatial scale and that the most influential scale differs between species. Furthermore multi-scale habitat models often yield better predictions than single-scale models (Grand, Buonaccorsi, Cushman, Griffin, & Neel, 2004). Each variable has thus been calculated for 10 different buffers (100, 200, 300, 400, 500, 600, 700, 800, 900 and 1000 m) by measuring cell statistics within different sizes of moving windows centered on each raster cell. For each variable/species pairs we selected the most relevant scale by first fitting 10 univariate models for the 10 different scales (Bellamy et al., 2013) using the AIC criteria (*Akaike Information Criterion*) (Akaike, 1974). Then we regrouped all the scaled-landscape variables in a full model for each species and we used a backward leave-one-out stepwise procedure of variables deletion to identify the most performing subsets of scaled-landscape variables and select the best model for each species (Parolo, Rossi, & Ferrarini, 2008). In order to avoid multicollinearity in the models, we evaluated the correlations among our selected scaled-landscape variables using Pearson's coefficient to detect obvious correlation (Zuur et al., 2009). Only scaled-landscape variables with correlation coefficients between -0.70 and 0.70 were included simultaneously in the models (Dormann et al., 2013). Secondly, we computed the Variance Inflation Factor (VIF) on the full sets of variables selected

for each models (Fox & Monette, 1992); all variables had $VIF < 5$, indicating no obvious problem of multicollinearity between the variables of our models. We tested for spatial autocorrelation on models residuals using Moran's I with 20 lags of 1 km. We found few significant spatial autocorrelations between 1 and 3 km, and those with significant values corresponded to low levels (Moran's $I < 0.17$) hence we considered we didn't have to take into account for spatial autocorrelation.

A.2. Method details for model performance evaluation

Models were trained with all data collected in 2015 and models performance evaluations were based on data from an independent field sampling. In 2016, we build another random stratified sampling in the exact same way as in 2015. Along the gradients of the three same landscape variables, we sampled 94 new recording points in the study area at the same period than 2015. All the 2016's recording locations were at least at 200 m away from recording locations sampled in 2015. We assessed the performance of presence/absence models by using: (1) the area under the receiver operating characteristic curve (AUC) (Leathwick, Elith, & Hastie, 2006; Lobo, Jiménez-valverde, & Real, 2008); (2) the specificity and (3) sensibility (Thuiller, Lafourcade, & Araujo, 2010). We assessed the predictive performance of our activity models by using the Root Mean Square Error (RMSE). In order to compare performance between different models, the RMSE was normalized by dividing the RMSE by the difference between the maximum predicted value and the minimum value (NRMSE) (Loague & Green, 1991). The greater the percentage of NRMSE, the less the model from 2015 is efficient into predicting the activity of 2016. We also used the Pearson correlation coefficient (COR) between the predictions of 2015 and observations of 2016 (Elith et al., 2006) as another index to evaluate our presence/absence and activity models performance. For presence/absence models evaluation, we classified the predicted values in 10 classes in which we calculated the number of actual presences observed weighted by the number of sampled cells in each prediction class, i.e. we calculated the COR between the prediction classes and the percentage of actual presences. The contribution of each landscape variable to the model predictions was assessed using the method described in Thuiller et al. (2010).

Appendix B. Light-reduction scenarios details

Light reduction scenarios on areas:

- Wetlands
- Main roads
- Urban parks and woodlands
- City center of municipalities of less than 10000 inhabitants
- City center of municipalities of more than 10000 inhabitants

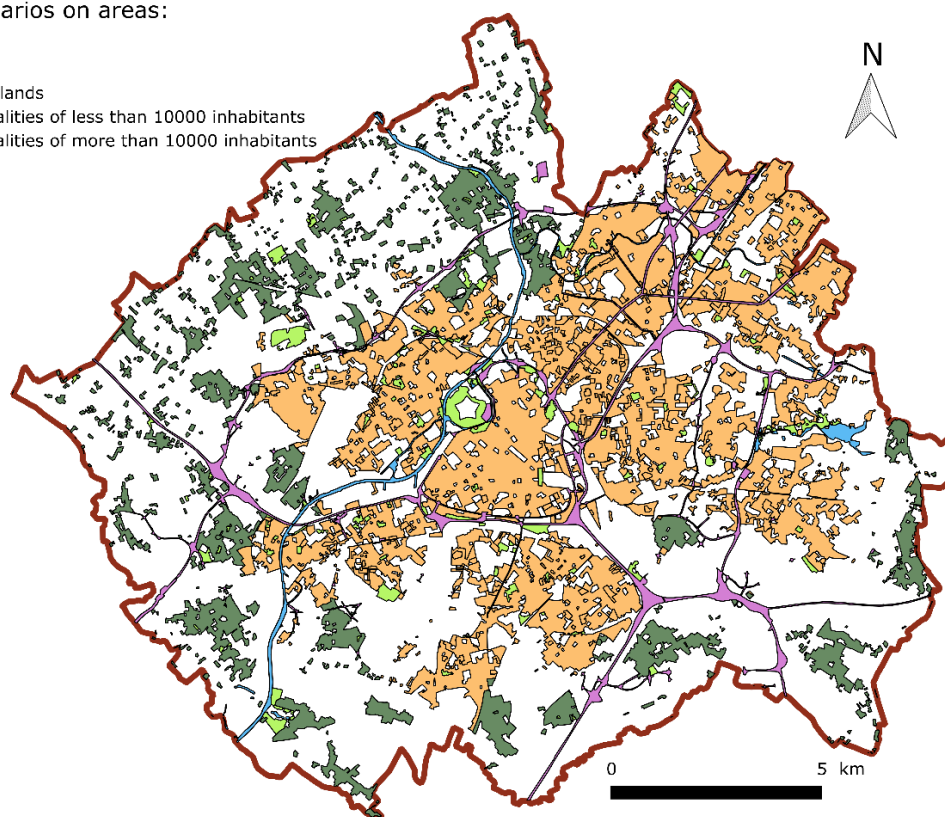


Fig. B1: Spatial distribution of unlit areas

Table B1: Information on areas where light reduction has been applied: (1) urban areas of municipalities of more than 10 000 inhabitants; (2) on urban areas of municipalities of less than 10 000 inhabitants; (3) on urban parks; (4) on main roads; (5) on wetlands.

	(1)	(2)	(3)	(4)	(5)
Radiance mean ($nW/cm^2 \cdot sr$)	28.6	10.2	27.6	24	18.6
SD	9.8	7.2	9.4	9.3	11.6
Surface area (ha)	8439	4087	468	4775	969

B2: List of private lighting areas not included in the light reduction scenarios.

Airports, aerodromes, Other public rights-of-way, Main railway axes and associated areas, Campsites, Quarries, Construction sites, Cemeteries, Landfills and depots, Commercial rights-of-way, Hospital facilities, Industrial rights-of-way, School and/or university rights-of-way, Golf courses, Harbour infrastructures, Working-class gardens, Stadiums, sports facilities

ARTICLE 4

FLYING THROUGH THE CITY: NEW LIGHTING TECHNOLOGIES ALTER LANDSCAPE CONNECTIVITY FOR BATS IN URBAN AREAS

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1. Introduction

Urban areas are expanding worldwide (Zhang & Seto, 2011) and threaten biodiversity through profound transformations of habitats and landscapes (Foley, 2005; McDonald, Kareiva, & Forman, 2008). Although urbanization is often studied as a process impacting surrounding ecosystems, it can also be considered as a particular type of ecosystem itself (Savard, Clergeau, & Mennechez, 2000) and which biodiversity is valuable and should be protected (Kowarik, 2011). Urban landscapes are often composed of few patches of vegetation and aquatic environments embedded in a matrix of impervious hence representing highly fragmented landscapes (Savard, Clergeau, & Mennechez, 2000). Landscape fragmentation reduces individuals' ability to move between habitats and is considered to be a key driver of global species loss (Fischer & Lindenmayer, 2007). Indeed, being able to move across the landscape is essential to fulfill daily needs (food, shelter) and dispersion to maintain populations' viability (demo-genetics process). Urbanization is accompanied by the emission of environmental stressors such as artificial light which can alter habitat quality and species movement (e.g., Stone, Jones, & Harris, 2009). Indeed, a large variety of behavioral and physiological impacts of light on species have been documented and artificial lighting is considered as a major biodiversity threat (Hölker, Wolter, et al., 2010; Davies & Smyth, 2017). Light may affect organisms' orientation through attraction (e.g., Eisenbeis, 2006), avoidance (e.g., Gal, Loew, Rudstam, & Mohammadian, 1999) or barrier effect (e.g., Hale, Fairbrass, Matthews, Davies, & Sadler, 2015). Thus in urban areas artificial light could have a cumulative effect to soil sealing and worsen landscape fragmentation in already highly fragmented areas.

Light pollution is expected keep on increasing in the future due to global increase in artificial light at night (ALAN) emissions (Hölker, Moss, et al., 2010) and to change in lighting technologies (Kyba, 2018). Indeed, there is a rapid development of new lamps such as light

emitting diodes (LED) that have a high energy-efficiency. Worryingly, this desirable attribute in a context of energy transition toward less CO₂ emissions makes LEDs cheaper than other lamps which could lead to an increase use of light (Tsao et al., 2010). Moreover, LEDs have a broad spectrum thus producing a “white” light that allows for better visual rendering for users. This means that they emit a higher proportion of short wavelengths (blue part of the spectrum) than older technologies such as low (LPS) and high (HPS) pressure sodium lamps (Falchi et al., 2011). Short wavelengths increase insects attraction to light (Pawson & Bader, 2014; Gaydecki, 2018) and can modify species orientation and movements across the landscape (E. L. Stone, Jones, & Harris, 2012; Van Grunsven et al., 2017). However LEDs have more directional flux and are generally implemented in fixture that better concentrate light toward the area to illuminate hence reducing the unintentional lighting of surroundings and the direct emission of light above the horizon. It is currently unclear how large scale changes in lighting technology will affect organisms and their ability to move in the landscape.

Since 2013, preserving and restoring landscape connectivity has been defined as an important goal to conserve biodiversity in the EU. The green infrastructure policy promotes the determination and improvement of ecological corridors. Landscape connectivity is the degree to which the landscape facilitates or impedes organisms movement between resource patches (Taylor et al., 1993). Corridor networks are helpful conservation tools to mitigate the impacts of landscape fragmentation on wildlife populations (Beier & Noss, 1998) and several modeling approaches have been developed and extensively used to design such linkages (Beier, Majka, & Spencer, 2008). However corridors are often designed simply following the structural elements of the landscape such as wooded without accounting for ecological processes which may greatly limit their potential for conserving biodiversity (Chetkiewicz, St. Clair, & Boyce, 2006). Measuring landscape functional connectivity requires to account for species-specific information on how individuals respond to landscape elements and the global spatial

configuration of the landscape (Kindlmann & Burel, 2008). The evaluation of the landscape permeability may be evaluated using expert opinion or literature reviews, data on occurrence or abundance or animal-movement data (genetic distance, GPS tracking). These data will be used to attribute different values to landscape elements or environment contexts. As ALAN affects nocturnal species perception of the landscape and modifies their movement behavior compared to what would be expected when only considering structural elements, accounting for artificial lighting is a key factor to consider when evaluating landscape connectivity for nocturnal species.

Despite (i) the important progression of artificial light emissions worldwide (Hölker, Moss, et al., 2010), (ii) the fact that a significant proportion of species are nocturnal (Hölker, Wolter, et al., 2010), and (iii) the development of policies promoting ecological corridors, to our knowledge, the direct impact of ALAN on landscape connectivity has never been studied (but see Hale et al., 2015). This may be due to both the difficulty to study organisms living by night (data accessibility) and to access data relative to artificial light. One of the major issue to measure landscape functional connectivity is to acquire biological data relating individuals' habitats preference when they are moving through the landscape (Chetkiewicz, St. Clair, & Boyce, 2006) and particularly when considering small and cryptic species. A review showed that only 13 studies evaluated landscape connectivity for small mammals (<1 kg) in urban landscapes within which four focus on bats (LaPoint et al., 2015). Indeed bats are a good model species to investigate landscape connectivity as they emit ultrasounds while flying thus measuring bat activity through recordings of bat calls allows to determine their habitat preferences when in movement. Another difficulty specific to the evaluation of landscape connectivity for nocturnal species is to access environmental data reflecting the distribution of artificial light in the landscape. Previous studies have used proxies such as roads (Hale et al., 2012) or locally available fine scale data such as nocturnal aerial pictures (Hale et al., 2015).

Recently, fine scale nocturnal pictures taken from the International Space Station (ISS) have come to be more accessible through the citizen science program Cities at Night (<http://citiesatnight.org/>). The calibration of these pictures allows to measure the radiance emitted upward at a resolution up to one meter. Moreover, pictures are composed of four color bands (one blue, one red and two green) which allows to have information on the spectral distribution of the emissions.

In this study we used ISS pictures taken at night to evaluate the landscape connectivity in cities for bats daily movements (e.g., foraging movements). The flight behavior of several bat species can be affected by ALAN (Polak et al., 2011) as some may avoid brightly lit areas (Kuijper, Schut, & Dulleman, 2008; E. L. Stone, Jones, & Harris, 2009) or perceive light as a barrier and hence turn back when encountering lit areas (E. L. Stone, Jones, & Harris, 2009; Hale et al., 2015). Some bat species are still present in large cities as they depend on man-made structures for roosting (Simon, Hüttenbügel, & Smit-Viergutz, 2004; Marnell & Presetnik, 2010) and hence present a rare case of species vulnerable and strictly protected at the European level living within urban environments (European Commission, 1992). Studies showed that bat activity is sensitive to landscape connectivity (Hale et al., 2012; Frey-Ehrenbold et al., 2013) and that a global increase in artificial light could reduce the proportion of accessible area in the landscape (Hale et al., 2015). As it is impossible to exhaustively locate all bat roosts and foraging areas, our work aims at predicting the landscape functional connectivity for bats daily movements between potential habitat patches.

In this study, we investigated how artificial light impacted the functional landscape connectivity for the daily movements of *P. pipistrellus* in urban areas and how changes in lighting could affect it. In addition, as the spatial arrangement of land cover types and the distribution of light may play an important role in the global landscape connectivity, we investigated ALAN's impacts in three study areas. Our aims were (i) to measure the

contribution of ALAN to the landscape fragmentation, (ii) to evaluate how much landscape connectivity would be affected by a change in lighting technology toward the generalized use of LEDs and (iii) to determine if light pollution and its potential evolution would affect different cities in the same way. To achieve these goals we evaluate the activity of *P. pipistrellus* in three large cities of France while including information on artificial light derived from ISS pictures. We compared the connectivity in the current state of lighting to three lighting scenarios. In one scenario, we considered cities with no light at all to measure the impact of the current lighting on the landscape connectivity. The two other scenarios reflected the shift of lighting toward the use of LEDs, the number of lighting points remaining unchanged, with one of them accounting for the potential of more directional flux to reduce global light emissions (Aubé et al., 2018). We predicted that, due to LEDs important proportion of blue wavelength, the change in lighting technology would have a negative impact on bat connectivity but that a better orientation of the light flux may help reduce this negative impact.

2. Methods

We studied three cities where we recorded bat activity and for which we calculated environmental data in order to build a model to predict bat activity (Fig. 1). Then we transformed the maps predicting bat activity to produce resistance maps and constructed landscape graphs for each city to represent landscape connectivity. Finally, we created three lighting scenarios and evaluated the changes in landscape connectivity for each of them in comparison to the current situation.

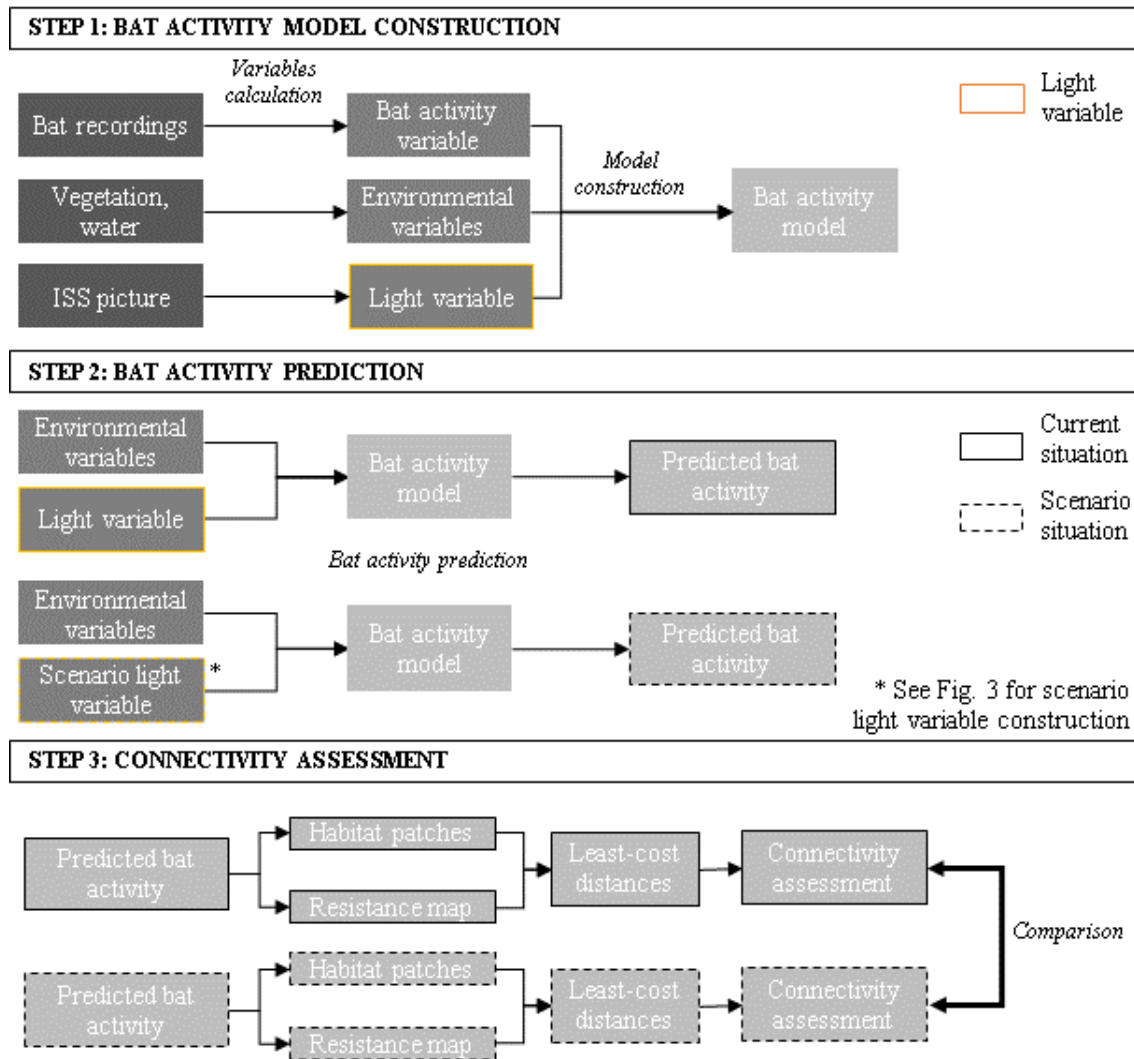


Fig. 1. Flow diagram representing the steps of the methodology

2.1. Study sites

We used three French cities as study sites, Paris, Lille, and Montpellier. They are amongst the 10 most populated cities of France and suffer high levels of light pollution. Light levels are 20 to 40 times higher than natural light levels in Lille and Montpellier and over 40 times higher in Paris (Falchi et al., 2016). Tree cover represents 21% of the surface in Paris and Montpellier and 14% of the surface in Lille. The three cities present a diversity in green areas distribution and sizes (Fig. 2). Paris, the largest of the three cities (105 km²), has 17 parks (mean size 0.13 km²) in its center and two woodlands on its border (10 and 8.5 km²); Lille only has a

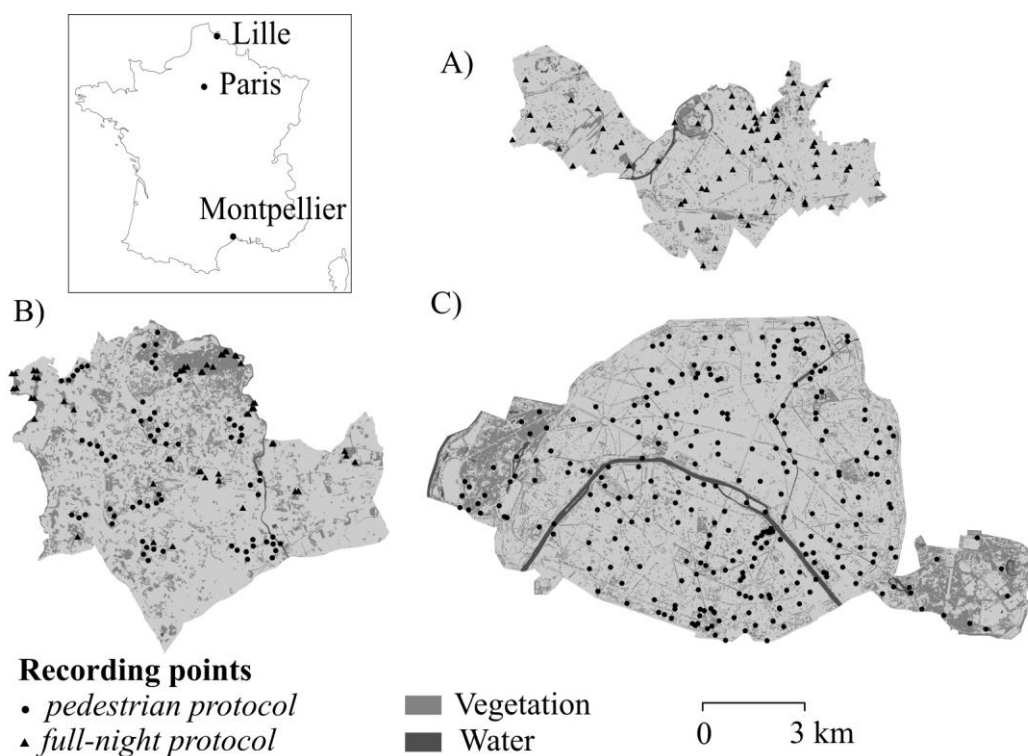


Fig. 2 Study sites: Lille (A), Paris (B), and Montpellier (C). Triangles represent locations of full-night recordings and dots represent locations of pedestrian recordings.

dozen parks (mean size 0.15 km²); and Montpellier has a large number of parks of various sizes spread across the city, the largest one being 1 km². The three cities were crossed by canalized rivers of differing width and with varying degrees of vegetation on their riversides.

2.2. Bat activity data

Data for Paris and Montpellier were provided by the French national bat-monitoring program Vigie-Chiro (<http://vigienature.mnhn.fr/page/vigie-chiro>). Recordings took place between June and October, the seasonal peak in bat activity, when the weather conditions were favorable (i.e. no rain, wind speed below 7 m/s, temperature at sunset above 12°C). Two protocols were used: the pedestrian protocol and the full-night protocol. For the pedestrian protocol, volunteers recorded bat activity for 6 minutes at 10 selected locations within a 4 km²

area starting the sampling 30 minutes after sunset. In Montpellier, volunteers used Song Meter SM2BAT detectors (Wildlife Acoustics Inc) and in Paris they used time expansion detectors (Tranquility Transect Bat detector, Courtpan Design Ltd, UK). For the second protocol, volunteers placed a SM2BAT detector at a selected location and recorded bats from 30 minutes after sunset until 30 minutes after sunrise. In Paris, 923 recordings at 282 different locations were taken following the pedestrian protocol between 2008 and 2013 (Fig 2. B). In Montpellier, 71 locations were sampled using the pedestrian protocol and 82 locations using the full-night protocol between 2011 and 2012 (Fig 2. C). For Lille, recordings were taken in 2015 by authors at 73 locations following the full-night protocol (Fig 2. A).

For recordings taken in Paris and Montpellier, all bat calls were identified by volunteers and then validated by expert using Syrinx version 2.6 (Burt, 2006). Data from Lille were run through the software SonoChiro (Bas et al., 2013) to automatically classify echolocation calls to the most accurate taxonomic level. Ambiguous calls were checked manually using Syrinx. We measured bat activity as the number of bat passes per 6 minutes. A bat pass was defined as the occurrence of one or several calls of the same bat species during a 5 second interval (Millon et al., 2015). We only had sufficient data in the three cities for *Pipistrellus pipistrellus* hence we only performed the analysis on this species. *P. pipistrellus* is often present in urban areas (Russo & Ancillotto, 2015) and is one of the most common species in France although its population tends to decline (Kerbiriou et al., 2015). In order to use data from both sampling protocol together, we split the full-night recordings in 6 minutes sequences and only kept sequences recorded during the first two hours of the night. Then we calculated the mean activity per point to avoid pseudo-replication.

Here, we studied echolocation calls emitted by bats when they are commuting and/or foraging but not feeding buzzes because their occurrence is too low (~1%). We did not distinguish between foraging and commuting behaviors as they are not fully disconnected (bats

often forage while commuting) but we considered that a high bat activity in a recording area likely reflects a high proportion of foraging behavior.

2.3.Light variables

To account for artificial light emissions, we used nighttime ISS pictures from the Cities at Night program (citiesatnight.org). We used one picture by city taken on a cloudless night. The images were corrected for linearity of the sensor, vignetting, and calibrated absolutely using reference stars on other lenses and relatively to the VIIRS image of May 2014 using synthetic photometry (Sánchez De Miguel, 2016). There was no atmospheric correction. The value of each pixel corresponded to the radiance which is the radiant flux reflected or emitted by a given surface (units $nW.cm^{-2}.sr^{-1}.A^{-1}$). For each of the four color bands of ISS pictures, we calculated two variables using QGIS 2.8.3 (QGIS Development Team, 2017): the mean radiance value within 100 m and within 200 m of the recording point (Table 1). Hence in total there were eight different light variables calculated using the same 60 m x 60 m grid. Four recording locations had a very high radiance value due to a singular context (e.g., Eiffel tower illuminations). We considered them as outliers and removed the recordings taken at these locations from the dataset ($n = 12$; 1% of the total dataset).

2.4.Environmental variables

Bat activity is positively correlated with the proximity of water (Rainho & Palmeirim, 2011) and with the extent and the distance to wooded areas (Boughey et al., 2011). We accounted for these effects by calculating three variables using BD TOPO data (<http://www.ign.fr/>): the distance to water in meters, the distance to tree cover in meters and the proportion of tree cover within 200 meter around each sampling point (Table 1). We also

controlled for recording conditions (city, protocol, temperature in °C, wind speed in m.s-1 and humidity in %) and date (year, Julian day).

Table 1. List of all the variables used in the models. Each light variables were used in a separate full model and all environmental variables were included in all full models. Light variables are defined for each color band of the ISS picture, the red (Red 1), the two green (Green 2 and Green 3), and the blue (Blue 4).

Variables name	Description and units
LIGHT VARIABLES	
Red 1 - 100 ; Green 2 - 100 ; Green 3 - 100 ; Blue 4 - 100	Mean pixel value in a 100 m radius (units: nW/cm2/sr/A)
Red 1 - 200 ; Green 2 - 200 ; Green 3 - 200 ; Blue 4 - 200	Mean pixel value in a 200 m radius (units: nW/cm2/sr/A)
ENVIRONMENTAL VARIABLES	
Dist. to water	Distance to the closest water surface (units: m)
Dist. to tree cover	Distance to the closest tree cover (units: m)
Prop. of tree cover	Proportion of tree cover within 200 m (units: %)
Temperature	Temperature at sunset (units: °C)
Humidity	Humidity at sunset (units: %)
Wind speed	Wind speed at sunset (units: km/h)
Year	Year of recording
Julian Day	Julian day of recording
City	City where the recording took place
Recording point	Identification of the recording point
Protocol	Recording protocol: fullnight or pedestrian protocol

2.5. Bat activity modeling

We built a statistical model to explain bat activity with the environmental variables defined earlier. As the eight light variables were correlated with one another, we built one full-model for each of the eight light variables and proceed to a model selection based on the AIC to evaluate which variable performed best. We aggregated the data from the three cities to a single dataset to analyze to produce a single general model with good statistical power. All the variables used within the same model had a VIF value below three (Heiberger & Holland, 2004) and the mean VIF for variables within a model was below two (Chatterjee & Bose, 2000) hence there was no obvious sign of multicollinearity. We built Generalized Linear Mixed Models

(GLMM ; glmmTMB 0.2.0 ; Brooks et al., 2017) using bat activity as the response variable and one light variable and all other variables as fixed effects. We also included an interaction between the proportion of tree cover and the light variable as a study showed that the response to light of *P. pipistrellus* could vary depending on the proportion of tree cover (Mathews et al., 2015). As the response variable were count data with over-dispersion, we used a negative binomial error distribution with a log link (Zuur et al., 2009). Some recording points were replicated hence we included a random effect on the recording location. We kept the city variable as a fixed effect in order to account for the difference in mean activity per city in the bat activity predictive maps. The full model could be written as follow:

$$\text{bat activity} \sim \text{light variable} * \text{proportion of tree cover} + \text{distance to water} + \text{distance to tree cover} + \text{city} + \text{protocol} + \text{temperature} + \text{humidity} + \text{wind speed} + \text{year} + \text{Julian day} + (\text{Julian day})^2 + \text{random}(\text{recording location})$$

where the light variable was one of the variables based on the ISS picture. For each of the eight full-models, we tested all possible combinations of fixed effects using the MuMIn package (Barton, 2013) in R (R Core Team, 2017) and selected the best model using Akaike's Information Criterion (AIC ; Burnham & Anderson, 2002). As the AIC tends to keep variables that do not improve the fit (Guthery et al., 2005), we selected the simplest model amongst those that had an AIC maximum two points higher than the best model. At the end of the selection process, we had eight best models, one for each light variables tested. We compared these eight models using the AIC and used the best one (lowest AIC) to produce predictive maps of bat activity. To limit border effects, we estimated bat activity for each pixel (60 m x 60 m) of the three study areas surrounded by a rectangle buffer which limit was at least 400 m away from the city border (henceforth, extended study area). All explanatory variables linked to the specific conditions of recording (e.g., date, wind speed) were fixed to their mean value while vegetation, water and light variables varied across the landscape.

2.6. Construction of landscape graphs

We used a landscape graph approach to investigate the landscape connectivity (Minor & Urban, 2008). We defined the landscape resistance and the patches of habitats using the bat activity predictions from the best model (lowest AIC). We assumed that our data mostly reflected foraging movements and that the level of activity reflected the habitat quality in terms of food resource. We defined habitat patches as the areas of the map where the activity was the highest (values above the 90th percentile). Indeed, we expected areas of high activity to be the best foraging areas. We defined a different level for high activity for each city as they did not have the same baseline activity. In addition, we only kept habitat patches of at least 1 ha to limit the number of patches and hence the computing time. Moreover foraging areas are expected to be larger than the minimum patch size by at least an order of magnitude (E. Stone et al., 2015) hence bats would have to travel between patches.

Because we recorded bats while flying (foraging and/or commuting), we made the assumption that bat activity was positively correlated with habitat permeability and thus a high level of bat activity indicated a landscape easy to travel through. Therefore we defined the resistance as the additive inverse of the activity (Zeller, McGarigal, & Whiteley, 2012). Resistance in each pixel was calculated as follow:

$$R_{px} = P_{max} - P_{px} + 1$$

where R_{px} is the resistance of the pixel, P_{max} is the maximum bat activity predicted in the study area and P_{px} the bat activity predicted for the pixel.

Using these resistance maps, we measured the connectivity between habitat patches using least cost distances calculated with the Linkage Mapper Toolkit v.1.0.9 (McRae & Kavanagh, 2011) in ArcGIS v.10.2.2 (ESRI, 2013). Least-cost distances are defined as the maximum efficiency paths to travel from one patch to another, i.e. the path that accumulates

the least cost in term of distance travelled and landscape resistance traversed (Etherington & Penelope Holland, 2013). This methodology main hypothesis is that individuals have a perfect knowledge of the entire landscape and will chose to travel along the optimal route (Coulon et al., 2015). Bats are long-lived territorial animals which tend to be faithful to their transit routes and foraging areas (Hillen, Kiefer, & Veith, 2009) thus being familiar with the surrounding landscape beyond their direct perception range hence we believe that the least-cost distance method is adapted to this species. Least cost distance were only calculated for a node and its direct neighbors in terms of resistance and distance as paths between more distant nodes passed through nodes that were in between.

2.7.Lighting scenarios

We constructed landscape graphs for the current situation and for three lighting scenarios produced by altering the ISS pictures. In two scenarios all lights sources were replaced by 3000K LEDs which is an increasingly used LED type for street lighting (Kinzey et al., 2017). The first scenario had the same radiance level as the current situation but a change in spectral emissions reflecting the spectrum of 3000K LEDs (LED scenario). The second scenario had the same change of spectrum but also a decrease of 30% in pixel radiance (LED-30 scenario). We created the two LED scenarios by modifying the original ISS picture using the relationships existing between color bands ratios and lamp types (Fig. 3 ;Sánchez De Miguel et al., submitted). For each study area, the current radiance level was considered to be given by the mean of the two green color bands. The 30% decrease in overall radiance in the LED-30 scenario was thus reflected in a 30% decrease in the mean green bands pixel values. Once the overall radiance was calculated, a modified blue color band was created to reflect changes in the spectral composition of light emissions. To mimic the spectrum of 3000K LEDs, we chose a Blue/Green ratio of 0.4 (see Fig. 2 and 10 in Sánchez De Miguel et al., submitted). In the

original ISS picture, the Blue/Green ratio is 0.38 in Paris, 0.36 in Lille and 0.30 in Montpellier. In both scenarios the spectrum and radiance were build considering that the number of light sources remained the same, i.e. spectrum and radiance were modified only within pixel which exhibit light in the current ISS picture. We also used a third scenario with no light at all (No Light scenario) to compare with the current situation and measure how much connectivity is lost due to lighting. Considering the extended study areas, 42% of Montpellier area, 29% of Lille area and 15% of Paris area were dark (pixel value $< 0.001 \text{ nW.cm}^{-2}\text{.sr}^{-1}\text{.A}^{-1}$) in the original ISS picture and thus remained so in all scenarios.

As we considered that a high bat activity likely reflects a high proportion of foraging behavior, we defined habitat patches as the 90th percentile of highest activity. The threshold

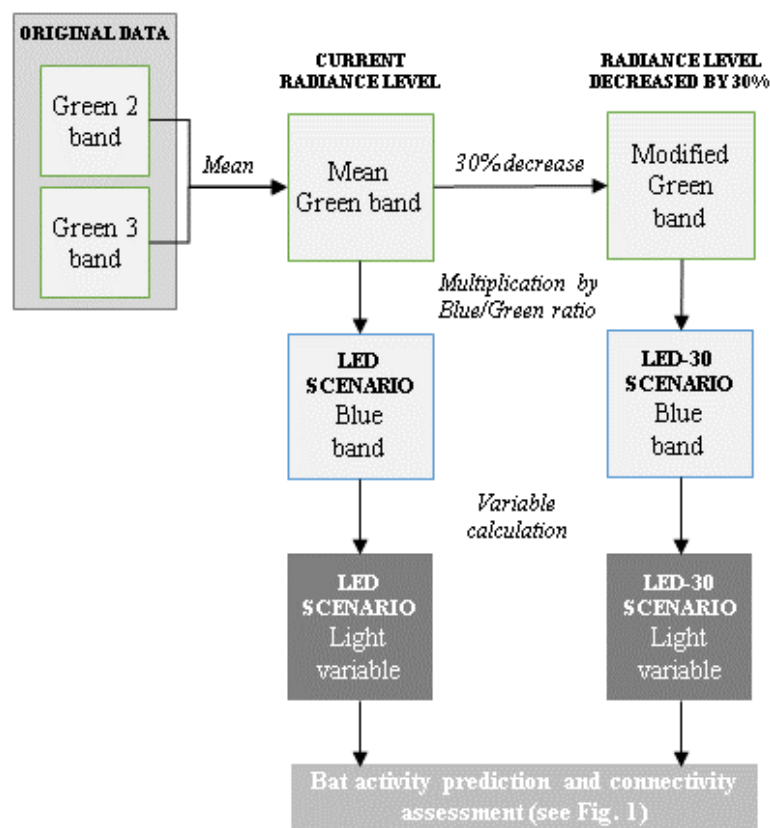


Fig. 3. Steps to create the light variables to evaluate the impact of lighting scenarios on bat activity and landscape connectivity

to define patches was set for the current situation and did not vary between scenarios. Thus the number and size of patches could vary between scenarios. To allow for direct comparisons of the connectivity between scenarios of a given study area, we defined the resistance relatively to the maximum bat activity predicted overall the scenarios. We linearly transformed habitat quality and least cost distance to a scale from 1 to 10 to ease the comparison between the results of the different scenarios of a same study area. However these re-scaled values were not directly comparable between study areas as their range in habitat quality and least cost distance values differed.

2.8.Connectivity measure

For each patch, we calculated the patch quality through the weighted area, i.e. the sum of the predicted activity values of all the pixels composing the patch (Dilts et al., 2016). In order to measure the global difference in landscape connectivity between the scenarios, we calculated the probability of connectivity index (PC) (Saura & Pascual-Hortal, 2007). It is defined as the probability that two individuals randomly placed in the landscape will fall into patches that are connected to each other. When compared with other widespread indices, PC was the only one to comply with all the requirements to adequately measure landscape connectivity (Saura & Pascual-Hortal, 2007). PC is defined as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_L^2}$$

where n is the total number of patches, a_i and a_j the weighted area of patches i and j , p_{ij}^* is the maximum probability of movement between patches i and j and A_L is the maximum weighted area of the landscape. The latter was calculated as the product of the maximum bat activity value of the study area and the study area's size. The probability to move between the patches i and j , p_{ij} , was defined with an exponential decay function (Saura & Pascual-Hortal, 2007):

$$p_{ij} = e^{-kCD_{ij}}$$

where CD_{ij} is the least cost distance between the patches i and j and k ($0 < k < 1$) expresses the intensity of decreasing probability of movement between patches resulting from the exponential function. For each city, we defined the value of k by setting the probability to travel between two patches to 0.05 when the path length corresponded to the maximum nightly flight range of *P. pipistrellus* (i.e. 4 km; Nicholls & Racey, 2006) for the median value of resistance (Saura & Pascual-Hortal, 2007). To assess the global change in connectivity, we measured the rate of variation in PC:

$$\Delta P = \frac{P_{scenario} - P_{current}}{P_{current}} \times 100$$

3. Results

3.1. Bat activity modeling

After variable selection on the eight best models, they all retained the light variable and performed better than the model without light variable (Table 2). In all models, the radiance level had a negative effect on bat activity. The three best models ($\Delta AIC < 2$) were based on three different color bands hence none seemed to be a better predictor than the others. Five out of the eight models retained the interaction between the light variable and the proportion of tree cover. The interaction showed that when the proportion of tree cover was low, the effect of the radiance level was negative whereas for high proportions of tree cover the radiance had a positive effect on bat activity.

Table 2. Selection of models explaining bat activity. Estimates for the effect of light variable (i.e. radiance) and for the interaction between the light variable and the proportion of tree cover when retain after model selection and model without a light variable. The three best models ($\Delta AIC < 2$) are above de dotted line. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Light variable *		Tree cover	AIC	ΔAIC	Weights
	Light variable					
Blue 4 - 100	-52.80	**		3331.3	0.00	0.33
Green 2 - 100	-29.10	***	78.50 .	3332.0	0.70	0.23
Red 1 - 200	-18.00	***	54.00 *	3333.1	1.80	0.14
Green 2 - 200	-33.60	***	99.00 *	3333.9	2.60	0.09
Red 1 - 100	-6.90	*		3334.5	3.20	0.07
Blue 4 - 200	-46.00	*		3334.8	3.50	0.06
Green 3 - 200	-30.70	**	107.00 *	3335.2	3.90	0.05
Green 3 - 100	-22.40	**	85.80 *	3336.3	5.00	0.03
None				3338.7	7.40	0.01

In the eight selected models and the model without light variable, the distance to water and at least one of the tree cover variables were selected (Appendix A). As found in the literature, the distance to water and tree cover had a negative effect on bat activity while the proportion of tree cover had a positive effect (Kaňuch et al., 2008; Boughey et al., 2011). The Julian day had a quadratic effect reflecting the reproductive phenology of bats. Contrarily to other studies, the wind speed had a positive effect on bat activity. However the wind speed considered here were low (below 5.5 m.s⁻¹ in over 90% of the data). The city had a strong effect, with the mean activity being lower in Montpellier than in Lille and even lower in Paris.

We used the overall best model, i.e. the one including the mean radiance value in a 100 m buffer for the blue color band, to produce predictive maps of bat activity across the study areas.

3.2. Lighting scenarios

To build both LED scenarios, we created modified blue color bands (reflecting the emission in the blue part of the spectrum) to simulate a global shift toward 3000K LED. In the LED scenario, where the overall radiance is kept the same as the current situation, 33 to 57% of the pixel of the new blue color band of the extended study area increased in radiance depending on the city considered (Fig. 4).

In the second scenario (LED-30) where we simulated a global shift toward LED

accompanied by a decrease of 30% in radiance, approximately the same proportion of pixels increased and decreased in blue emissions for all three study areas (Fig. 4). In the third scenario (No Light), simulating a global light extinction at the city scale, 58 to 85% of the pixels decreased in blue emissions.

In Montpellier, for all scenarios, the repartition of the pixels which values of blue emissions increased or decreased were fairly homogenous (Fig. 5). For Paris, the repartition was also fairly homogenous except for the two woodlands on the outer borders which blue emissions remained mostly unchanged. In Lille, the decrease in blue emissions was mostly visible in the city center and more globally on the center and East part of the city.

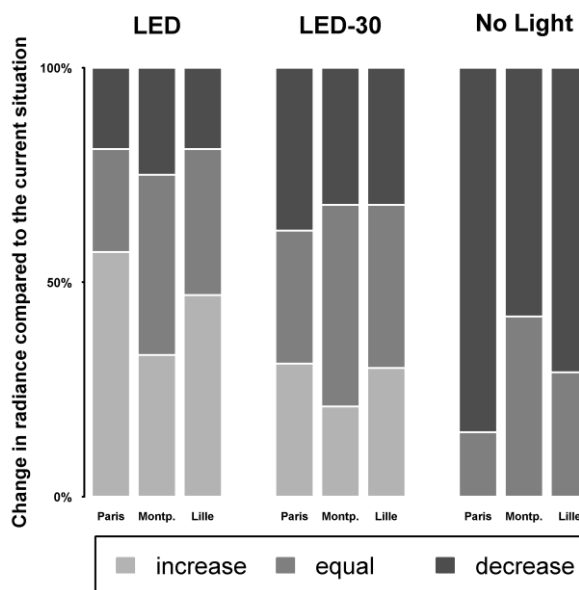


Fig. 4 Proportion of pixel (extended study areas) of the modified ISS picture that increased, stayed the same ($\Delta < 0.001 \text{ nW.cm}^{-2}.\text{sr}^{-1}.\text{A}^{-1}$) or decreased in radiance value compared to the current situation (i.e. the original ISS picture).

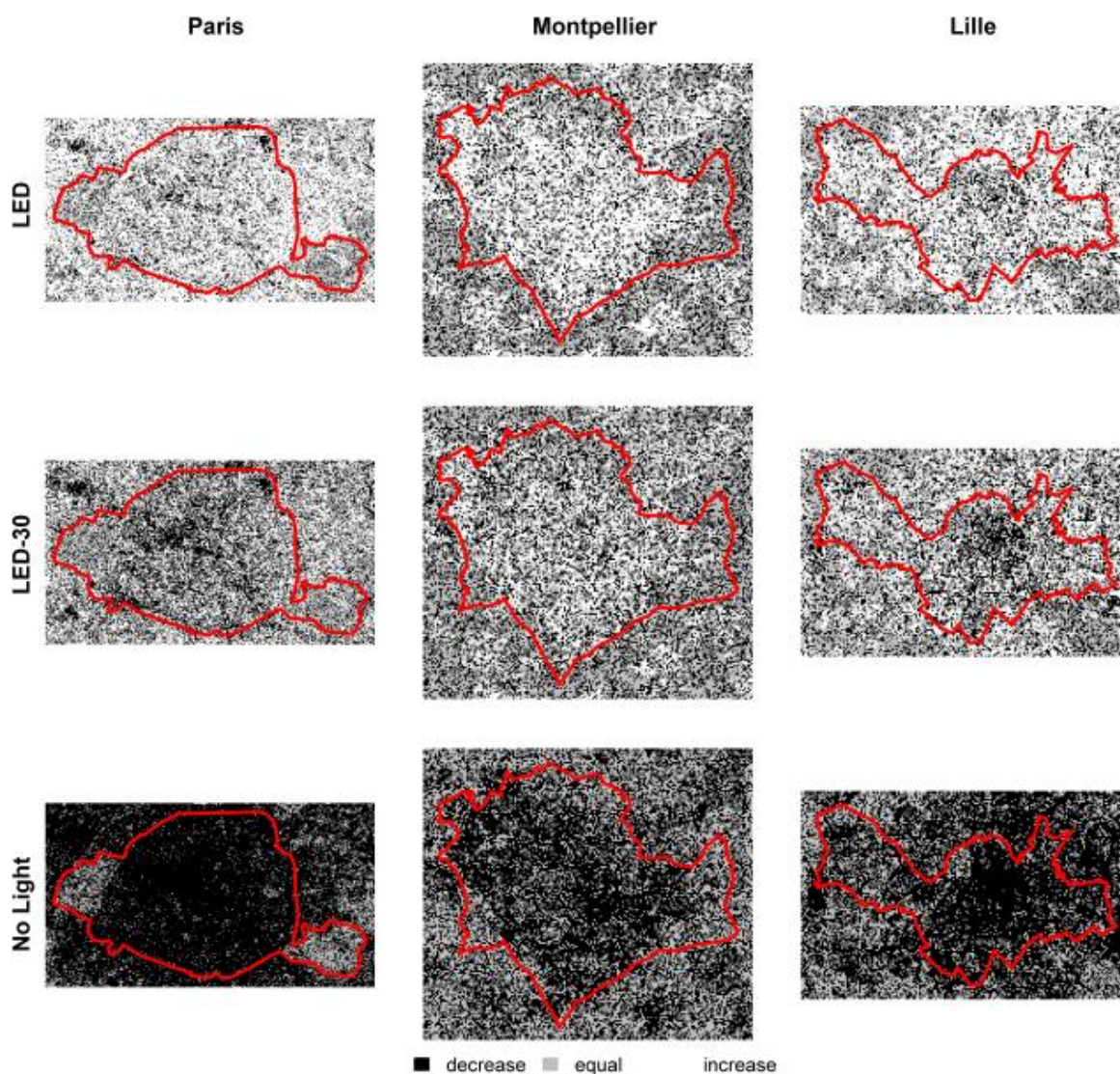


Fig. 5 Spatial repartition of the change in radiance for the 3 study areas and the three scenarios compared to the current situation.

3.3.Habitat patches

Globally, habitat patches, .i.e. the areas for which bat activity was in the 90th percentile of highest activity, included a large proportion of tree cover (53 to 80%; Table 3). For all cities, the number of habitat patches decreased in the LED scenario compared to the current situation (2 to 13% less patches). When all lights were replaced by LEDs, a decrease of 30% in radiance increased the number of habitat patches (5 to 15% more patches). The No Light scenario highly increased the number of habitat patches compared to the current scenario (27 to 43% more

patches) and hence the higher total patch area although the mean patch size did not vary much (range -0.4 km^2 - $+0.3 \text{ km}^2$).

Table 3. Habitat patches characteristics.

	Paris				Montpellier				Lille			
	Current	LED-D	LED-30	No Light	Current	LED-D	LED-30	No Light	Current	LED-D	LED-30	No Light
Number of patches	69	65	70	122	41	40	47	57	63	55	58	86
Mean patch size (km ²)	0.26	0.26	0.26	0.22	0.27	0.27	0.24	0.24	0.12	0.12	0.14	0.15
Total patch area (km ²)	17.7	16.6	18.4	27.3	11.0	10.8	11.5	13.8	7.6	6.8	7.9	12.5
Ratio between total patch area and study area	0.10	0.09	0.10	0.15	0.10	0.09	0.10	0.12	0.09	0.08	0.09	0.15
Global proportion of tree cover in patches	68%	69%	67%	58%	80%	80%	79%	76%	61%	62%	61%	53%
Proportion of tree cover in the study area			21%				21%				14%	
Mean patch quality	1.20	1.17	1.19	1.16	1.29	1.30	1.26	1.28	1.33	1.38	1.38	1.49

The habitat patches mostly corresponded to urban parks and the largest ones had the highest quality (Fig. 6). Patches quality did not change much in Montpellier between the four situations but for Lille and Paris, patches quality increased in the No Light scenario compared to the two LED scenarios and the current situation.

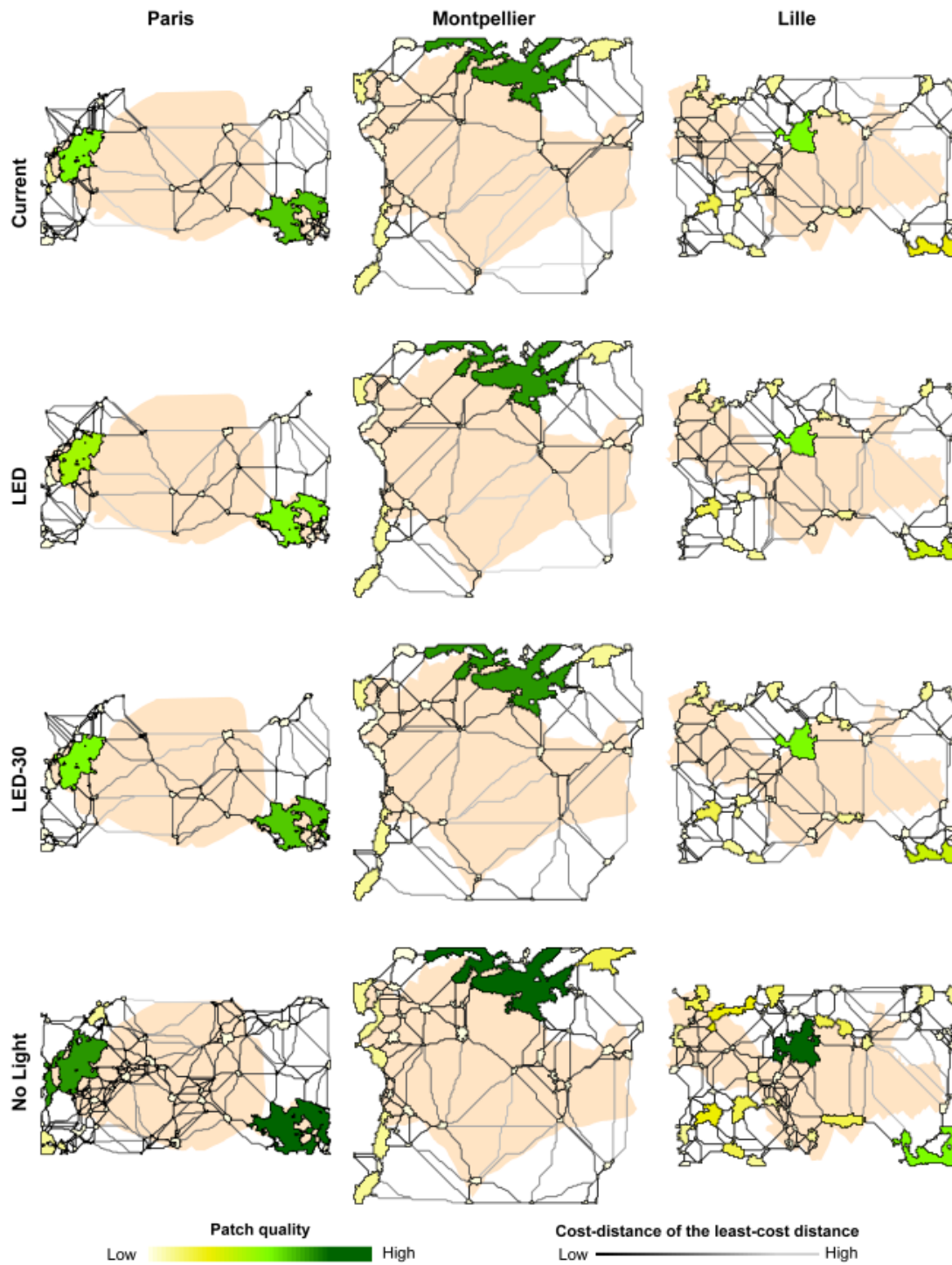


Fig. 5. Maps of habitat patches and least-cost paths for each study area and each scenario. The light orange shape represent the area of the cities.

3.4. Connectivity assessment

We measured the overall connectivity with the probability of connectivity (PC) index and measured its variation between scenarios (Fig. 7). Compared to the current lighting situation, the LED scenario had a weaker overall connectivity in all study areas (Paris -10%, Montpellier -3%, Lille -42%). The change to LED lights accompanied by a decrease in overall radiance (LED-30) had a positive effect on the connectivity for Paris and Montpellier (respectively +20% and +6%) but not for Lille (-24%) although it increased the connectivity compared to the LED scenario (+18%). The No Light scenario provoked the higher increase in connectivity for all cities but it was relatively weak in Montpellier (+18%) compared to Paris (+114%) and Lille (+210%). Overall, the three scenarios had a small impact on Montpellier's landscape connectivity compared to Paris and Lille.

4. Discussion

Our study shows that artificial lights has a negative effect on urban landscapes' connectivity for *P. pipistrellus* daily movements. In addition, a transition toward LEDs would increase light emissions in short wavelengths compared to the current situation and hence decrease the landscape connectivity. Moreover, the magnitude of ALAN's influence on the overall connectivity is dependent on the context and varies considerably between cities.

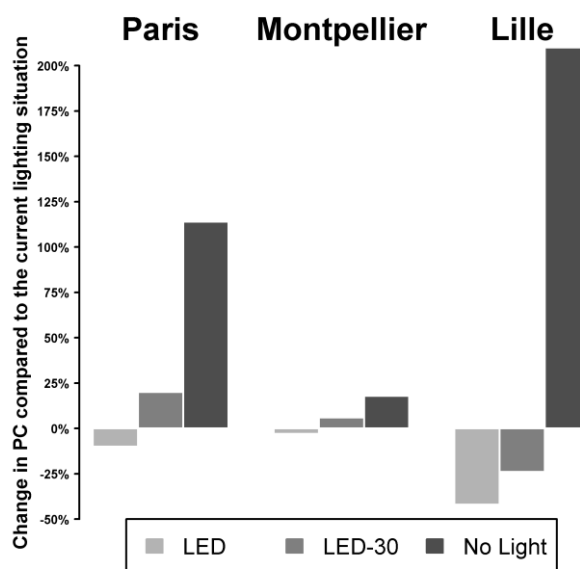


Fig. 7. Change in overall landscape connectivity for the lighting scenarios compared to the current situation.

Globally, a change of lighting technology toward broad spectrum lamps would have adverse effects on cities' already highly fragmented landscapes and potential decrease in light trespass due to a better flux orientation (here, simulated through the scenario LED-30) might not suffice to cancel out this negative effect.

Our results show that light has a significant negative effect on landscape connectivity for bats as the PC index was always higher in the scenario with no light than in any situation with lighting. This is coherent with another study which found that light reduced the proportion of landscape accessible around ponds for bats compared to a dark situation (Hale et al., 2015). Although *P. pipistrellus* is considered as light tolerant due to its ability to forage under streetlight to take advantage of the insects attracted to light (Rydell, 1992), at the national scale, its activity is negatively affected by the radiance level (Azam et al., 2016) and our results show that both its activity and its ability to move across the landscape is reduced by ALAN. *P. pipistrellus* is more resilient to anthropogenic pressures than other species hence it is still present in urban areas but relatively less than in other more suitable landscapes (Kerbiriou, Parisot-Laprun, & Julien, 2018). Therefore other species that are more sensitive to light may suffer even greater impacts which stress the importance to account for biodiversity in lighting planning.

We found that a change toward LED lighting without changing the number of light sources would decrease landscape connectivity for bats daily movements. Currently, the outdoor public lighting in Paris and Lille is mostly constituted of HPS lamps, representing approximately 66 and 56% of light sources respectively (data given by Lille and Paris public lighting company) and we can suppose that the situation is similar in Montpellier. HPS lamps have a narrower spectrum than LEDs and emit a smaller amount of short wavelengths (Falchi et al., 2011) hence the transition to LEDs globally increased the three cities radiance in short wavelength emissions. This result is coherent with a simulation of lamps change at the scale of

Europe which showed that a change from current lighting to LED lighting while keeping the same flux would yield a 2.5 increase in light pollution mostly due to an increase in blue light emissions (Falchi et al., 2016). Moreover, a similar lighting transition at the scale of urban areas in Hawaii considering that new fixtures would eliminate all light emissions above the horizon was predicted to counter balance the negative impact of LEDs hence not worsening the light pollution but not improving it either (Aubé et al., 2018). Although a study suggested that the change from LPS lamps (very narrow spectrum with no blue light emissions) to LED lamps did not affect bat activity at the local scale (Rowse, Harris, & Jones, 2016), we found that, at the city scale, bat activity was negatively affected by an increase in blue wavelengths emissions and that a transition toward LED lights would deteriorate landscape functional connectivity for bats.

Our work allowed to globally predict the influence of the predicted change in lighting technologies (Mckinsey, 2012) on bats daily movements. As we used ISS pictures to determine the radiance, the resolution of the light data is relatively coarse (60 m) and include both public and private lighting. Hence it does not allow to identify individual light sources and indicate which might be particularly problematic. However very fine scale data for both public and private lighting are not available yet but they may become available through drone nighttime imaging in the near future. Even so, as the detection distance of *P. pipistrellus* ultrasound calls is approximately 30 m with current recording equipment (Barataud, 2015), our methodology could not yield more precise outputs by using higher resolution light data. A limit of the approach we developed is that we cannot produce scenarios simulating an increase in the number of light sources. Indeed the quantity of light emitted and reflected upward that is measured with ISS pictures is the resultant of a large number of parameters such as the light characteristics (e.g. spectrum, illuminance, flux distribution), the light fixture characteristics (e.g., height, lamp head), the presence of obstacles (e.g., buildings, trees) and the capacity of

surfaces to reflect light (e.g, type of soil surface, windows). Therefore simulating new light sources would require fairly complex models. The progress in LED lighting technologies is accompanied by a reduction in lighting cost thus potentially leading to an increase in the number of lighting points (Tsao et al., 2010). Therefore, future studies should investigate how the extension of urban areas and the increase in light sources may impact landscape connectivity.

Our results show that the degree to which lighting impacts landscape connectivity for bats varies considerably among cities and accordingly, the simulated technological evolution affected them to different extent. The variation in global connectivity throughout all scenarios was weak for Montpellier which may be due to the fact that initially 42% of the extended study area in Montpellier was dark and thus remained dark in all scenarios. Hence, considering the actual repartition of light, Montpellier may be less sensitive to changes in lamp types than the two other study areas. Moreover, although Paris and Lille had similar radiance changes in the three scenarios, the change in overall connectivity differed significantly. This might be explained by a difference in the spatial repartition of the changes. In the LED scenario, the changes in Paris were homogenously distributed whereas in Lille the radiance mostly decreased in the highly urbanized city center, the least suitable zone of the study area for bats, and increased in the rest of the city. Hence, this scenario induced a greater decrease in connectivity for Lille than for Paris. These results show that although there is a similar general pattern in the landscape connectivity variations for the three cities, it is not straightforward to estimate the influence of a change in lighting technology as it depends on the landscape context in terms of land use and current lighting distribution. Moreover, our study highlights the importance to take several parameters into account to prioritize areas where the reduction of light would most benefit bats as some light changes may have more or less impact on the landscape connectivity.

As the awareness on the need to preserve ecosystems rise and the potential of urban parks and biodiversity to increase human well-being is more and more recognized (Ulrich et

al., 1991; Carrus et al., 2015), land management in urban areas tends to give more attention to the promotion of biodiversity. Tools such as revegetation can help increase landscape connectivity (Shanahan et al., 2011) and integrating lighting within sustainable landscape planning by delineating areas with biodiversity issues within which light source should be removed or adapted to limit their impact may greatly benefit to nocturnal biodiversity.

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ARTICLE 4

APPENDICES

Appendix A. Detailed models outputs

Table A.1. Modeling bat activity. Estimates of all the variables retained in the 20 best models and best model without light variable. After model selection on the full models, for five models, the light variable was not retained and the best model was the one without light variable.

Light variable in the model	Estimates														AIC	ΔAIC	Weights
	Interce pt	City - Paris	City - Montpelle	Julian Day	Julian day ²	Wind speed	Dist. to water	Dist. to tree	Prop. of tree	Light variable	Light variable						
Blue 4 - 100	-9.39 *	-3.05 ***	-2.59 ***	0.11 **	-0.0002 **	0.03 •	-0.0004 **		1.46 *	-52.80 **		3331.3	0.00	0.33			
Green 2 - 100	-9.21 *	-3.11 ***	-2.58 ***	0.11 **	-0.0002 **	0.03 •	-0.0005 **		1.35 *	-29.10 ***		3332.0	0.70	0.23			
Red 1 - 200	-9.40 *	-3.15 ***	-2.59 ***	0.11 **	-0.0002 **	0.03 •	-0.0005 **		1.07	-18.00 ***		3333.1	1.80	0.14			
Green 2 - 200	-9.69 *	-3.23 ***	-2.67 ***	0.11 **	-0.0002 **	0.03 *	-0.0005 **		1.19 •	-33.60 ***		3333.9	2.60	0.09			
Red 1 - 100	-9.20 *	-3.02 ***	-2.55 ***	0.11 **	-0.0002 **	0.03 *	-0.0004 **		1.50 *	-6.90 *		3334.5	3.20	0.07			
Blue 4 - 200	-9.59 *	-3.16 ***	-2.68 ***	0.11 **	-0.0002 **	0.03 •	-0.0004 **		1.52 *	-46.00 *		3334.8	3.50	0.06			
Green 3 - 200	-9.62 *	-3.25 ***	-2.65 ***	0.11 **	-0.0002 **	0.03 •	-0.0005 **		1.26 •	-30.70 **		3335.2	3.90	0.05			
Green 3 - 100	-9.30 *	-3.19 ***	-2.57 ***	0.11 **	-0.0002 **	0.03 •	-0.0005 **		1.56 **	-22.40 **		3336.3	5.00	0.03			
None	-9.42 *	-3.17 ***	-2.56 ***	0.11 **	-0.0002 **	0.03 •	-0.0004 *		1.96 ***			3338.7	7.40	0.01			

“You can't study the darkness by flooding it with light.”

Edward Abbey

CHAPTER 4

**LOCAL SCALE EFFECTS OF LIGHT
CHARACTERISTICS**

ARTICLE 5

Pauwels J., Kerbiriou C., Bas Y., Valet N., Le Viol I. Adapting street lighting to limit light pollution impacts on bats in protected areas. *Submitted in Animal Conservation.*

Introduction

In the two previous chapters, I evaluated the impact of light pollution on bat activity, its spatial distribution and the landscape connectivity at intermediate scales corresponding to landscape management scales for lighting planning such as cities. Indeed in most cases outdoor public lighting is managed at the scale of cities or municipality. These studies may be valuable for global landscape planning as they allow to determine the areas to prioritize when taking action to limit light impacts on biodiversity. They provide empirical evidence that can be used for the delineation of ecological corridors for nocturnal species in the framework of the green infrastructure policy. Indeed, since 2010, French municipalities are asked to enhance, restore and conserve the ecological integrity of green areas and aquatic ecosystems in their land-use planning strategies (Trame Verte et Bleue, Grenelle de l'Environnement 2010). However, to implement actions aimed at reducing the impact of light pollution at the local scale, information on fine scale behavior of species is needed. Implementing biodiversity-friendly management requires concrete recommendations on how light sources should be placed, in what amount and with which spectrum. This need was well summarized by a question asked by a lighting engineer during meeting I organized with land managers: "I'm inclined to try to adapt streetlights to limit their impact on biodiversity but really, how should I change lighting to do so?"

Studies revealed that restoring darkness during part of the night through the extinction of public lighting in the middle of the night is unlikely to effectively reduce the negative impact of light on nocturnal species (Azam et al., 2015; Day et al., 2015). Indeed, the majority of crepuscular and nocturnal species are most active immediately after dusk and before dawn which corresponds to hours where streetlights are on to allow for human activities (Gaston et al., 2012; Newson, Evans, & Gillings, 2015). Therefore, it appears necessary to preserve dark

refuges and corridors all night long to efficiently limit the impacts of ALAN on light sensitive species habitats. This involves, in a first step, to define what is a dark refuge or corridor. Indeed, as species have different response to light, the notion of what is dark enough to be used as habitat or transit route may be species-specific. Such information may be acquired through field work measurement of bat behavior in different lighting contexts. Empirical studies can be used to find threshold values of lighting parameters (Azam et al., 2018) that can thence be translated into criteria to define dark areas ultimately allowing to transpose landscape level plans into local scale ecological dark corridors.

Due to the species-specificity of the behavioral response to light, it appears important to study several species. More specifically, it is crucial to carry out experiment to define what dark areas are for species highly sensitive to light. Such species are often sensitive to low levels of light (Lacoeuilhe et al., 2014; Azam et al., 2018) and, due to the important light levels in urban areas and the absence of suitable habitats, are therefore mostly absent from densely urbanized and lit contexts. They can be more abundant in semi-natural areas but they may still be affected by light diffusing from urban areas which may reduce the habitat they can use. To further understand how the type, quantity and distribution of light impact their behavior, study needs to be carried out in relatively preserved areas where these sensitive species are present and protected.

Aims of the chapter

In the study presented in this chapter, I intended to evaluate the impact of light on bat communities in a protected area in the South of France both around streetlights and at hedges. Most local scale studies evaluate the impact of light in the direct vicinity of a streetlight (Stone et al., 2015; Rowse, Harris, & Jones, 2016; Lewanzik & Voigt, 2017) thus mostly capturing the impact on bat species foraging insects trapped in the halo of light. Nevertheless, two studies

investigated the effect of light away from its source (Lacoeuilhe et al., 2014; Azam et al., 2018). Here, I intended to both capture the impact of light, compared to dark sites, on bat activity around streetlight and at hedges which are known to be important for bats (Verboom & Huitema, 1997). More generally, hedges can act as movement corridors for numerous species and increase the functional landscape connectivity (Burel, 1996). Therefore they are interesting landscape elements to preserve in the framework of landscape planning and their preservation for bats movement is likely to have benefits for other species. Azam et al. (2018) evaluated the distance effect of light sources positioned along hedges but here I investigate the impact of streetlights away from hedges on their potential as habitats for bat communities. Moreover, the field work took place in a protected area within a Mediterranean biogeographical region which allowed to study a large diversity of species.

In addition, this study aims at simultaneously evaluating five characteristics of light: presence, illuminance, lamp type, lamp height and distance to hedge. The three first characteristics have been explored in other studies (Stone, Jones, & Harris, 2012; Mathews et al., 2015; Lewanzik & Voigt, 2017) but not always simultaneously which make it difficult to compare them. The latter two characteristics have never been explored although Azam et al. (2018) evaluated the distance effect of light sources positioned along hedges. Thus, in the study presented in this chapter, I intended to **evaluate the importance of five characteristics of**

streetlights in the impact of ALAN on a large cohort of bat species (n=15) both around light sources and at potential transiting routes. I carried out field work

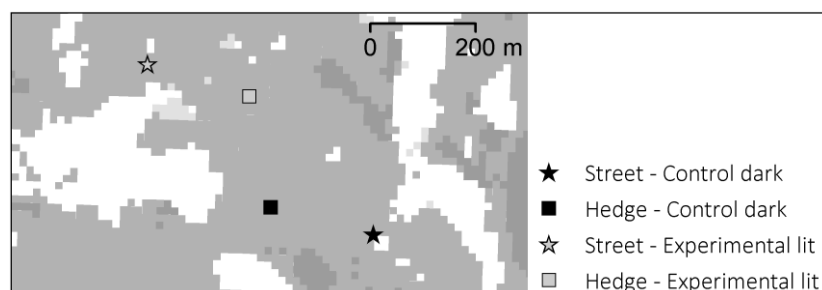


Fig. 28. Example of a site with the experimental lit pair (grey) and the control dark pair (black) both composed of a recording point on a street (stars) and a recording point at a hedge (squares). The sampling included 28 such sites.

sampling bat activity at specific location around streetlight and at lit hedge and also at control dark sites (Fig. 28 ;112 recording points). The species recorded were studied independently and by groups based on ecological traits in order to allow for generalization to other species presenting similar traits. The aerial group included nine high to medium-altitude fast-flying species and the clutter group included six low-altitude slow-flying species.

Principal results & discussion

The study revealed that, **regardless of streetlight characteristics, the presence of light had a negative effect on clutter species activity and a positive effect on aerial species activity around streetlights** (Fig. 29). This pattern is coherent with Azam et al. (2018) although in the present study, effect size and significance are higher. The negative response of clutter species only hold for one species at hedges. Nonetheless, these results highlight the importance properly selecting areas that need lighting as the presence of streetlights has profound effects on local bat communities. In the context of preserved areas such as protected areas where sensitive species are present in higher numbers (Kerbiriou et al., 2018), it is essential to limit the spread of artificial light. Although globally the increase of light pollution in protected areas is lower in protected than non-protected areas (Bennie et al., 2015; Guetté et al., 2018), it is nevertheless increasing and may severely impact light sensitive species.

The result showed no effect of the distance between the light source and the hedge for clutter species activity at the hedge but the illuminance at the hedge had a negative effect on their activity. As neither the presence nor the distance to the streetlight impacted clutter bat activity at the hedge, we may conclude that it is not the bright light point of the lamp but the light level that affects their behavior at least away from the streetlight. Hence the distance of a streetlight to a potential dark area is not a convincing measure to limit light effects on bats. The distance of impact of a light source depends on several parameters in addition to the distance such as the quantity of light and the orientation of the light flux. Software used by lighting engineers allow to model the halo cast by a streetlight while accounting for all its characteristics. Such tools could be valuable to preview the distribution of the light emitted by new streetlights and adapt its fixture or lamp to limit its impact on surrounding vegetation ahead of their implantation if need be. We detected a negative response of the clutter group for very low light levels (range 0.1-13.2 lx, 3rd quartile = 0.3 lx) thus showing that even minor lighting trespass may decrease their habitat use. To preserve dark areas for sensitive species, it is therefore needed to limit light trespass on vegetation to less than 0.1 lx as proposed by Azam

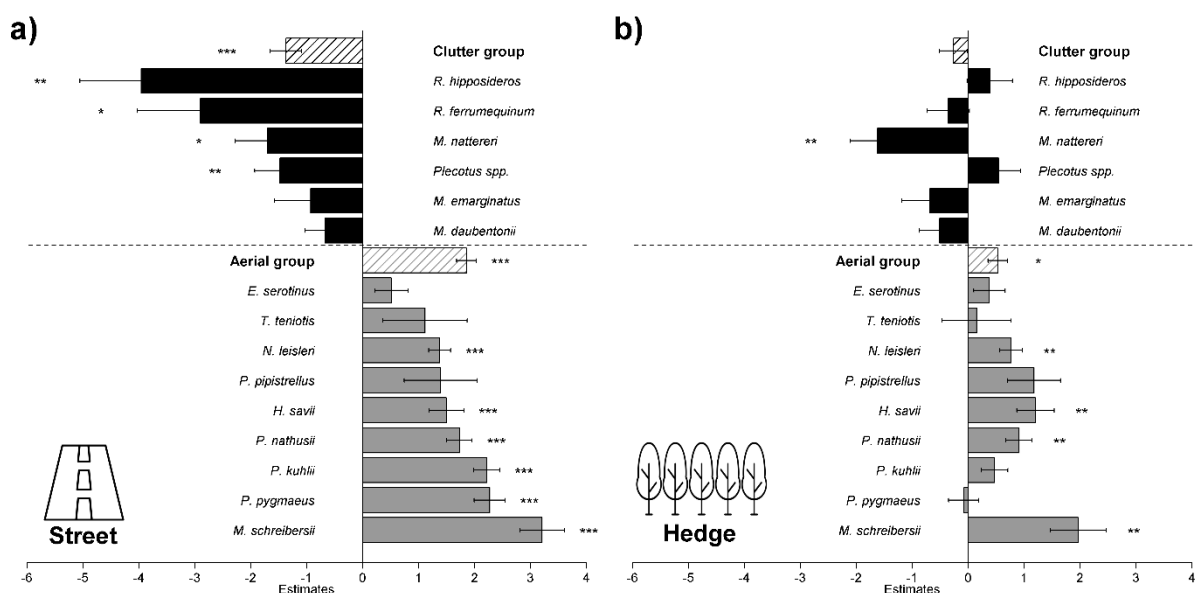


Fig. 29. Effect of the presence of a streetlight on bat activity at the street points (a) and at the hedge points (b) for clutter species (black), aerial species (grey) and groups (hatched). Bars represent estimates of the difference of activity between experimental lit points and control dark points and error bars represent standard errors (* refers to p-value < 0.05; ** refers to p-value < 0.01; *** refers to p-value < 0.001) (extracted from Pauwels et al., Article 5).

et al. (2018). A study on two protected areas in Italy (1800 km² and 150 km²) showed that moderate decrease in ALAN could result in substantial gains of dark areas: Reducing light pollution by 10% increased dark areas by 15% and decreasing light pollution by 20% increased dark areas by up to 46% (Marcantonio et al., 2015). Hence strategies such as dimming may have a high potential to reduce trespass while and help preserve dark areas for light sensitive species. Moreover, dimming strategies have the potential to achieve light levels compatible with human activities while limiting the impact on bats therefore providing both economic (decreased energy cost) and ecological benefits (increased dark habitat) (Rowse, Harris, & Jones, 2018).

Perspectives

Although the present study shows a positive response of fast flying species to light at the local scale, studies presented in the previous chapters revealed that the same bat species could be negatively impacted by light at the landscape level. At the local, bat activity around streetlight is estimated to mostly correspond to foraging activity (Rydell, 1992) thus the negative effect detected at the landscape level may reflect the adverse impact of light in other types of behavior such as transiting (Hale et al., 2015) or the diminution of resource quantity due to the decline in insect prey caused by light (Wilson et al., 2018). This ambivalent behavior, it may prove difficult to evaluate how dimming strategies may affect local activities of these bat species. Nonetheless, dimming was identified as a lever of action to increase the surface of dark patches hence potentially increasing the area of suitable habitat for sensitive species that often correspond to rarer and more highly protected species.

Globally, artificial light exposure increases in terrestrial ecosystems (Bennie et al., 2015) and as population growth now occurs almost entirely within towns and cities (United Nations, 2018) it is critical to plan urban development in a way that minimize its harm on biodiversity (Lin & Fuller, 2013). The impacts of urbanization on ecosystems depend largely

on the spatial extent and the intensity of land-use change which generated a debate on whether land-sparing or land-sharing urban development should be favored (Lin & Fuller, 2013). The land-sparing strategy would imply to concentrate urban development in some areas while natural areas would be set-aside for conservation. The land-sharing strategy would be to spread low-intensity development within which species may persist. Urbanization and the impact of anthropogenic land use are often measured by impervious surfaces spatial extent but the development of outdoor lighting in connection with urban growth may have a further reaching effect than soil sealing due to its diffuse nature. A study showed that land-sparing may be a more desirable type of development for the preservation of bat communities as even low level of housing densities can have important effects on several species presence and abundance (Caryl et al., 2016). This study evaluated the impact of urbanization through housing density. This proxy, although valuable, does not account for diffuse anthropogenic pollutions such as light and noise. The land-sharing strategy entails the spread of build structure which will most probably be accompanied by the use of artificial light sources. Hence this type of development would potentially increase the spread of light pollution and further extend its reach into natural areas through light trespass. As most of the species studied at the landscape level showed a negative response to the radiance level and as light sensitive species are impacted by low levels of illuminance, it is likely that such spread-out urban development will have far reaching negative implication for numerous bat species. The study presented in this chapter highlighted the importance to preserve dark areas henceforth the protection of natural areas aside from urban development may be more effective to conserve bat species. However, dark habitat patches are not sufficient to maintain local populations and the necessary gene-flow between populations. The connectivity between dark areas is as much an important element in species conservation as the preservation of suitable habitat patches.

ARTICLE 5

ADAPTING STREET LIGHTING TO LIMIT LIGHT POLLUTION'S IMPACTS ON BATS IN PROTECTED AREAS

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Abstract

The spread of artificial light at night (ALAN) is dramatically changing the nocturnal lightscape. Protected areas tend to be darker than their surroundings but in Europe, most of them include a significant part of human activities making them more prone to suffer increased light levels especially close to urban areas. Our study investigates the impact of ALAN, and in particular the importance of streetlights characteristics, on bat activity in a protected area in order to define pertinent levers of action to limit ALAN's effects. We measured the activity of 15 bat species in lit and dark conditions along streets and at hedges (foraging habitats for bats) 7 to 192 m away from streetlights. We then analyzed how streetlights height, lamps type, illuminance and the distance to a streetlight could influence bat species activity and the activity of two species groups based on flight and foraging behavior. We found that lighting had a negative effect on clutter bats activity and a positive effect on aerial bats activity. Illuminance was the most relevant characteristic and caused contrasted responses for the two groups. Notably, clutter species activity at hedges was negatively impacted by illuminance. Half of the species in this group are cited in the Annex II of the Habitat Directive which imply the designation of special areas of conservation. Since the diffusion of light into surrounding habitats alters the conservation potential of protected areas, we recommend to suppress light sources or at least to reduce light illuminance close to environments with conservation issues.

1. Introduction

The spread of artificial light at night (ALAN) across the world in the past decades has dramatically changed the nocturnal lightscape (Falchi et al., 2016). Through the modification of natural light levels, ALAN is disrupting the natural cycle of day and night, i.e. the circadian rhythm, arguably the most important cue to life organization (Bradshaw & Holzapfel, 2010). It has major impacts on nocturnal species (Hölker et al., 2010) as it can change their behavior (e.g. Downs et al., 2003) and disrupt interactions (e.g. Knop et al., 2017). Light pollution has come to be considered as a global environmental change (Lyytimäki, 2013) that not only affects urban areas but also natural and protected areas (Gaston, Duffy, & Bennie, 2015). Protected areas play a key role in buffering biodiversity from diverse anthropogenic pressures (Margules & Pressey, 2000; Gaston, Pressey, & Margules, 2002) and albeit they are often darker than their surroundings, globally, they suffered an increase in nighttime lighting in recent years (Gaston et al., 2015; Guetté et al., 2018).

Amongst protected areas, there is a gradient of management objectives from a strict protection of pristine nature (IUCN categories Ia and Ib) to the preservation of ecosystems while also developing sustainable socio-economic activities (IUCN categories IV, V and VI). In Europe, protected areas represent 21% of the land and three quarters of them belong to category IV and V (European Environment Agency, 2012) thus including a significant part of human activities and prone to suffer increased levels of light. In protected areas including small and discontinuous urban areas, habitats surrounding urban areas could be impacted by light spillover and hence be avoided by sensitive species. To limit this effect, it is important to know how light affects the use of natural areas by species and on which light parameters it is possible to act to reduce this impact.

European Microchiroptera are good model species to study the effects of artificial light as they are nocturnal and have contrasting sensitivity to light (Lacoeuilhe et al., 2014; Stone, Harris, & Jones, 2015). Fast-flying species foraging in open spaces such as *Pipistrellus* spp. and *Nyctalus* spp. (hereafter referred to as “aerial” species) can benefit from localized increase in preys abundance due to the attraction of insects to light (Eisenbeis, 2006; van Langevelde et al., 2011). *Rhinolophus* and *Myotis* species are described as light-sensitive as they avoid lit areas (Stone, Jones, & Harris, 2009, 2012) and are not present in highly urbanized cities contrarily to some aerial species (Bartonicka & Zukal, 2003; Rainho, 2007). They are characterized by a slow low-altitude flight and forage in cluttered vegetation (referred to as “clutter” species). In the EU all bat species are protected and thirteen of them have high conservation issues requiring the designation of special areas of protection in the Natura 2000 network (Council Directive 92/43/EEC, 1992). Light diffusing outside towns illuminate forest edges and hedgerows which are landscape elements of great importance for bats to transit and forage (Verboom & Huitema, 1997; Boughey et al., 2011a; Lacoeuilhe et al., 2016). Their lighting may result in a decrease of habitat quality and a degradation of ecological corridors (Stone et al., 2009; Hale et al., 2015) leading to a reduction of the conservation potential of protected areas that include urban areas.

It is urgent to produce recommendations regulating lighting to limit the increase in ALAN and preserve dark areas. Street lighting is the most persistent, aggregated and intense source of lighting (Gaston et al., 2012) but it is within the range of action of land managers. Actions have already been taken through the implementation of extinction schemes although it does not seem to be efficient for bats (Azam et al., 2015; Day et al., 2015). However streetlights parameters need to be tested to find out if they could be interesting levers of actions to help reduce the impact of light pollution.

Our study investigates the impact of ALAN, and in particular the importance of streetlights characteristics, on bat activity in a protected area in order to define pertinent levers of action to limit ALAN's effects and produce recommendations for a more environment-friendly lighting. In partnership with land managers, we carried out the field work in a protected area of category V examining the influence of streetlights height (3.6 to 9 m), lamp type (HPS or LED), illuminance (0.1 to 51 lux) and the distance to the streetlight (7 to 192 m) on bat activity. We worked on 15 bat species pertaining to the clutter and aerial groups (including four species listed in the Annex II of the Habitats Directive) and hence potentially presenting various behavioral responses to light (Lewanzik & Voigt, 2017; Azam et al., 2018). We evaluated the activity of each bat species around streetlights and at forest edges or hedgerows facing a streetlight in regard with the characteristics of the streetlight. In order to generalize our results, we also explored the response to those characteristics at the level of the two groups. We expected antagonistic effects on the activity of aerial and clutter species with the latter group being negatively impacted by light.

2. Material and methods

2.1 Study area

The experiment was carried out in the Parc Naturel Régional du Luberon, a protected natural park of 1850 km² located in the South-East of France (Fig 1a). It is a protected area of category V hence the main aims are the protection of nature, the preservation of landscapes of cultural value and the maintenance of balanced interactions with people through traditional management practices. The park includes nine Natura 2000 sites covering one third of its surface. It is also recognized as part of a hot spot of bat species richness, harboring 21 of the 34 French bat species (Biotope, 2016). Urban areas represent only 10% of the park surface and

arable lands 14% while semi-natural areas represent 76% of the land (42% of low vegetation and 33% of high vegetation semi-natural areas). The largest city in the park (Cavaillon, 26000 inhabitants) has a light level 12 times higher than the natural background sky brightness. Aside from this city, the park has a mean artificial brightness about twice as high as the mean natural background sky brightness which means it is within the 40% of France surface receiving the least light pollution (Falchi et al., 2016). Almost 60% of the municipalities have a public lighting extinction scheme but we did not work in these municipalities to avoid biases.

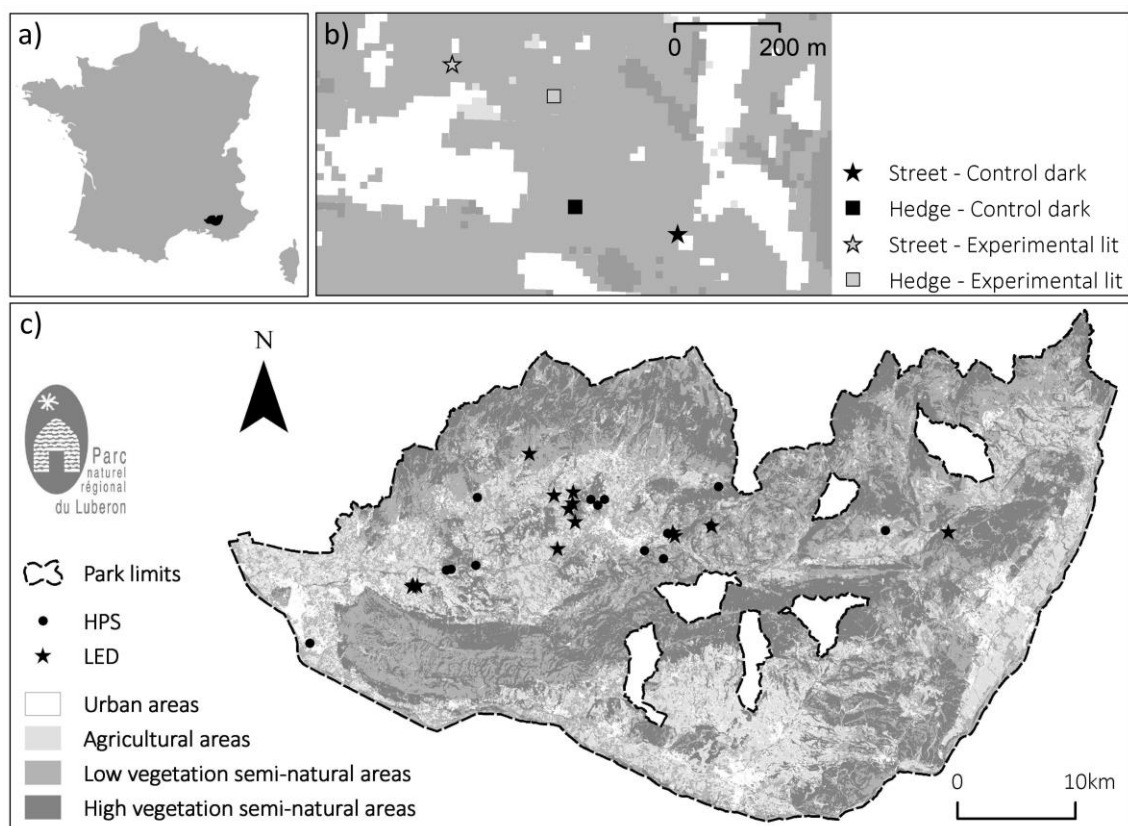


Fig. 1 Presentation of the study area and the sampling design with (a) the location of the Parc Naturel Régional du Luberon (black); (b) an example of site with the experimental lit pair (grey) and the control dark pair (black) both composed of a recording point on a street (stars) and a recording point at a hedge (squares); and (c) the location of the 28 sites with an indication of the lamp type.

2.2 Sampling design

We selected 28 study sites located at the limit between towns and their semi-natural surroundings to measure bat activity both under streetlights and at hedgerows or forest edges (thereafter, “hedges”) directly facing streetlights (Fig 1b and 1c). We sampled bat activity at hedges because they represent potential bat commuting routes (Verboom & Huitema, 1997; Boughey et al., 2011b; Lacoeuilhe et al., 2016). In our study hedges were mostly composed of tall oak trees. On each site we placed two pairs of recording points, an experimental lit pair and a control dark pair separated by 450 meters on average (min = 56m, max = 1982m). For the lit pair, one recording point was placed under a streetlight and the second was placed along a hedge lit by this streetlight. Half of the lit pairs had High Pressure Sodium lamps (HPS, n=14) and the other half Light Emitting Diode lamps (LED, n=14). For the dark pairs, the recording points were placed along a street and at a hedge in a similar fashion and in similar habitats as experimental points but in a dark environment. For a given site, the distance between the two recording points of a pair (i.e. street point and hedge point) was the same for the lit and the dark pair and varied between sites from 7 to 192 meters (see Appendix A – Table A.1)

2.3 Environmental variables

At each recording point, we measured the vertical illuminance at 1.20 m above the ground with a lux meter (Digital Light Meter YF-170) while facing the street point. The vertical illuminance is the measure of the luminous flux received by a 1m² vertical surface such as trees and hedgerows. We also measured streetlights height. While selecting study sites we paid particular attention to the surroundings land use composition to avoid confounding effects. For each site, experimental lit points and their associated control dark points had a similar environmental context. We computed the proportion of urban area, agricultural area and semi-natural area for low and high vegetation in a 200 meter buffer around the recording points using

the CES-OSO (Cesbio <http://www.cesbio.ups-tlse.fr/multitemp/?p=6178>) land use map of France (10 meter resolution) and did not find any difference in the environmental variables values distribution between experimental and control points either at the street point or at the hedge point (Appendix A – Table A.2). In addition, there was no important correlation between environmental variables and light variables (Spearman $|r| \leq 0.6$, Dormann et al., 2013) (Appendix A – Table A.3). However, environmental variations between sites were taken into account within models.

2.4 Bat monitoring

The fieldwork was carried out between the 28th of August and the 7th of September 2016 when the weather conditions were favorable according to the recommendation of the French national bat-monitoring program Vigie-Chiro (no rain, wind speed below 7 m/s, temperature $> 12^{\circ}\text{C}$; Kerbiriou et al., 2018). This period was also between the third and the first quarter of moon to limit the interaction between natural and artificial light (Saldaña-Vázquez & Munguía-Rosas, 2013).

Bat activity was sampled at each point with a Song Meter SM2BAT (<http://wildlifeacoustics.com/>) which automatically recorded all ultrasounds with an SMX-US omnidirectional microphone. The four recording points of each site were sampled on the same night from 30 minutes before sunset until 30 minutes after sunrise, allowing for direct comparison of bat activity between the experimental lit points and their paired dark control point.

As it is impossible to identify individual bats from their echolocation calls, we calculated bat activity as the number of bat passes per species. A bat pass is defined as the occurrence of a single or several echolocation calls of the same bat species during a 5-second interval (Millon

et al., 2015). Echolocation calls were detected and classified to the most accurate taxonomic level using the software TADARIDA (Bas, Bas, & Julien, 2017) in its latest version (online repository <https://github.com/YvesBas>). We used an independent dataset comprising 8405 bat passes recorded throughout France as part of the Vigie-Chiro bat-monitoring program and both checked manually and ran through TADARIDA to perform a logistic regression between the success/failure of automatic species assignment and the confidence index provided by the software. We could hence associate each confidence index with an identification success probability and calculate for each species the minimum confidence index required to tolerate a given maximum error risk, i.e. confidence threshold (methodology detailed in Appendix B). We used the confidence thresholds calculated on the national dataset to create two subsets of this study's dataset: one with a 0.5 maximum error risk tolerance (MERT) and another subset with a 0.1 maximum error risk tolerance. We performed the analysis on both subsets and found similar results. Hereafter we show results for a 0.5 MERT while results for a 0.1 MERT are presented in Appendix C.

An overlap of the detection volumes of the two recording points of a pair could occur depending on the distance between the points and the species maximum distance of detectability. For example, *Rhinolophus hipposideros* can be detected at a maximum of 5 m hence volumes of detection overlapped for only 11% of pairs. For *Tadarida teniotis* which can be detected at 150 m, volumes of detection overlapped for all pairs. When simultaneously detected at the two recording points of a pair, bat passes were associated to the point which recorded the longest sequence of bat calls since it was most probably the closest to the bat flight path. Then we applied a correction on the number of bat passes to account for the subsequent unevenness in the sampling volume of the recording points (Appendix D).

We studied each species activity and also the activity of two groups of species based on their flying and foraging preferences. The “aerial” group was composed of 9 species which are

medium to high-altitude fast-flying species: *Pipistrellus kuhlii*, *P. pipistrellus*, *P. pygmaeus*, *P. nathusii*, *Hypsugo savii*, *Miniopterus schreibersii*, *Eptesicus serotinus*, *Nyctalus leisleri*, *Tadarida teniotis* (Blake et al., 1994; Lacoëuilhe et al., 2014; Azam et al., 2015; Roemer et al., 2017). The “clutter” group was composed of 5 species and 1 genus of low-altitude slow-flying bats that generally forage in cluttered vegetation: *Myotis daubentonii*, *M. emarginatus*, *M. nattereri*, *Plecotus spp.*, *Rhinolophus ferrumequinum* and *R. hipposideros* (Blake et al., 1994; Stone et al., 2012; Lacoëuilhe et al., 2014; Azam et al., 2015).

2.5 Statistical analysis

2.5.1 Effect of the presence of the streetlight

We tested the effect of the treatment (experimental lit vs control dark) to measure the effect of the presence of a streetlight on bat activity. For each species and group of species, we performed a generalized linear mixed model (GLMM) (package *glmmTMB* v.0.2.0; Brooks et al., 2017) using the number of bat passes as the response variable and the recording point type (four levels: street-lit, hedge-lit, street-dark and hedge-dark) as a fixed effect. To account for the paired design in the species models, we used the site as a random effect. Models for the aerial and clutter groups contained a random effect on the recording point nested within the site and a second random effect to account for the species effect. According to the nature of the response variable (i.e. count data) we used a Poisson error distribution or a negative binomial error distribution if overdispersion was detected in the data (Zuur et al., 2009). We performed all models with and without a zero-inflation parameter and to identify the best model, we used AIC scores and examined the dispersion parameter. We did not run models when occurrence was below 10% or the number of contacts was below 20.

We used a principal component analysis (PCA) (package FactoMineR v.1.39; L  , Josse, & Husson, 2008) to summarize the information included in the 4 environmental variables (proportion of urban, agricultural, high and low vegetation semi-natural areas) and 3 meteorological variables (wind speed, temperature and proportion of visible moon). As the proportion of variance explained by the two first principal components of the PCA was greater than 50%, we only included these two as fixed effects in all models. This technique allowed us to limit the number of co-variables (from seven to two) and thus to avoid over-parametrisation and multi-collinearity problems by using uncorrelated linear combinations of the original co-variables (principal components). The models to test the effect of the presence of the streetlight were written as follow:

$$\textit{Species activity} \sim \textit{recording point type} + \textit{PC1} + \textit{PC2} + (1/\textit{site})$$

$$\textit{Group activity} \sim \textit{recording point type} + \textit{PC1} + \textit{PC2} + (1/\textit{species}) + (1/\textit{site}/\textit{recording point})$$

They were applied on data for all recording points (n=112). We performed a post-hoc Tukey HSD test to obtain comparison between experimental lit and control dark points at the street and at the hedge (package lsmeans v.2.27-67; Lenth, 2016).

2.5.2 Effect of the illuminance on bat activity

We evaluated the effect of the illuminance level on bat activity at street and hedge points using both experimental and control recording points. For each species and group of species we performed two GLMMs using bat activity as the response variable and illuminance as a fixed effect, one model focusing on street points and a second model focusing on hedge points. We used the same random effect structures as previously and also included the two first components

of the PCA on environmental and meteorological variables. The models to test the effect of the illuminance were written as follow:

$$\textit{Species activity} \sim \textit{illuminance} + \textit{PC1} + \textit{PC2} + (1/\textit{site})$$

$$\textit{Group activity} \sim \textit{illuminance} + \textit{PC1} + \textit{PC2} + (1/\textit{species}) + (1/\textit{site}/\textit{recording point})$$

Both models were applied separately on data for street points (n=56) and on data for hedge points (n=56).

2.5.3 Effect of the streetlights characteristics on bat activity

We measured the effect of three other streetlight characteristics on bat activity: the lamp type (HPS or LED), the streetlight height and the distance to the streetlight. As those variables could only be measured for experimental lit points, we did not consider control points in the following models. For each species and light variable (lamp type, streetlight height and distance to the streetlight), we built two GLM, one for bat activity at the streetlights and one for bat activity at the lit hedges except for the distance variable which could only be measured at hedges. In each model we included one of the three light variables and the two principal components of the PCA as fixed effects. Aerial and clutter groups' models were built as GLMMs with the same fixed effects and two separate random effects, one on the recording point and one on the species.

The models to test the effect of the streetlight characteristics were written as follow:

$$\textit{Species activity} \sim \textit{streetlight characteristic} + \textit{PC1} + \textit{PC2}$$

$$\textit{Group activity} \sim \textit{streetlight characteristic} + \textit{PC1} + \textit{PC2} + (1/\textit{species}) + (1/\textit{recording point})$$

Both were applied separately on data for lit street points (i.e. at streetlights; n=28) and on data for lit hedge points (n=28). As we looked at the effect of each characteristics in separate models, we applied a Bonferroni correction on the p-values. In order to be significant, effects of models on street points needed to have a p-value below 0.025 (2 models: lamp height and lamp type) and effects of models on hedge points needed to have a p-values below 0.017 (3 models: lamp height, lamp type and distance to the streetlight). All the analyses were performed in R 3.3.3 (R Core Team, 2017).

3. Results

3.1 Bat monitoring

In the dataset allowing for a maximum error risk of 0.5, there was a total of 187 885 bat passes belonging to 20 species. Five species were not included in the analysis as the number of

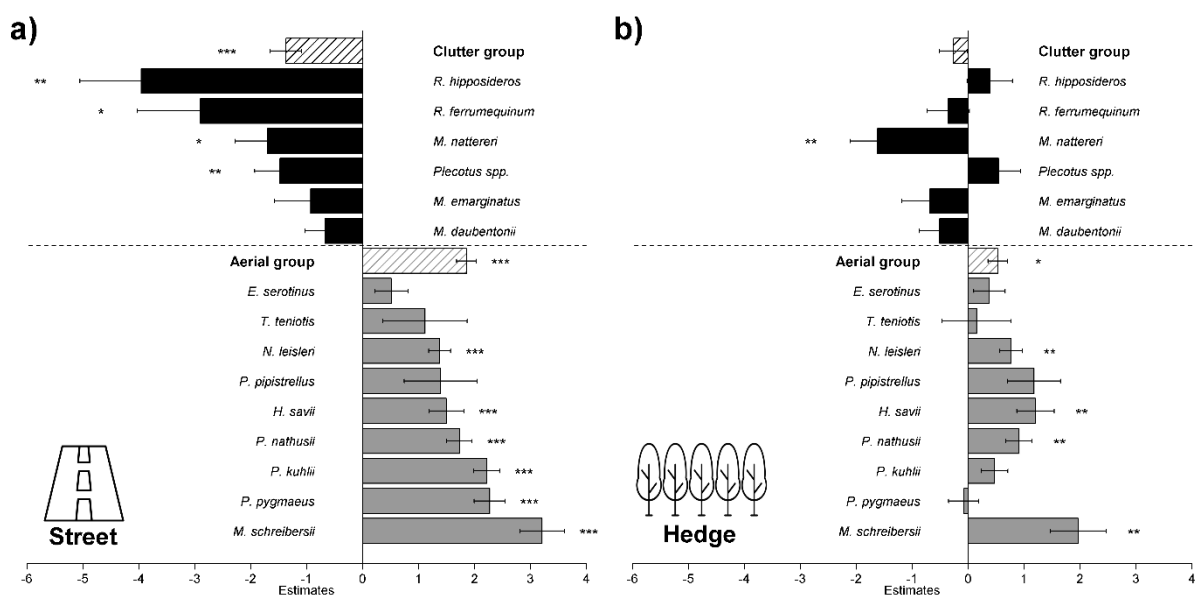


Fig. 2 Effect of the presence of a streetlight on bat activity at the street points (a) and at the hedge points (b) for clutter species (black), aerial species (grey) and groups (hatched). Bars represent estimates of the difference of activity between experimental lit points and control dark points and error bars represent standard errors ('*' refers to p-value < 0.05; '**' refers to p-value < 0.01; '***' refers to p-value < 0.001).

bat passes recorded was too low ($n < 50$). The most abundant species were *P. kuhlii* ($n = 89\,773$), *P. pipistrellus* ($n = 45\,194$) and *P. pygmaeus* ($n = 32\,380$) (Table 1). Almost all bat passes were attributed to aerial species with only 1% of bat passes being of clutter species ($n = 1277$) (see Appendix E for more details).

3.2 Effect of the presence of the streetlight

The presence of a streetlight had a significant positive effect on all aerial species activity except for *P. pipistrellus*, *T. teniotis* and *E. serotinus* and on the aerial group activity at the street points compared to a similar environment with no light (Fig. 2a). At the hedge, this positive effect was significant but weaker for the aerial group and for *P. nathusii*, *H. savii*, *M. schreibersii* and *N. leisleri* (Fig. 2b). All these effects were also significant for the 0.1 maximum error risk tolerance (MERT) dataset except for *P. nathusii*. This species number of bat passes dropped drastically from 5122 at the 0.5 MERT to 74 at the 0.1 MERT due to difficulties in its acoustic identification. A significant negative effect was detected on the activity of *M. nattereri*, *R. ferromequinum*, *R. hipposideros* and *Plecotus spp.* and at the clutter group level at the streetlight. It was only significant for *M. nattereri* activity at the hedge. Results on the dataset with a 0.1 MERT are detailed in Appendix C.

3.3 Effect of the light illuminance on bat activity

Light illuminance had a significant positive effect on the aerial group activity both at the street and hedge points (Fig 3). At the species level, illuminance had a significant positive effect on *P. kuhlii*, *P. pygmaeus*, *P. nathusii*, *M. schreibersii* and *N. leisleri* but these effect disappeared for the 0.1 MERT dataset for *P. pygmaeus* and *P. nathusii*. This positive effect was also present and stronger at the hedge for *P. kuhlii*, *P. nathusii* and *N. leisleri*. Again, it was not significant for *P. nathusii* when using the 0.1 MERT dataset. The illuminance had a negative

impact on the clutter group activity at the hedge. At the species level, the illuminance only had a significant negative effect on *R. hipposideros* at street points but it was at least twice as strong as the higher positive effect for aerial species.

Table 1 Number of bat passes, overall occurrence and protection status of the 15 species studied. Protection status refer to the level of protection given by the Habitat Directive in the EU.

	Number of bat passes	Occ.	Protection status
Aerial species			
<i>P. pipistrellus</i>	45 194	79%	Annex IV
<i>P. kuhlii</i>	89 773	100%	Annex IV
<i>P. pygmaeus</i>	32 380	98%	Annex IV
<i>P. nathusii</i>	5 122	97%	Annex IV
<i>H. savii</i>	2 818	85%	Annex IV
<i>M. schreibersii</i>	2 754	76%	Annex II
<i>E. serotinus</i>	991	87%	Annex IV
<i>N. leisleri</i>	2 234	93%	Annex IV
<i>T. teniotis</i>	5 342	55%	Annex IV
Clutter species			
<i>M. daubentonii</i>	169	57%	Annex IV
<i>M. emarginatus</i>	59	29%	Annex II
<i>M. nattereri</i>	196	39%	Annex IV
<i>Plecotus spp.</i>	547	61%	Annex IV
<i>R. hipposideros</i>	240	44%	Annex II
<i>R. ferrumequinum</i>	66	22%	Annex II

3.4 Effect of the streetlight characteristics on bat activity

The lamp height had a negative effect on *P. natusii* activity at the streetlight but this effect was not significant with the 0.1 MERT dataset. HPS lamps had a significant negative impact on *H. savii* activity at the streetlight compared to LED lamps. There was no other effect of the lamp height or type for any other species or for the two groups either at the streetlight or at the hedge. The distance to the streetlight had a significant negative effect on all aerial species activity except for *T. teniotis* and *E. serotinus* and it was also significant for the aerial group (Fig. 4). The distance to the streetlight had no significant effect on clutter species and group.

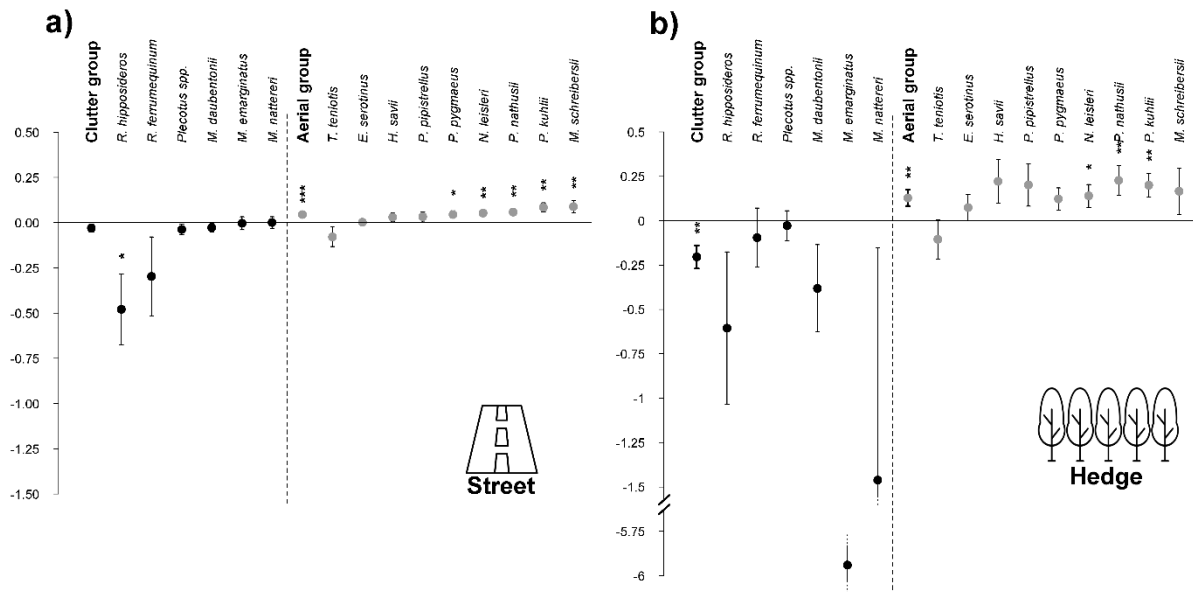


Fig. 3 Effect of the illuminance level on bat activity at the street points (a) and hedge points (b) for clutter species (black) and aerial species (grey). Dots represent the estimates of the effect of illuminance and error bars represent standard errors ('*' refers to p-value <0.05; '**' refers to p-value <0.01; '***' refers to p-value <0.001). For graphical reasons, we broke the y axis on graph (b) to represent *M. emarginatus* estimates but we did not represent the full extent of this species and *M. nattereri* standard error bars.

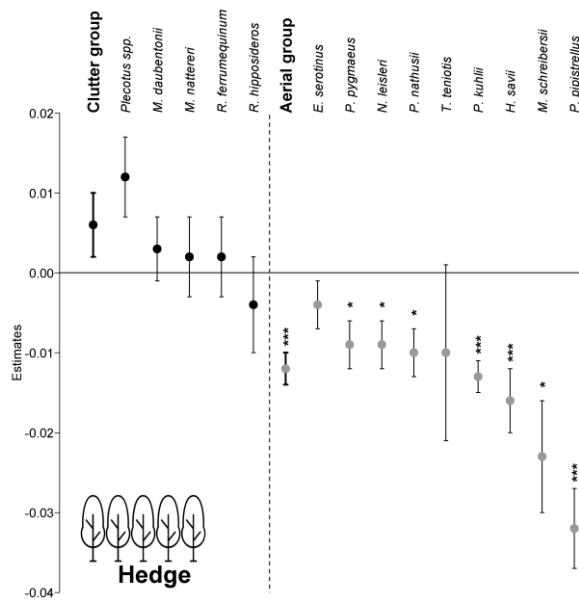


Fig. 4 Effect of the distance of the streetlight on bat activity at the hedge for clutter species (black) and aerial species (grey). Dots represent the estimates of the effect of the distance and error bars represent standard errors. As we tested 3 variables in separate models, we used a Bonferroni correction hence effects are significant for p-values < 0.017 ('*' refers to p-value <0.017; '****' refers to p-value <0.0001). We did not run a model for *M. emarginatus* as we had less than 20 contacts in the dataset considered for this model.

4. Discussion

We evaluated the impact of ALAN on 15 bat species activity in a protected area and found opposite effects on aerial (9 species) and clutter (6 species) species. Clutter species activity was negatively impacted by the presence of light which could be explained by a possible intrinsic perception of increased predation risk of these slow-flying species when in lit environments (Rydell, Entwistle, & Racey, 1996). On the opposite, aerial species activity was higher in lit environment both along streets and hedges which reflects the foraging behavior adaptation of most aerial species to take advantage of the accumulation of insects close to lights (Stone et al., 2012; Lewanzik & Voigt, 2017). The illuminance level affected all bat species and notably it negatively impacted clutter bats activity at hedges. Light diffusing outside urban areas and onto potential habitats for bats can decrease their quality and this might alter protected areas capacity to preserve species with conservation issues. We performed all the models (n=125) on two datasets including a different maximum error risk tolerance (0.5 and 0.1). This allowed us to confirm the robustness of our findings except for five models. Four of these were for *P. nathusii* which acoustic identification is difficult notably due to confusions with *P. kuhlii* (Obrist & Fluckiger, 2004) hence results for this species should be considered with caution.

4.1 Influence of light on bat communities

We found a negative effect of lighting at street points on four out of six clutter species activity and a positive effect on six out of nine aerial species activity which is coherent with other studies (Stone et al., 2009; Azam et al., 2015). At the hedge (7 to 192 m away from streetlights), we only found a negative impact of the streetlight presence on one clutter species. In Azam et al. (2018), the activity of *Myotis spp.* at hedges seemed to be lower in lit conditions as far as 50 m away from the streetlight (positioned along the hedge) but no significant effect was detected further than 10 m away. The difference of sensitivity to light pollution between

bat species causes a competition disadvantage for species that cannot forage for insects gathered at light sources. This is most probably accentuated by the “vacuum cleaner” effect, i.e. the long-distance attraction of light-susceptible species to lamps (Voigt & Kingston, 2016), leading surroundings of lit areas to have less food resource available for light-avoider species. This further loss of foraging habitats for light-sensitive species could lead to a distortion in the community composition in favor of aerial species (Arlettaz, Godat, & Meyer, 2000; Polak et al., 2011). Therefore light pollution might not only impact activity levels but also bat communities and lead to less rich and more generalist communities thus contributing to a biotic homogenization process. However, the impact of light pollution is not as permanent as land use conversion. If we were to turn off lights illuminating a habitat previously used by light-sensitive bats, we could expect sensitive bats to come back (Stone et al., 2009, 2012) although no research has been done to study bat activity after the extinction of sites lit for a long period of time.

4.2 Effect of the illuminance on bats

We found a significant negative effect of the illuminance on the clutter group at hedge points where illuminance values were low (range 0.1-13.2 lx, 3rd quartile = 0.3 lx). This is coherent with another study that showed a negative impact of illuminance on *Myotis spp.* and *Plecotus spp.* while most sampling sites (77%) had an illuminance level below 5 lx (Lacoeuilhe et al., 2014). Moreover, full moon light which correspond to 0.1 to 0.3 lx (Gaston et al., 2013) can influence bat activity levels (Saldaña-Vázquez & Munguía-Rosas, 2013) thus small changes in natural light level such as light trespass may have important impacts on bats. As in Stone et al., 2012, we found a significant negative effect of illuminance at street points for *R. hipposideros* but we did not find significant effect for any other clutter species or at the group level. However our results showed a strong negative effect of the presence of streetlights on clutter species activity at street points when compared to control dark points. The mean number

of clutter bat passes was 5 times higher at lit hedges than at streetlights thus it is possible that we find no effect of illuminance at the streetlight because gleaner bats avoid coming close to light sources irrespective of the illuminance level. Moreover, as there was no significant difference in clutter bats activity level between the dark control points along streets and at hedges (p-value = 0.375), our sample design allow us to conclude that the low activity at streetlights is not due to the higher proximity to urban areas of street points.

Studies on artificial light often measure bat activity at streetlights in urban areas and hence mostly record the activity of species exploiting insects attracted by light (Stone, Wakefield, et al., 2015; Rowse, Harris, & Jones, 2016; Lewanzik & Voigt, 2017). Studying the impact of ALAN in a protected area and at varying distances from streetlights allowed us to evaluate the impact of low levels of light (under 5 lx) on sensitive species. Our results showed that light trespass onto semi-natural areas such as hedges that represent important potential foraging habitats or transiting routes (Verboom & Huitema, 1997; Boughey et al., 2011a; Lacoeuilhe et al., 2016) can reduce habitat quality to a point where light-adverse species will completely avoid the area.

4.3 Streetlight characteristics

We found a negative impact of the distance to streetlights on seven out of nine aerial species activity. Similarly, a study undertaken in a protected area in the North of France, showed that the positive effect of light on *P. nathusii*, *P. kuhlii*, *P. pipistrellus* and *N. leisleri* activity disappeared rapidly with increasing distance steps (no effects at more than 10 m from the streetlight; Azam et al., 2018). However here, while considering distances between 7 and 192 m, we detect a linear negative effect for most aerial species. This is consistent with the positive effect of illuminance on aerial activity as the illuminance decreases proportionally to the inverse of the distance squared ($R^2 = 0.9$ in our dataset). We did not find any effect of the distance on

clutter species either at the species or group level and Azam et al. (2018) showed that the negative effect of light on *Myotis spp.* lost its significance when further than ten meters away from the streetlight. This could suggest that clutter bats are not sensitive to the brilliance of a light source perceived from a distance but only to the illuminance level at the point where they are located.

4.4 Recommendations & conclusion

New lighting technologies have a higher energy efficiency which decreases the cost of lighting and might trigger a multiplication of light points and an increase in power input (Tsao et al., 2010). Hence it is urgent to consider the impact of light pollution on biodiversity. The constant renovation of public lighting (estimated replacement rate of 3% in France in 2011, ADEME, 2011) and the current shift toward more adaptable technologies is also an opportunity to develop lighting planning schemes less harmful to ecosystems. Gaston et al. (2012) proposed five management options to reduce light pollution. According to our result, it appears that three of them are of major importance: reducing the quantity of light, increasing light flux directionality and avoiding lighting at all.

The quantity of light, often measured through illuminance in ecological studies, affects the majority of bat species. Clutter species are negatively impacted and sensitive to low levels of light hence they might be disturbed by light trespass. Thus it is important to use the lowest amount of light possible considering pedestrians and vehicles use of the area to limit excessive lighting and light spillover into semi-natural habitats. New technologies light flux can be changed even after being installed. Thus an evaluation of local ecosystems sensitivity to light could technically be followed by a modification in installed streetlights parametrization. In addition, new streetlights are very often installed in full cut-off luminaires that allow for a more directional flux and hence results in less light spillover (Kinzey et al., 2017). It is also possible

to add shielding on the streetlight or to plant a hedge to help reduce trespass and preserve dark refuges. However, the most important parameter to control is the position of the streetlight. The presence of a streetlight irrespective of its characteristics had an impact on the activity of 10 out of the 15 bat species studied. The decision to keep an installed streetlight or add a new one remains the first and principal lever of action to limit light pollution and even more so in protected areas where protected sensitive species are.

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ARTICLE 5
APPENDICES

APPENDIX A: Recording points detailed information

Site	Treatment	Location	Meteorological variables				Environmental variables (Proportion in a 200m buffer around the recording point)				Light variables			
			Temperature (°C)	Wind speed (m/s)	Proportion of visible moon	Arable land	Urban area	High vegetation	Low vegetation	Illuminance (lx)	Lamp height (m)	Lamp type	Distance to the streetlight	
														0.01
1	Control	Streetlight	20	4	0.04	0.01	0.2	0.08	0.7	0.2	—	—		
1	Control	Hedge	20	4	0.04	0.01	0.2	0.09	0.69	0.2	—	7		
1	Experimental	Streetlight	20	4	0.04	0.04	0.08	0.36	0.48	17.2	4.3	HPS		
1	Experimental	Hedge	20	4	0.04	0.04	0.09	0.36	0.49	8.1	4.3	HPS		
2	Control	Streetlight	23	0	0.01	0.12	0.31	0.08	0.46	0.2	—	—		
2	Control	Hedge	23	0	0.01	0.15	0.26	0.12	0.44	0.1	—	47		
2	Experimental	Streetlight	23	0	0.01	0.12	0.33	0.16	0.38	2.1	9	HPS		
2	Experimental	Hedge	23	0	0.01	0.15	0.32	0.11	0.41	0.5	9	HPS		
3	Control	Streetlight	22	9	0.09	0.05	0.06	0.32	0.58	0.2	—	—		
3	Control	Hedge	22	9	0.09	0.04	0.05	0.33	0.57	0.2	—	21		
3	Experimental	Streetlight	22	9	0.09	0.01	0.17	0.04	0.78	39.2	5	HPS		
3	Experimental	Hedge	22	9	0.09	0.01	0.14	0.05	0.8	1.1	5	HPS		
4	Control	Streetlight	22	5	0.16	0.04	0.11	0.24	0.6	0.2	—	—		
4	Control	Hedge	22	5	0.16	0.06	0.13	0.21	0.59	0.1	—	53		
4	Experimental	Streetlight	22	5	0.16	0	0.26	0.07	0.67	10.3	5.5	LED		
4	Experimental	Hedge	22	5	0.16	0	0.32	0.07	0.6	0.3	5.5	LED		
5	Control	Streetlight	21	4	0.04	0.08	0.16	0.02	0.76	0.2	—	—		
5	Control	Hedge	21	4	0.04	0.08	0.16	0.02	0.75	0.2	—	11		
5	Experimental	Streetlight	21	4	0.04	0.01	0.74	0	0.23	1.7	8	HPS		
5	Experimental	Hedge	21	4	0.04	0.01	0.76	0	0.22	1.6	8	HPS		
6	Control	Streetlight	23	0	0.09	0.16	0.1	0.03	0.7	0.2	—	—		
6	Control	Hedge	23	0	0.09	0.07	0.04	0.26	0.61	0.3	—	192		
6	Experimental	Streetlight	23	0	0.09	0.39	0.23	0.01	0.36	1.2	6	LED		
6	Experimental	Hedge	23	0	0.09	0.27	0.25	0.08	0.38	0.2	6	LED		
7	Control	Streetlight	23	1	0.01	0.27	0.22	0	0.49	0.2	—	—		

7	Control	Hedge	23	1	0.01	0.56	0.1	0	0.34	0.2	-	-	172
7	Experimental	Streetlight	23	1	0.01	0.1	0.35	0	0.54	1.7	6	HPS	-
7	Experimental	Hedge	23	1	0.01	0.27	0.2	0.01	0.51	0.2	6	HPS	167
8	Control	Streetlight	19	0	0.23	0.41	0.16	0	0.43	0.1	-	-	-
8	Control	Hedge	19	0	0.23	0.59	0.05	0.01	0.32	0.1	-	-	159
8	Experimental	Streetlight	19	0	0.23	0.57	0.14	0	0.29	1.5	8	LED	-
8	Experimental	Hedge	19	0	0.23	0.48	0.09	0	0.44	0.2	8	LED	169
9	Control	Streetlight	23	0	0.01	0.17	0.2	0.35	0.27	0.2	-	-	-
9	Control	Hedge	23	0	0.01	0.18	0.19	0.36	0.25	0.2	-	-	30
9	Experimental	Streetlight	23	0	0.01	0.39	0.19	0.13	0.28	51	3.7	LED	-
9	Experimental	Hedge	23	0	0.01	0.35	0.19	0.19	0.26	0.2	3.7	LED	30
10	Control	Streetlight	23	9	0.09	0.06	0.28	0.1	0.55	0.1	-	-	-
10	Control	Hedge	23	9	0.09	0.04	0.2	0.2	0.56	0.2	-	-	62
10	Experimental	Streetlight	24	9	0.09	0.04	0.27	0	0.7	5.1	7.9	HPS	-
10	Experimental	Hedge	24	9	0.09	0.03	0.23	0.07	0.66	0.2	7.9	HPS	61
11	Control	Streetlight	20	0	0	0.22	0.18	0.12	0.5	0.3	-	-	-
11	Control	Hedge	20	0	0	0.25	0.17	0.04	0.56	0.1	-	-	118
11	Experimental	Streetlight	20	0	0	0.05	0.42	0	0.51	15.4	3.7	LED	-
11	Experimental	Hedge	20	0	0	0.09	0.47	0	0.43	0.1	3.7	LED	121
12	Control	Streetlight	20	0	0.23	0.01	0	0.71	0.27	0.2	-	-	-
12	Control	Hedge	20	0	0.23	0.01	0	0.54	0.45	0.2	-	-	93
12	Experimental	Streetlight	20	0	0.23	0.01	0.01	0.26	0.72	7.4	6.3	LED	-
12	Experimental	Hedge	20	0	0.23	0.14	0.01	0.13	0.71	0.3	6.3	LED	98
13	Control	Streetlight	20	5	0.16	0.1	0.4	0	0.48	0.1	-	-	-
13	Control	Hedge	20	5	0.16	0.07	0.18	0.12	0.61	0.1	-	-	180
13	Experimental	Streetlight	20	5	0.16	0.01	0.07	0.18	0.74	1.5	6.1	HPS	-
13	Experimental	Hedge	20	5	0.16	0.04	0.06	0.18	0.71	0.2	6.1	HPS	186
14	Control	Streetlight	23	0	0.05	0.18	0.3	0.01	0.51	0.3	-	-	-
14	Control	Hedge	23	0	0.05	0.24	0.21	0	0.54	0.2	-	-	95
14	Experimental	Streetlight	23	0	0.05	0.09	0.28	0.04	0.57	30.4	3.6	HPS	-
14	Experimental	Hedge	23	0	0.05	0.06	0.25	0.11	0.56	0.1	3.6	HPS	96
15	Control	Streetlight	23	0	0.09	0.2	0.26	0.01	0.55	0.2	-	-	-
15	Control	Hedge	23	0	0.09	0.18	0.25	0.01	0.56	0.2	-	-	12

15	Experimental	Streetlight	21	0	0.09	0.05	0.33	0.36	0.27	5.4	6	HPS	-
15	Experimental	Hedge	21	0	0.09	0.04	0.3	0.39	0.26	3.8	6	HPS	13
16	Control	Streetlight	22	0	0.01	0	0.29	0	0.7	0.3	-	-	-
16	Control	Hedge	22	0	0.01	0	0.16	0.02	0.82	0.2	-	-	55
16	Experimental	Streetlight	22	0	0.01	0	0.21	0	0.77	14	3.9	LED	-
16	Experimental	Hedge	22	0	0.01	0	0.17	0	0.8	0.2	3.9	LED	53
17	Control	Streetlight	22	0	0.09	0.1	0.18	0.02	0.69	0.2	-	-	-
17	Control	Hedge	22	0	0.09	0.17	0.18	0.02	0.64	0.2	-	-	109
17	Experimental	Streetlight	22	0	0.09	0.09	0.47	0.01	0.43	19.9	8.5	LED	-
17	Experimental	Hedge	22	0	0.09	0.07	0.53	0.01	0.38	0.2	8.5	LED	103
18	Control	Streetlight	23	0	0	0.03	0.43	0	0.54	0.2	-	-	-
18	Control	Hedge	23	0	0	0.03	0.42	0	0.55	0.2	-	-	8
18	Experimental	Streetlight	23	0	0	0.03	0.51	0	0.46	1.6	4.3	LED	-
18	Experimental	Hedge	23	0	0	0.03	0.51	0	0.46	13.2	4.3	LED	8
19	Control	Streetlight	23	0	0.05	0.37	0.28	0	0.34	0.3	-	-	-
19	Control	Hedge	23	0	0.05	0.38	0.27	0.01	0.34	0.2	-	-	23
19	Experimental	Streetlight	24	0	0.05	0.26	0.31	0.02	0.41	3.6	4.8	LED	-
19	Experimental	Hedge	24	0	0.05	0.31	0.3	0.02	0.36	1	4.8	LED	23
20	Control	Streetlight	22	5	0.16	0.23	0.06	0.04	0.68	0.2	-	-	-
20	Control	Hedge	22	5	0.16	0.13	0.14	0.05	0.68	0.3	-	-	114
20	Experimental	Streetlight	22	5	0.16	0.03	0.2	0.11	0.66	13.6	5	HPS	-
20	Experimental	Hedge	22	5	0.16	0.07	0.21	0.06	0.65	0.2	5	HPS	120
21	Control	Streetlight	21	5	0.16	0.19	0.19	0	0.63	0.2	-	-	-
21	Control	Hedge	21	5	0.16	0.26	0.12	0	0.62	0.1	-	-	71
21	Experimental	Streetlight	22	5	0.16	0.33	0.33	0	0.34	13.1	4.2	LED	-
21	Experimental	Hedge	22	5	0.16	0.45	0.24	0	0.32	0.1	4.2	LED	69
22	Control	Streetlight	20	1	0.01	0	0.07	0.33	0.59	0.2	-	-	-
22	Control	Hedge	20	1	0.01	0	0.06	0.53	0.41	0.3	-	-	93
22	Experimental	Streetlight	20	1	0.01	0	0.07	0.32	0.6	13.7	4.4	HPS	-
22	Experimental	Hedge	20	1	0.01	0	0.05	0.45	0.48	0.1	4.4	HPS	86
23	Control	Streetlight	23	9	0.09	0	0.2	0.17	0.63	0.1	-	-	-
23	Control	Hedge	23	9	0.09	0.01	0.21	0.17	0.62	0.1	-	-	17
23	Experimental	Streetlight	23	9	0.09	0.01	0.21	0.04	0.74	1.1	7.7	LED	-

23	Experimental	Hedge	23	9	0.09	0.01	0.21	0.04	0.74	0.5	7.7	LED	18
24	Control	Streetlight	20	5	0.16	0.04	0.17	0.48	0.31	0.1	-	-	-
24	Control	Hedge	20	5	0.16	0.04	0.17	0.47	0.3	0.1	-	-	8
24	Experimental	Streetlight	20	5	0.16	0	0.19	0.47	0.33	11.6	4.3	HPS	-
24	Experimental	Hedge	20	5	0.16	0	0.19	0.47	0.32	6.9	4.3	HPS	8
25	Control	Streetlight	20	1	0.01	0.33	0.11	0	0.53	0.2	-	-	-
25	Control	Hedge	20	1	0.01	0.33	0.17	0	0.49	0.2	-	-	65
25	Experimental	Streetlight	20	1	0.01	0.23	0.21	0.01	0.54	21.5	4.8	HPS	-
25	Experimental	Hedge	20	1	0.01	0.25	0.16	0.01	0.56	0.3	4.8	HPS	70
26	Control	Streetlight	18	0	0.23	0.01	0.25	0.1	0.65	0.3	-	-	-
26	Control	Hedge	18	0	0.23	0.01	0.19	0.06	0.73	0.2	-	-	146
26	Experimental	Streetlight	18	0	0.23	0.01	0.26	0	0.7	18.3	3.8	LED	-
26	Experimental	Hedge	18	0	0.23	0.02	0.12	0.04	0.8	0.2	3.8	LED	147
27	Control	Streetlight	25	0	0	0.16	0.29	0.27	0.26	0.2	-	-	-
27	Control	Hedge	25	0	0	0.21	0.26	0.25	0.25	0.2	-	-	78
27	Experimental	Streetlight	25	0	0	0.13	0.32	0.09	0.45	2.8	7.3	HPS	-
27	Experimental	Hedge	25	0	0	0.13	0.18	0.14	0.51	0.5	7.3	HPS	80
28	Control	Streetlight	22	5	0.16	0.01	0.18	0.38	0.42	0.2	-	-	-
28	Control	Hedge	22	5	0.16	0.01	0.16	0.42	0.38	0.2	-	-	25
28	Experimental	Streetlight	22	5	0.16	0.01	0.21	0.24	0.53	1.1	6	LED	-
28	Experimental	Hedge	22	5	0.16	0.01	0.21	0.29	0.48	0.2	6	LED	25

Table A.2 Results of the Wilcoxon signed rank tests of whether the proportions of the different land cover types around recording points differ between experimental and control points at the streetlight or at the hedge

	Under the streetlight		At the hedge	
	W	p-value	W	p-value
Arable land	321.5	0.249	344.5	0.440
Urban area	503.5	0.069	508.5	0.057
High vegetation	360.5	0.606	355.0	0.548
Low vegetation	378.5	0.831	366.5	0.682

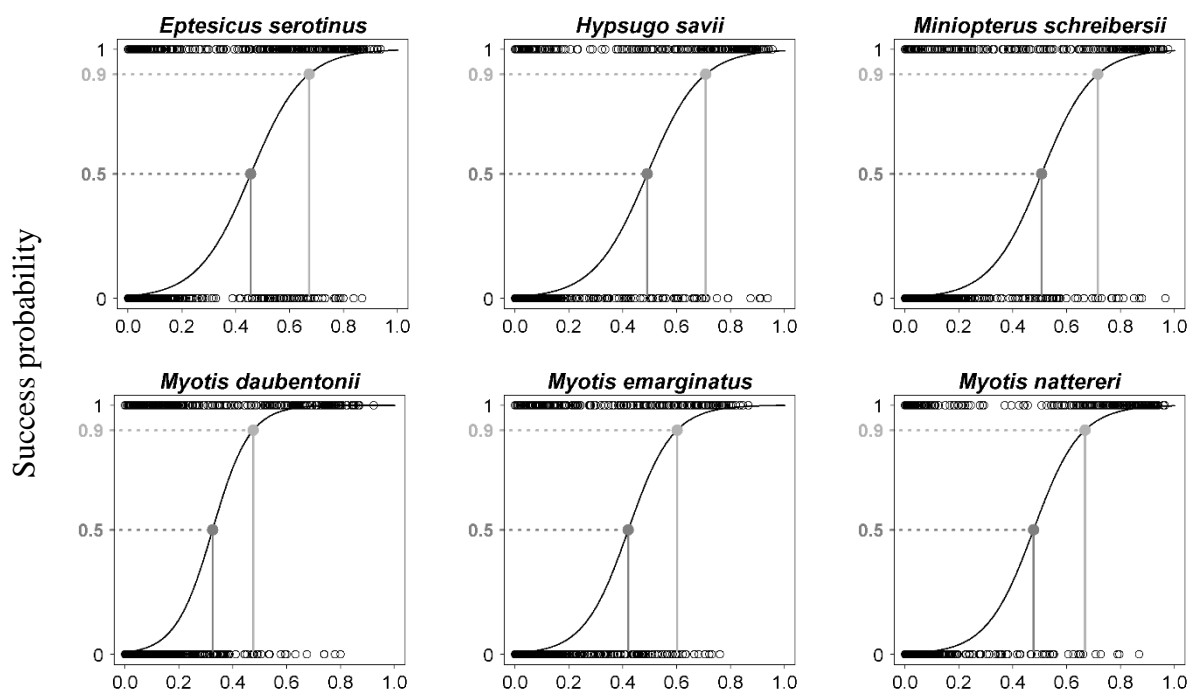
Table A.3 Spearman correlation between light, meteorological and environmental variables

	illuminance	Lamp height	Distance to streetlight	Temperature	Wind speed	Proportion of visible moon	Arable land	Urban area	High vegetation	Low vegetation
illuminance	-									
Lamp height	0.60	-								
Distance to streetlight	0.01	0.09	-							
Temperature	0.23	0.15	0.18	-						
Wind speed	0.12	0.14	0.24	0.03	-					
Proportion of visible moon	0.15	0.20	0.23	0.40	0.33	-				
Arable land	0.02	0.08	0.28	0.34	0.44	0.21	-			
Urban areas	0.12	0.10	0.11	0.42	0.28	0.41	0.29	-		
High vegetation	0.05	0.04	0.27	0.15	0.15	0.16	0.27	0.53	-	
Low vegetation	0.14	0.09	0.21	0.05	0.37	0.15	0.56	0.40	0.02	-

APPENDIX B: Error risk modelling for bat species identification

A national dataset of 17 531 species occurrences (including 8405 bat passes) underwent automatic identification using the software Tadarida (Bas et al., 2017) (online repository: <https://github.com/YvesBas>) to be classified to the most accurate taxonomic level and assigned a confidence probability between 0 and 1. The same dataset was also manually checked using BatSound© (Pettersson Elektronik AB, Sweden) and Syrinx (John Burt, Seattle, WA, USA) softwares. The dataset contained data for 28 out of the 34 bat species present in France and all species considered in this study.

For each species, we build a generalized linear model (package stats; R Core Team, 2017) using the success/failure of automatic identification as a binomial response variable and the probability given for that species by the random forest classifier as an explanatory variable. We selected the *probit* link which better fitted the binomial distribution of manual checking for all species. Reading the logistic regression curves produced, we could hence determine the needed confidence index to tolerate a given maximum error risk, i.e. confidence thresholds (Figure B.1).



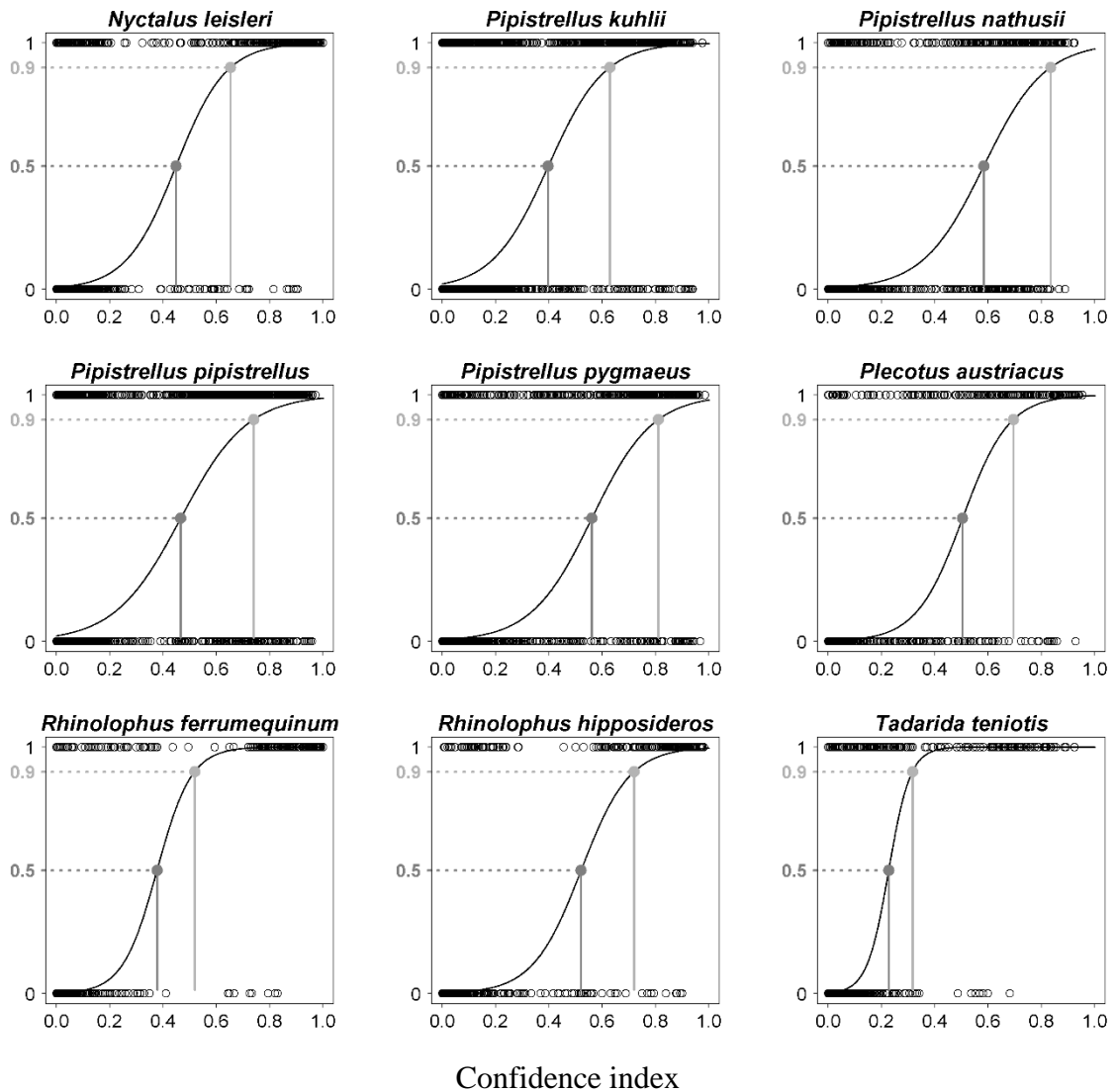


Fig. B.1. Logistic regressions between the success probability and the confidence index of the automatic identification for the 15 bat species studied. Horizontal dotted lines show identification success probabilities (0.5 and 0.9) corresponding to the maximum error risk tolerance thresholds used in the analysis (respectively, 0.5 and 0.1) and corresponding confidence thresholds (vertical solid lines). Each open circle represent a bat pass taking an identification success probability value of 1 when correctly identified by Tadarida software and 0 otherwise.

APPENDIX C: Models results for the dataset at a 0.1 maximum error risk

Table C.1 Effect of the presence of a streetlight on species and species group activity at the street and hedge points ('.' refers to p-value <0.1; '*' refers to p-value <0.05; '**' refers to p-value <0.01; '***' refers to p-value <0.001). The model for *M. emarginatus* for street points was not be because occurrence was too low (<10%).

	Illuminance	
	Street points	Hedge points
	$\beta \pm SE$	$\beta \pm SE$
Aerial species	1.88 ± 0.20 ***	0.56 ± 0.20 *
<i>P. pipistrellus</i>	0.85 ± 0.62	1.53 ± 0.60
<i>P. kuhlii</i>	2.29 ± 0.27 ***	0.36 ± 0.58
<i>P. pygmaeus</i>	2.38 ± 0.44 ***	0.22 ± 0.41
<i>P. nathusii</i>	-0.04 ± 0.97	-1.71 ± 0.41
<i>H. savii</i>	1.15 ± 0.40 *	1.63 ± 0.54 *
<i>M. schreibersii</i>	3.34 ± 0.41 ***	2.14 ± 0.45 ***
<i>N. leisleri</i>	1.30 ± 0.21 ***	0.73 ± 0.21 **
<i>T. teniotis</i>	1.56 ± 0.76	0.32 ± 0.56
<i>E. serotinus</i>	-0.26 ± 0.58	0.38 ± 0.48
Clutter species	-2.15 ± 0.37 ***	-0.23 ± 0.29
<i>M. daubentonii</i>	-1.02 ± 0.42	-0.76 ± 0.41
<i>M. emarginatus</i>	–	-0.50 ± 0.619
<i>M. nattereri</i>	-3.63 ± 1.18 *	-1.83 ± 0.62 *
<i>R. ferrumequinum</i>	-2.90 ± 1.13 *	-0.35 ± 0.38
<i>R. hipposideros</i>	-3.91 ± 1.12 **	0.51 ± 0.47
<i>P. austriacus</i>	-2.96 ± 0.89 **	1.01 ± 0.47

Table C.2 Effect of streetlight illuminance on species and species group activity under the streetlight and at the hedge ('.' refers to p-value <0.1; '*' refers to p-value <0.05; '**' refers to p-value <0.01; '***' refers to p-value <0.001). The model for *M. emarginatus* at the streetlight was not run because occurrence was too low (<10%).

	Illuminance	
	Street points	Hedge points
	$\beta \pm \text{SE}$	$\beta \pm \text{SE}$
Aerial species	0.04 \pm 0.01 **	0.14 \pm 0.05 **
<i>P. pipistrellus</i>	0.04 \pm 0.04	0.18 \pm 0.08 *
<i>P. kuhlii</i>	0.08 \pm 0.04 *	0.15 \pm 0.07 *
<i>P. pygmaeus</i>	0.04 \pm 0.02 .	0.23 \pm 0.14 .
<i>P. nathusii</i>	-0.02 \pm 0.08	-7.04 \pm 4.94
<i>H. savii</i>	0.05 \pm 0.03 .	0.36 \pm 0.28
<i>M. schreibersii</i>	0.08 \pm 0.04 *	0.13 \pm 0.13
<i>N. leisleri</i>	0.05 \pm 0.02 *	0.16 \pm 0.08 *
<i>T. teniotis</i>	-0.1 \pm 0.07	-0.2 \pm 0.09 *
<i>E. serotinus</i>	-0.11 \pm 0.05 *	0.05 \pm 0.15
Clutter species	-0.14 \pm 0.04 ***	-0.58 \pm 0.19 **
<i>M. daubentonii</i>	-0.05 \pm 0.03	-0.74 \pm 0.59
<i>M. emarginatus</i>	–	-5.21 \pm 3.19
<i>M. nattereri</i>	-0.15 \pm 0.09 .	-1.24 \pm 1.65
<i>R. ferrumequinum</i>	-0.3 \pm 0.22	-0.1 \pm 0.17
<i>R. hipposideros</i>	-0.47 \pm 0.2 *	-0.66 \pm 0.49
<i>P. austriacus</i>	-0.21 \pm 0.11 .	-1.22 \pm 1.49

Table C.3 Effect of streetlight characteristics on species and species group activity under the streetlight and at the hedge. Using Bonferroni correction, effects under the streetlight are significant for p-values <0.025 and at the hedge for p-values <0.017 ('.' refers to p-value <0.05; '*' refers to p-value under the significance threshold; '**' refers to p-value <0.001; '***' refers to p-value <0.0001). Several models were not run because the occurrence was too low (<10%) or there were too few bat passes recorded (<20).

	Streetlight height		Lamp type		Distance to the streetlight
	Street points	Hedge points	Street points	Hedge points	
	$\beta \pm SE$	$\beta \pm SE$	$\beta \pm SE$	$\beta \pm SE$	
Aerial species	-0.02 ± 0.08	-0.23 ± 0.24	-0.05 ± 0.10	-0.02 ± 0.33	-0.011 ± 0.002 ***
<i>P. pipistrellus</i>	-0.39 ± 0.23	0.50 ± 0.33	0.83 ± 1.12	0.54 ± 3.15	-0.084 ± 0.033 *
<i>P. kuhlii</i>	-0.22 ± 0.11	0.02 ± 0.17	0.48 ± 0.41	-0.21 ± 0.43	-0.013 ± 0.003 ***
<i>P. pygmaeus</i>	-0.12 ± 0.15	-0.11 ± 0.28	0.19 ± 0.60	0.26 ± 0.82	-0.021 ± 0.006 ***
<i>P. nathusii</i>	0.36 ± 0.46	–	-2.43 ± 2.76	–	–
<i>H. savii</i>	-0.55 ± 0.22 *	0.58 ± 0.21 *	-1.87 ± 0.73 *	-0.06 ± 1.03	-0.017 ± 0.006 *
<i>M. schreibersii</i>	-0.02 ± 0.19	0.01 ± 0.23	-0.85 ± 0.58	-1.22 ± 0.66	-0.023 ± 0.007 *
<i>N. leisleri</i>	-0.07 ± 0.12	0.14 ± 0.17	0.12 ± 0.33	0.27 ± 0.42	-0.010 ± 0.003 *
<i>T. teniotis</i>	0.63 ± 0.66	-0.89 ± 0.34 *	5.10 ± 1.95 *	0.57 ± 1.07	-0.010 ± 0.013
<i>E. serotinus</i>	0.71 ± 0.32	-0.77 ± 0.25 *	1.52 ± 1.30	0.91 ± 0.74	0.004 ± 0.008
Clutter species	-0.00 ± 0.18	-0.11 ± 0.65	-0.09 ± 0.15	-0.64 ± 0.49	0.009 ± 0.005
<i>M. daubentonii</i>	–	-0.12 ± 0.15	–	-0.43 ± 0.47	0.005 ± 0.005
<i>M. emarginatus</i>	–	–	–	–	–
<i>M. nattereri</i>	–	–	–	–	–
<i>R. ferrumequinum</i>	–	0.21 ± 0.18	–	-0.69 ± 0.52	0.002 ± 0.005
<i>R. hipposideros</i>	–	-0.01 ± 0.36	–	-1.47 ± 0.80	-0.004 ± 0.007
<i>P. austriacus</i>	–	0.19 ± 0.41	–	2.69 ± 1.34	0.028 ± 0.012 .

APPENDIX D: Detection volumes overlap between recording points & corrected number of bat passes

We applied a correction on the number of bat passes for each species and each point for which there was an overlap in the detection volume (Table S4-1) to account for the subsequent unevenness in the sampling volume of the recording points. The corrected number of passes was calculated as follow:

$$N_{cor} = N \times \frac{\textit{Theoretical detection volume}}{\textit{Truncated detection volume}}$$

where N is the original number of bat passes and N_{cor} the corrected number of bat passes.

We used N_{cor} as the response variable in all the analysis.

Table D.1 Proportion of the dataset concerned with the volume of detection correction for each species.

Species	Species group	Distance of detection	Proportion of pairs with overlap	Number of bat passes recorded at both points of a pair	Proportion of bat passes detected at both points of a pair
<i>Rhinolophus hipposideros</i>	clutter	5	11%	2	1%
<i>Myotis emarginatus</i>	clutter	10	21%	1	2%
<i>Rhinolophus ferrumequinum</i>	clutter	10	21%	1	1%
<i>Myotis daubentonii</i>	clutter	15	36%	11	6%
<i>Myotis nattereri</i>	clutter	15	36%	6	3%
<i>Pipistrellus pygmaeus</i>	aerial	25	39%	7101	20%
<i>Miniopterus schreibersii</i>	aerial	30	45%	312	11%
<i>Pipistrellus kuhlii</i>	aerial	30	45%	30296	29%
<i>Pipistrellus pipistrellus</i>	aerial	30	45%	13639	26%
<i>Eptesicus serotinus</i>	aerial	40	59%	101	11%
<i>Plecotus austriacus</i>	clutter	40	59%	14	3%
<i>Hypsugo savii</i>	aerial	40	59%	399	15%
<i>Nyctalus leisleri</i>	aerial	80	88%	401	20%
<i>Tadarida teniotis</i>	aerial	150	100%	357	9%

APPENDIX E: Bat calls identification & associated error risk

Table E.1 Number of bat passes, occurrences and predicted error rates for the raw data and the two datasets used for the analysis (maximum error risk tolerance or 0.5 and 0.1).

	Raw data	Maximum error risk tolerance			Raw data	Maximum error risk tolerance	
		0.5	0.9			0.5	0.9
<i>Pipistrellus kuhlii</i>				<i>Myotis nattereri</i>			
Confidence index	–	0.401	0.63	Confidence index	–	0.494	0.691
Nb of bat passes	113 737	75 691	70 863	Nb of bat passes	304	192	151
Occurrences	1	1	0.94	Occurrences	0.64	0.39	0.27
Error rate	0.09	0.04	0.02	Error rate	0.37	0.07	0.03
<i>Pipistrellus nathusii</i>				<i>Myotis daubentonii</i>			
Confidence index	–	0.585	0.833	Confidence index	–	0.325	0.475
Nb of bat passes	6 797	4 554	73	Nb of bat passes	639	164	121
Occurrences	0.99	0.97	0.15	Occurrences	0.83	0.57	0.47
Error rate	0.39	0.27	0.09	Error rate	0.67	0.09	0.03
<i>Pipistrellus pipistrellus</i>				<i>Myotis emarginatus</i>			
Confidence index	–	0.469	0.739	Confidence index	–	0.421	0.601
Nb of bat passes	55 872	37 845	16 940	Nb of bat passes	229	57	38
Occurrences	1	0.79	0.29	Occurrences	0.71	0.29	0.19
Error rate	0.2	0.15	0.07	Error rate	0.75	0.11	0.04
<i>Pipistrellus pygmaeus</i>				<i>Plecotus austriacus</i>			
Confidence index	–	0.562	0.81	Confidence index	–	0.511	0.702
Nb of bat passes	42 059	28 326	20 573	Nb of bat passes	1 266	506	265
Occurrences	1	0.98	0.7	Occurrences	0.94	0.61	0.29
Error rate	0.21	0.1	0.05	Error rate	0.58	0.16	0.04
<i>Hypsugo savii</i>				<i>Rhinolophus ferrumequinum</i>			
Confidence index	–	0.5	0.719	Confidence index	–	0.378	0.518
Nb of bat passes	3 995	2 193	860	Nb of bat passes	75	66	66
Occurrences	0.96	0.85	0.49	Occurrences	0.22	0.22	0.22
Error rate	0.38	0.2	0.05	Error rate	0.1	0.01	0.01
<i>Miniopterus schreibersii</i>				<i>Rhinolophus hipposideros</i>			
Confidence index	–	0.507	0.715	Confidence index	–	0.522	0.72
Nb of bat passes	4 916	2 565	2 414	Nb of bat passes	278	240	229
Occurrences	0.8	0.76	0.71	Occurrences	0.5	0.44	0.38
Error rate	0.46	0.04	0.03	Error rate	0.14	0.03	0.01
<i>Eptesicus serotinus</i>				<i>Tadarida teniotis</i>			
Confidence index	–	0.472	0.694	Confidence index	–	0.272	0.38
Nb of bat passes	1 178	815	316	Nb of bat passes	6 330	3 511	2 033
Occurrences	0.99	0.87	0.38	Occurrences	0.71	0.55	0.41
Error rate	0.3	0.18	0.06	Error rate	0.42	0.11	0.03
<i>Nyctalus leisleri</i>							
Confidence index	–	0.463	0.672				
Nb of bat passes	2 601	1 650	1 551				
Occurrences	0.97	0.93	0.88				
Error rate	0.21	0.03	0.02				

“Failure to abate the environmental consequences of a man-made disturbance [artificial light] using available viable solutions would not inspire confidence in our ability to solve the apparently insurmountable challenges posed by global climate change phenomena.”

Davies 2017

GENERAL DISCUSSION

GENERAL DISCUSSION

1. Principal results

Throughout my PhD thesis, I investigated the impact of light pollution on bat species activity at the local scale and at the city scale. All the analysis presented here were based on bat acoustic data either resulting from a national scale citizen science monitoring program (Vigie-Chiro) or gathered during field work. Passive acoustic recording of bats produces large amounts of data which identification have recently been facilitated by semi-automated identification software. To exploit these data, the identification success of the software Tadarida was evaluated in regard to the confidence index associated to each identification (**Article 1**). Such analysis allowed to define confidence threshold subsequently used to constitute bat activity datasets suitable for further analysis.

The large majority of studies on the impact of light pollution on bats focus on local scale effects. However, bats perception of the landscape may be different depending on the scale studied and it is therefore important to consider this to conceive efficient bat conservation measures (Gallo et al., 2018). Hence, I investigated bats response to light at an intermediate scale revealing that a bat species considered to be light tolerant is negatively affected by ALAN at the city scale (**Article 2**). A similar analysis at a conurbation scale demonstrated that bat species may show a diversity of response to light being either positive, negative or dependent on the light level (**Article 3**). Both studies highlighted the need to preserve dark areas in urban context to promote several bat species activity. Nevertheless, conserving habitats is insufficient to maintain population. The promotion of landscape connectivity is also a crucial element to individuals to move between dark habitat patches to fulfill their everyday needs and to enhance gene-flow. Thus I examined the impact of artificial lighting on bats landscape connectivity and

showed that it was highly context-dependent, conditional to the original distribution of tree cover and light (**Article 4**). In addition, I evaluated the potential of lighting planning schemes to modify the landscape connectivity through the comparison of the current lighting situation with scenarios of light extinction in specific areas. These comparisons indicated that light extinction in environments suitable for bats had the potential to enhance landscape connectivity (**Article 3**). Moreover, I investigated the potential impact of a global change in lighting technology toward the use of LEDs and showed that it would have a negative influence on landscape connectivity for bats (**Article 4**). The results arising from intermediate scale studies may be used to provide recommendation for landscape planning. Yet, local scale implementation require more specific indication on how to adapt lighting to limit its influence on biodiversity. I thus investigated the influence of several light characteristic on the impact of light on bats and found that regardless of streetlights characteristics, the presence of streetlight negatively influenced slow-flying bat species activity (**Article 5**). Moreover, the results of this study showed that the impact of light on hedges could not be avoided through the determination of a distance threshold be only through the limitation of light trespass.

The work carried out during this PhD thesis allowed to improve the knowledge on bat species response to light and to propose tools to evaluate and mitigate the impact of ALAN on biodiversity. In the following paragraphs, I discuss the implication of the study presented, in relation to the current knowledge, on the technical challenges faced while using acoustic data, the importance to evaluate ALAN's impact at several spatial scales and how the expansion and evolution of lighting may greatly threaten biodiversity including humans.

2. Technical challenges of the study of bats

Acoustic data are increasingly employed to study animal biodiversity. Indeed they are noninvasive, cost-effective and may be more efficient than traditional methods such as capture to evaluate species richness and abundance (Fig. 30 ;MacSwiney et al., 2008). Passive acoustic sampling allow to generate considerable amounts of data that can be used to study species presence, abundance and behavior at small and large spatiotemporal scales (Froidevaux et al., 2014). Semi-automated identification software such as Tadarida (Bas, Bas, & Julien, 2017) allow to rapidly identify bat calls while associating identifications with a confidence index (CI). However to be able to use the CI to decide which data should be kept for the analysis, I participated in the development of a methodology allowing users to determine the maximum error risk of a given acoustic sequence identification (**Article 1**). The results showed that it was necessary to only consider data with at least a 0.5 maximum error risk to minimize false positives and have consistent responses of bat activity in models. This 0.5 maximum error risk threshold means that each data has a 0.5 or higher probability to be well identified hence in the total dataset the realized identification error rate is lower than 0.5. This study provides new opportunities, starting with a time gain in manual checking in experimental studies. Moreover,

semi-automated identification allows to remove the bias linked to the observer identification experience which may vary between observer and across time as observer gain in experience. This aspect is of particular importance for large-scale monitoring of bats where a large number of observers participate. Moreover, an important advantage of acoustic data is that

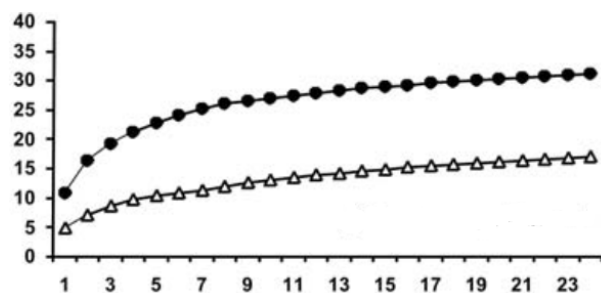


Fig. 30. Neotropical bat species accumulation curves in pastureland habitats (Yucatan peninsula). (Δ) represent species recorded with capture methods only and (\bullet) represent species recorded with capture methods and acoustical sampling (extracted from MacSwiney, Clarke, & Racey, 2008).

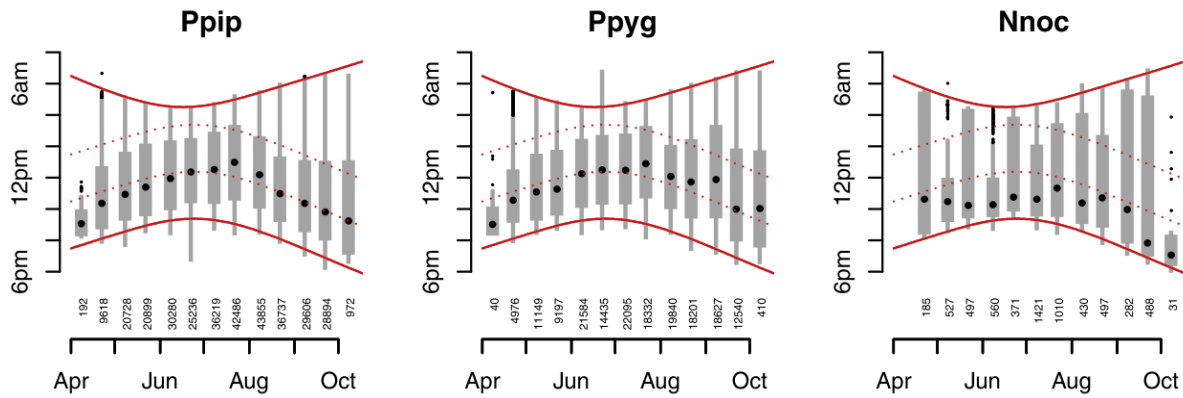


Fig. 31. Patterns of nightly activity through the season with respect to sunset time for three bat species (Ppip: *P. pipistrellus*, Ppyg: *P. pygmaeus* and Nnoc: *N. noctula*) measured using data from a PAM citizen-science program). Individual box plots summarize the timing of bat passes during half-month periods. The solid curved lines show sunset and sunrise times and the two dashed lines indicate 3 h and 6 h after sunset. For box plots, wide bars show quartiles, lines extend up to 1.5 times the interquartile range, large dots show the median and small dots show outliers. Numbers give the total number of recordings in each period (extracted from Newson et al., 2015).

they can be reanalyzed following the improvement of identification techniques or the development of new methodologies hence extracting new information from data accumulated over the years. For example, Tadarida is still being developed to enhance identification but also identify new species and taxa such as birds and insects. These improvements may generate a huge amount of data on newly acoustically identified species arising from already collected data. Acoustic data are mostly used for species-specific studies on a variety of taxa such as bats (Fig. 31 ;Newson, Evans, & Gillings, 2015), insects (Chesmore & Ohya, 2004) and apes (Kalan et al., 2015) but recent studies propose to use global soundscapes to evaluate spatial and temporal patterns of variation in animal diversity (Depraetere et al., 2012) thus opening new horizon for the use of acoustic data.

3. Importance of scale in the evaluation of light pollution's effects

Bats scale-dependent response to light

The studies undertaken during this PhD showed that the measured response to light of a bat species can be markedly different depending on the spatial scale considered. Indeed, at the scale of a light source, we found that *P. pipistrellus* and other fast flying species had a higher level of activity close to streetlight and with increasing illuminance (**Article 5**). This attraction to light has long been observed (see Rydell, 2006) and then measured in numerous studies (Emma Louise Stone, Jones, & Harris, 2012; Emma Louise Stone et al., 2015; Lewanzik & Voigt, 2017; Azam et al., 2018). It is due to fast-flying species ability to use light source as foraging grounds thus taking advantage of the high abundance of prey insects attracted to light (Eisenbeis, 2006). This behavior lead to the consideration of species foraging at streetlight as light tolerant. However a recent national scale study (Azam et al., 2016) and city and conurbation scale studies presented in this thesis (**Article 2 & 3**) demonstrate that even fast flying species can be negatively impacted by light pollution. This difference may be explained by the fact that small scale experiments give insight into the context-specific behavior of individuals while large scale analysis allow to study population dynamics hence cumulating all the behavioral and physiological responses to light pollution and addition to potential effect on resources. Most studies at fine scale measure bat activity at light sources and therefore the bat activity of fast-flying bats recorded mostly corresponds to foraging activity. Few studies evaluated the impact of light on other flying behavior such as roost emergence (Downs et al., 2003) or transit (Hale et al., 2015) and found negative effects on fast-flying species. Therefore, the term “light tolerant” only holds for one aspect of these species biology and hinder their consideration as species that are also negatively affected by light. Nevertheless, some species present the same response to light across scales such as light sensitive *Myotis* species that have

been shown to be negatively influenced by ALAN both at the local scale (Azam et al., 2018) and in this thesis at the conurbation scale (**Article 3**). Large scale studies allow to account for the global impacts of light on behaviors, physiology and interactions together with their downstream influence on population dynamics. The example of so-called light tolerant bats highlight the necessity to undertake large scale studies in addition to small scale ones to have the full picture of the effects of light on a species. Such studies investigating population level effects of light require large spatial sampling and can benefit from the data gathered through citizen science monitoring programs. In the long run, such sampling scheme could also allow to investigate the temporal evolution of populations jointly with the development of lighting and explore long-term demographic effects.

Knowledge gaps in light's large scale effects on low trophic level species

Bat species spatial distribution and population trends tend to be similar to those of their insect preys (Jones et al., 2009; Stahlschmidt & Brühl, 2012). As study showed that nighttime lighting could explain 20% of the variation in long-term changes in moth abundance and therefore brought evidence that light pollution contributes significantly to moth species decline (Wilson et al., 2018), large scale effects of light on insect populations may have indirect consequences on bat populations. More generally, it may be of particular interest to study the large-scale impacts of artificial night-time light on population dynamics of primary producers (e.g., phytoplankton, plants) and species at low trophic levels (e.g., zooplankton insects). As a direct or indirect source of energy for higher trophic levels, changes in their distribution and abundance may have vast cascading effects on a large number of species. For example, only one study evaluated the large scale effect of artificial lighting on plants phenology (ffrench-Constant et al., 2016). This study showed that deciduous trees budburst in lit areas could be advanced by up to 7.5 days thus potentially disrupting the synchronization of herbivorous

species phenology with the appearance of new leaves and impacting their fitness and reproductive success (Visser & Holleman, 2001). In turn, predators of these herbivorous species may be indirectly affected through a decreased availability or quality of preys. Changes in primary producers phenology may have wide reaching consequences and should therefore be explored to evaluate the extent to which they occur and the intensity of their impact.

Another taxa representing the source of food of numerous other species are insects. Within this taxa, numerous species are known to be attracted to light and this behaviour has been exploited to develop trapping methods (e.g., van Langevelde et al., 2017; Roeleke, Johannsen, & Voigt, 2018; Fig. 32). However methods to evaluate insect abundance in dark areas are lacking hence rendering impossible the comparison of lit and dark sites. Light induces a vacuum cleaner effects (Eisenbeis, 2006), i.e. long distance attraction of individuals to light sources, however little is known on the distance to which insect are attracted and how insect communities are affected at different distance step from the light source. A study attempted to measure the attraction distance of a 10 W UV lamp on large moths using a mark-release-recapture technique and found that the attraction range could be up to 10 m depending on the species however their analysis did not evaluate recapture rates (Truxa & Fiedler, 2012). Such methodology associated with further statistical analysis may be of interest to evaluate the attraction range of streetlights which power input may range from 10 to over 100 W (Rowse, Harris, & Jones, 2016) although they often emit less UV than the lamp used by Truxa et al. In addition to insects that can be trapped in light halos, some may become incapacitated by light from afar. For example, a study



Fig. 32. Common light trapping technique using a white sheet and a mercury vapor lamp (© T. SYRE)

showed that 50% of moths approaching a light trap stopped their flight on the ground (Hartstack, Hollingsworth, & Lindquist, 1968). Therefore light's range of impact is greater than a light source halo and may thus possibly affect insects tens of meters away. Insectivorous species that are very sensitive to light such as slow flying bat species (Emma Louise Stone, Jones, & Harris, 2009) avoid lit areas possibly due to an intrinsic perception of increased predation risk (Rydell, 1992) but may also be impacted by the insect depletion of dark areas at the vicinity of light sources. Newly developed Lidar systems allow to quantify insect biomass without using light traps and can also be used to measure bat activity (Malmqvist et al., 2018). Future studies could use this technology to evaluate the quantity of insect biomass at different distance from a light source jointly with bat activity. This would allow to evaluate the distance to which the vacuum cleaner effects is detectable and if an effect on bat activity can be linked to it. However further technological development is needed for such technology to be able to identify individual bat or insect species.

Large scale impacts of skyglow

The illuminance values tested in most experiments range from levels that can be measured in very close proximity to light sources (up to 100 lx) to light trespass at tens of meters away from a lamp (down to 0.01 lx). However, some species may be sensitive to even lower levels of light. For example, studies showed that zooplankton diel vertical migration could be altered or inhibited by artificial light (Moore et al., 2000) at light levels below what most commercial sensors can detect (Ludvigsen et al., 2018). Such low and nearly unmeasurable light quantity may be produced by skyglow. Although this phenomenon is believed to extend the effect of light pollution tens or maybe hundreds of kilometres away from the light source (Kyba et al., 2015), its actual reach is unknown and we do not have yet the technical means to measure it accurately. Indeed, the measure of skyglow is dependent on the

spectral distribution of light (Kyba, 2018). Measures taken with Sky Quality Meters, a device used by amateur astronomers to measure skyglow, before and after a change from 5%-uplight HPS to 0%-uplight LEDs would show a decrease in skyglow as they are based on one colour band although in reality the radiance measured would double (Sánchez de Miguel et al., 2017). Thus the potential of skyglow remains scarcely explored whereas its effects could be important. In aquatic ecosystems, the diel migration of zooplankton to consume near-surface phytoplankton constitutes a major pathway in the carbon cycle and adaptive behaviour of predators to vertical movements of their preys results in the daily migration of entire food webs (Davies et al., 2014). The skyglow effect hence has the potential to have extremely wide reaching impacts through the disruption of what may be the most substantial synchronized movement of biomass and carbon (Gaston et al., 2017).

Population level impacts of artificial light is multifactorial stemming from direct or indirect effects on individuals' physiology, behaviour and interactions. Some of these effects can modify species movement abilities. Light can act as a barrier to individuals' movement and in this thesis, I showed that light could reduce landscape connectivity for the movement of urban bat species (**Article 3 & 4**). However, bats are highly mobile species and their ability to fly may give them more possibility to avoid lit areas than other less mobile species such as gastropods. The functional landscape connectivity is species-specific and depends on the perception of the landscape, the habitat preferences and the capacity to move through different habitats. Light may have a stronger fragmenting effect on light sensitive nocturnal species with low movement abilities. In the context of green infrastructure development, to properly include light pollution as a criteria to define ecological corridors, it would be valuable to evaluate the influence of light on other nocturnal species landscape connectivity perception.

4. The future of lighting

The most persuasive arguments for lighting control are economic ones (Smith, 2009). Global strategies aiming at reducing energy expenditure and greenhouse gas emissions also contribute to the evolution of lighting such as the phasing out of incandescent light bulbs in the EU, the USA and many other countries. Local light schemes such as part-night lighting are implemented in more and more cities primarily to reduce electricity cost and to save energy (Azam et al., 2015). During my fieldwork, the mayor of small town told me she had to battle with political opponents of the municipality to start a part-night lighting scheme and in the end the decisive argument was the unequivocal reduction in electricity bills. The replacement of dilapidated lighting equipment by LEDs is more and more frequent and in the span of a year, two of the 14 sites with HPS lights I used in my field experiment were changed to LEDs. In the context of a global strategy toward the reduction of greenhouse gas emissions, the energy efficiency of LEDs associated with a lower cost of electricity input drove them to account for nearly half of the lighting market by 2016 (McKinsey, 2012). A vast technological change toward LED lighting thus seems inevitable and this change has the potential to double the current level of light pollution (Fig. 33 ;Falchi et al., 2016). I demonstrated that such a large scale modification in light spectrum may have important implications for bats landscape connectivity (**Article 4**). However, LEDs light emissions can be tailored in terms of duration, spectrum, intensity and directionality through a panel of technical tools. These possibilities should be the primary focus of future studies on light impacts on biodiversity and ecosystems. In addition, to increase the potential to reach realistic compromise for lighting planning, future studies should address the issue of light pollution through an interdisciplinary point of view by intersecting biology, physics and human sciences point of views. For example, the Haut de France region financed a study aiming at defining dark corridors in the city of Lille (from which arise the studies presented in the third chapter) while concurrently evaluating its acceptability

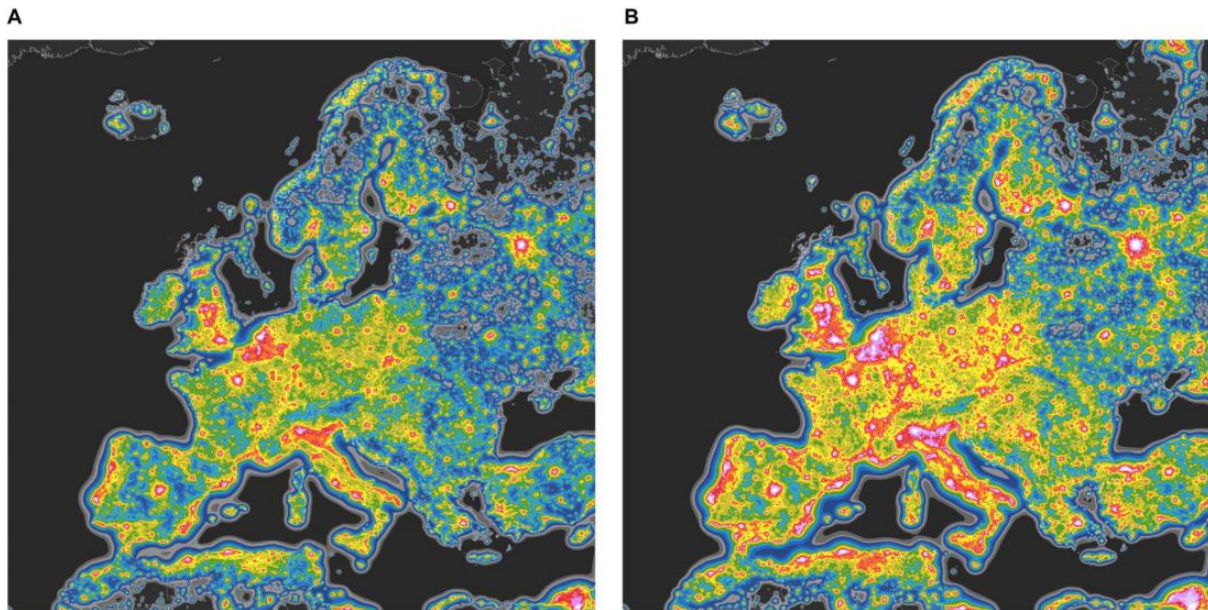


Fig. 33. Maps of Europe’s artificial sky brightness (A) currently and (B) as forecasted after a transition toward 4000K CCT LED technology, without increasing the photopic flux of currently installed lamps.

through surveys addressed to the local population and carried out by the social science department of the University of Lille 1. Although political actors feared that citizens would not agree with a decrease in light levels this exploratory study showed that citizens seemed to be ready to renounce to part of the comfort artificial light brought to limit its impact on biodiversity.

Yet another arising concern on the effect of light pollution is how it can impact human health (Haim, Scantlebury, & Zubidat, 2013). Recent studies linked blue light emissions with sleep disruption (Green, Haim, & Dagan, 2017) and increased risk of prostate and breast cancer (Haim & Portnov, 2013; Rybnikova & Portnov, 2018) and more generally, the exposure to artificial light at night may have profound impacts on human metabolism through the disruption of hormones secretion (Bonmati-Carrion et al., 2014). Those results may have an important influence on future decision concerning lighting (Haim & Zubidat, 2015).

Integrating darkness in ecological corridors

With green infrastructure policies, for the first time, conservation policies integrate the notion of scale and consider the dynamic nature of biodiversity (Sordello, Vanpeene, & Azam, 2014). These policies promote landscape connectedness throughout Europe, nation-wide and at regional and local scales which may have the potential to improve individual's daily movements, migration, dispersal, gene-flow and ecosystem functioning. In this PhD I focused on a scale only integrating bats daily movements however landscape connectivity is desirable at all scale and it would be valuable to carry out connectivity studies at larger scales studying gene-flow or migration routes for example. At the time when green infrastructure policies were first developed, the importance of the impact of light pollution on biodiversity was not clear yet and therefore not included as a criteria to define ecological corridors (Sordello, 2017). Nonetheless, along the elaboration of their ecological corridors network (SRCE), 21 one of the 22 regions of France mention the issue of light pollution and 6 raise need to acquire further knowledge on this topic (Sordello, 2017). This shows that land managers are aware of the issue but are in demand of proper recommendation to apply them to their territory.

At local and intermediate scale, outdoor lighting planning could be amended to include dark refuges and ecological corridors with low light level to allow for nocturnal species movements. Indeed, landscape connectivity may be greatly improved through the extinction of specific areas such as urban parks and wetlands (**Article 3**). Lighting planning should first be considered at a relatively large scale, coherent with a lighting management scale such as municipalities. The methodology presented in the second chapter could be used to define potential dark corridors for bats (**Article 3 & 4**) and adapted to evaluate such corridors for other nocturnal species. The superposition of several species dark corridors would lead to the determination of a network of links between habitat patches and could allow to delineate areas where lighting need to be reduced or modified to improve landscape connectivity. Then the

knowledge arising from small scale studies may be used to determine how locally the lighting should be ameliorated. Lighting management should be adapted to the context to allow for solutions both suitable for human activities and ecosystem functioning. For example, motion detector could be used in low traffic areas so the area would be lit when used by pedestrians and vehicles but stay dark otherwise. However such type of lighting hasn't been studied yet and its potential benefits or impacts need to be evaluate. The implementation of different lighting regime across a municipality with partial part-night lighting, diming or motion sensor detection may also be technically impossible as public lighting in towns and villages are often all linked and can only be controlled all together and have fairly old underground electrical installations. The emphasis should be put on the decision to install new light sources or not and thoroughly evaluate their pertinence in regard to the impact they will have on the surrounding environment. Whichever the mitigations measures employed to limit the effects of artificial lighting on biodiversity, their effectiveness needs to be evaluated (Mair et al., 2018) and even more so as for now such evaluation of biodiversity-friendly lighting planning has only been carried out on part-night lighting schemes and showed their low potential to benefit biodiversity (Azam et al., 2015; Day et al., 2015).

Rethinking outdoor lighting efficiency

Modern society relies on light as a security measure (Smith, 2009) and public lighting has become a highly political topic. Most political actors I met during my PhD were not inclined to decrease light level due to the perception that citizens won't be in favor of such actions. In addition, European standard EN13201 recommends light levels depending on the urban context. Although following this norm is not compulsory, lighting installation can be controlled and if the norm is not applied, municipalities should thoroughly justified why and may be fined. The norm includes minimal lighting levels but no maximum and often, municipalities chose to apply

light levels above the minimum recommended (Hale et al., 2013). Lighting engineers I met during my PhD also mentioned that it is made even worse by the increased use of street video-surveillance which requires important light levels. The EN13201 standards recommends to uniformly lit pedestrians pathways at a minimum of 7.5 lx although it has been demonstrated that a light level of 0.9 lx was sufficient for pedestrians to detect a 1 cm high obstacle over 3 m ahead (Fotios & Uttley, 2018). In order to find the best compromise between the need of light for human activities and the limitation of light pollution, energy efficiency for outdoor lighting should be redefined through a new approach, the efficient provision of light which implies to provide only the minimum amount of light necessary for a given task while minimizing negative environmental effects and energy use (Kyba, Hänel, & Hölker, 2014).

Raising awareness

The spread of artificial light at night has recently grown to be considered as a major threat to biodiversity and ecosystems. Scientific studies on this topic aim at defining what is

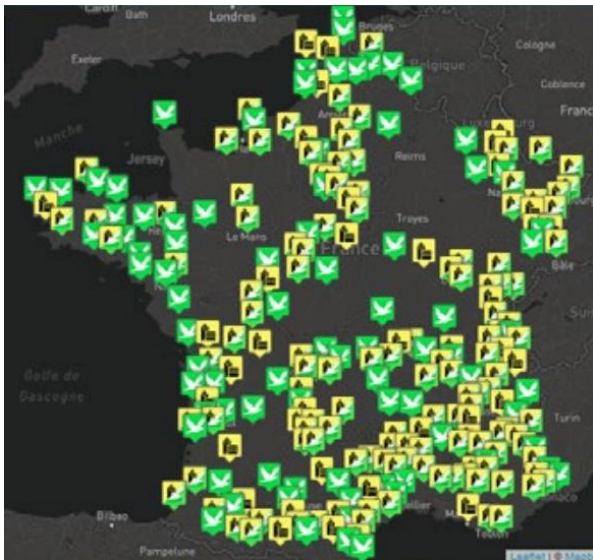


Fig. 34. Manifestations that took place during the Day of the Night in France in 2016. Yellow pictograms indicate outdoor lighting extinctions (n=357) and green pictograms indicate animations organized (n=329).

bad or undesirable about certain types and use of lighting. Yet, in order to raise the general public's awareness, it might be beneficial to adopt another approach by communicating on the values of darkness (Stone, 2017). Since 2009, the Day of the Night (Jour de la Nuit) is celebrated in France in October and is the occasion to organise activities to inform the public on nocturnal biodiversity and invite to the observation of the stars (around 350 animations organized nation-wide each years;

Fig. 34). In 2017, for this occasion, 350 cities across France turned all or part of their public lighting off (www.jourdelanuit.fr). This nation-wide operation is entirely organised by the volunteer association Agir pour l'Environnement which is helped by numerous local volunteer associations across the country to propose activities. In the same spirit, towns and villages amending their public lighting to reduce light pollution can be awarded a starry-sky village label by the association for the protection of the starry-sky (ANPCEN). Awareness and improvement may also be gained through the implication of citizens in the decision-making process of lighting planning.

Importance of interdisciplinary work & mitigation action effectiveness evaluations to propose efficient and functional biodiversity conservation measures

The impact of artificial light at night on biodiversity and ecosystems is tremendous both in its intensity, diversity and spatial extent. There is an urgent need for applied research in conservation biology that will both address the ecological issues and the societal questions linked to it. A recent study showed that research contribution displayed a lack of interest in socio-political questions and action planning. The number of publications on implementation and monitoring declined over time thus suggesting a decreasing interest in the measure of plan effectiveness (Mair et al., 2018). However, in the field of light pollution, large scale research projects have been developed in collaboration with local NGOs and with the financial help of lighting companies (e.g. Philips ;Fig. 35 ;Spoelstra et al., 2015), local authorities develop projects with land managers, lighting engineers and scientific from both ecology and social sciences (project in the Haut de France mentioned above) and environmental consultants like Auddicé Environnement finance research such as my PhD thesis. This type of projects should be encouraged as they are the necessary link between biological research and conservation planning. The integration of the social sciences and the development of interdisciplinary



Fig. 35. Pictures of the installations of the large scale project LichtOpNatuur testing the effect of different color spectra on a diversity of taxa (photos by K. Spoelstra)

collaboration may prove indispensable to assure the success of conservation efforts (Mair et al., 2018). I would add that due to the speed to which lighting technologies evolve, most *in situ* studies evaluate the impact of lamp types that are not used anymore and it would be more productive to directly work with lamp constructors to provide useful insight for future lighting installations. Scientifics need to bridge the gap between research studies results and land managers. Implementation evaluation are seldom performed and scientific papers are not often accessible to land managers thus conservation actions remain based on personal experience (Pullin et al., 2004). The improvement of exchanges between scientists and land managers, environmental consultants and lighting engineers through collaborative projects are key to the development of research project with the potential to propose mitigation measures congruent with human activities and ecosystem functioning.

“Young fool, only now, at the end, do you realize the power of the Dark side...”

Darth Sidious

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ANNEX

ARTICLE 6

Claireau F., Bas Y., Pauwels J., Puechmaille S J., Julien J.-F., Machon N., Allegrini B. and Kerbiriou C. Large effects of major roads on the insectivorous bat activity. *In prep.*

ARTICLE 6

LARGE EFFECTS OF MAJOR ROADS ON THE INSECTIVOROUS BAT ACTIVITY

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Abstract

Transport has been identified as one of the ten main pressures on biodiversity. Although the effects of transport have been very well documented for terrestrial mammals, birds, amphibians... there are lack of studies interested on effects of roads on bats. In order to improving the knowledge, we conducted acoustic surveys on 306 sample points on a whole night at different distance from a major road in 3 study site in France. In order to assess the relationship between bat activity and distance from major roads, we used generalized linear mixed models for 13 different taxa. Our results found a significant linear negative effect of major roads on bat activity for 5 taxa (low-flying species) up to 5 km. This study confirms the two previous peer-reviewed studies but generalize for another species and reports an even strong effect. We believe major roads act as a barrier for bats and can cause dramatic change on bat population. Considering our results and the road-effect zone, 35,32 % of the European union and 5,19 % of Natura 2000 areas in European union are concerned. These worrying results must be take into account in plan management. Avoidance of new roads by alternatives is necessary. Finally, in order to improve habitat connectivity or foraging areas in the actual road-effect zone, mitigations and offset measures should be employed.

1. Introduction

Transport (e.g., roads) has been identified as one of the ten main pressures on biodiversity (Maxwell et al. 2016) due to destruction of natural habitat, and landscape fragmentation including edge effects, barrier effects. In addition, traffic induce direct mortality by collision with vehicles (i.e., roadkills) generate light and noise disturbance and chemical pollution (Forman & Alexander 1998; Forman & Deblinger 2000). These dramatic changes in landscape configurations have consequences on many levels: from individual behaviour to population dynamics to the overall functioning of ecosystems (Quinn & Harrison 1988; Saunders, Hobbs & Margules 1991; Fischer & Lindenmayer 2007; Krauss et al. 2010).

Since 2000, worldwide roadway network length increased by approximately 12 million lane-km, and previsions are that global roads are likely to grow by nearly 25 million paved lane-km by 2050 (Dulac 2013). Road ecology is now increasingly studied, road effects studies covering currently a variety of taxa: terrestrial mammals, amphibians and birds, except notably bats (Berthinussen & Altringham 2012b). However, the effects of roads on bats are potentially numerous including habitat loss, reduced habitat quality, mortality by collision and barrier effects among habitats (Bontadina, Schofield & Naef-Daenzer 2002; Zurcher, Sparks & Bennett 2010; Bennett & Zurcher 2013; Frey-Ehrenbold et al. 2013; Medinas, Marques & Mira 2013; Kitzes & Merenlender 2014; Abbott et al. 2015; Fensome & Mathews 2016; Møller et al. 2016). The cumulative effects of these factors could be deleterious on bat populations (Altringham & Kerth 2016).

Bats use linear elements, such as hedgerows, to commute nightly (Frey-Ehrenbold et al. 2013) partly because a majority of them are reluctant to fly in open grounds or due to their sensitivity to light (Azam et al. 2018). Moreover, major roads may be barriers for bats because roads disconnect existing flight paths along linear features (e.g. hedgerows) and interrupt bat

commuting movements between breeding colonies and foraging areas (Bennett & Zurcher 2013). Even small gaps in linear element can affect drastically the probability of crossing. Indeed, in Indiana (USA), gaps of 5 m in tree or shrub cover along flight routes have been shown to significantly impact bat commuting movements (Bennett & Zurcher 2013). In United Kingdom, it has been stated that a gap of as little as 10 m may deter a bat from its flight path (Entwistle et al. 2001). Furthermore, Pinaud et al. (2018) demonstrated that bat movements were significantly affected by gap width: the probability of crossing falls down 0.50 for gaps larger 38 m i.e., similar to a gap caused by major roads. Moreover, Hale et al. (2012) demonstrated that bat activity in an habitat patch increased with the degree of connectivity of the surrounding landscape. This point is all the more important because, for a majority of bat species, nocturnal activity implies moving far from their roosts [0.6 - 11.7 km for *Rhinolophus ferrumequinum*, (Flanders & Jones 2009; Dietz, Pir & Hillen 2013); 0.2 - 4.7 km for *R. hipposideros* (Bontadina, Schofield & Naef-Daenzer 2002; Reiter et al. 2013); 0.5 - 11.5 km for *Eptesicus serotinus* (Catto et al. 1996); 0.9 - 3.7 km for *Pipistrellus pipistrellus* (Nicholls & Racey 2006; Davidson-Watts, Walls & Jones 2006); 2.3 - 9.2 km for *Myotis daubentonii* (Encarnacao et al. 2005; Nardone et al. 2015); 1 - 13 km for *Nyctalus leisleri* (Szentkuti et al. 2013)]. The necessity for bats to move on long distances implies a high likelihood for their populations to be impacted by road network within their home range.

Many European bats are endangered throughout much of their range and numerous causes of this situation have been identified, including habitat loss and degradation and roadkills which can cause by roads (Temple & Terry 2007). According to their life cycle (i.e. low fecundity, late maturation), population growth rate heavily depends on adult survival. Thus, mortality by roads is expected to increase their local extinction risk (Medinas, Marques & Mira 2013). All European bats are legally protected in European countries through national or European laws (Council Directive, 1992; Convention on Migratory Species, 1985–2008, and

Agreement on the Conservation of Populations of European Bats). Some of these protection status involve considering the negative effects of project development on biodiversity and limiting them through mitigation hierarchy (avoiding, reducing, restoring, and offsetting effects) with the aim to achieve a no net loss of biodiversity or a net environment (Regnery, Couvet & Kerbiriou 2013). And although bats benefit of strict protection status in many countries and road impacts appear potentially deleterious for bats, surprisingly, bats are very rarely taken into account in project road designs. Indeed, most of mitigation measures dedicated to bats in Europe are more focused on the reduction of impact such as bat overpasses than the compensation of habitat loss (Møller et al. 2016). Moreover, on the Conservation Sciences side only two studies focussing on road impact on bat activities have been published (Berthinussen & Altringham 2012b; Kitzes & Merenlender 2014). Berthinussen & Altringham reported the correlations existing between distance to major roads and bat activities. Bat activities were measured by the recording of the echolocation cries emitted by the bats. Thus, they found a decline of bat activity for a common species: *P. pipistrellus*, to a distance of at least 1,6 km (i.e. the maximum extent of their study area) on both sides of a road in Cumbria (United Kingdom). Kitzes & Merenlender also found a negative effect of roads on bat activity within 300 m (corresponding to the extent of the study area) for 4 common bat species in California state (USA): *Tadarida brasiliensis*, *Eptesicus fuscus*, *Lasiurus cinereus* and *Lasionycteris noctivagans*.

According to bat home range sizes and the importance of landscape connectivities for bat daily movements, we hypothesis that road may affect bat activity at the landscape scale. We conducted acoustic surveys in three sites in France (10 km squared) at different distance of major roads in five main habitats. We tested effect of distance to major roads on several taxa activities considering the habitat.

2. Materials and methods

2.1. Study sites

We selected three sites located in rural areas in western France including in each site, at a central position, an highway but exhibiting variations in land-uses composition (Fig. 1 & A.1). The extent of each study site is a 10 km square allowing studying potential impact of road at landscape scale (i.e. a scale of the same magnitude than a majority bat home-range (Catto et al. 1996; Davidson-Watts & Jones 2005; Hillen, Kiefer & Veith 2009; Bernd-Ulrich, Alois & Von Helversen 2009; Razgour, Hanmer & Jones 2011; Dietz, Pir & Hillen 2013). The first site was surrounded by intensive farming and located in the "Vendée" county near Niort (46°24'N, 0°35'W) and focused on the road A83 (which became operational in 2001; road with tarmac; 4 lanes with emergency lane on both sides; speed limit: 130 km/h, annual average daily traffic: 16 218 vehicles in 2015). The second site was mainly surrounded by woodlands and grasslands and located in the "Charente-Maritime" county near La Rochelle (45°50'N, 0°37'W) and focused on the road A10 (which became operational in 1994; same features as A83; annual average daily traffic: 27 377 vehicles in 2015). The last site was mainly surrounded by woodlands and grasslands in the "Ille-et-Vilaine", and located in Britany near Rennes (48°2'N,14°57'W) and focused on the road N24 (became operational in 1981; road with tarmac; 4 lanes without emergency lane on both sides; speed limit: 110 km/h; annual average daily traffic: 33 800 vehicles in 2015).

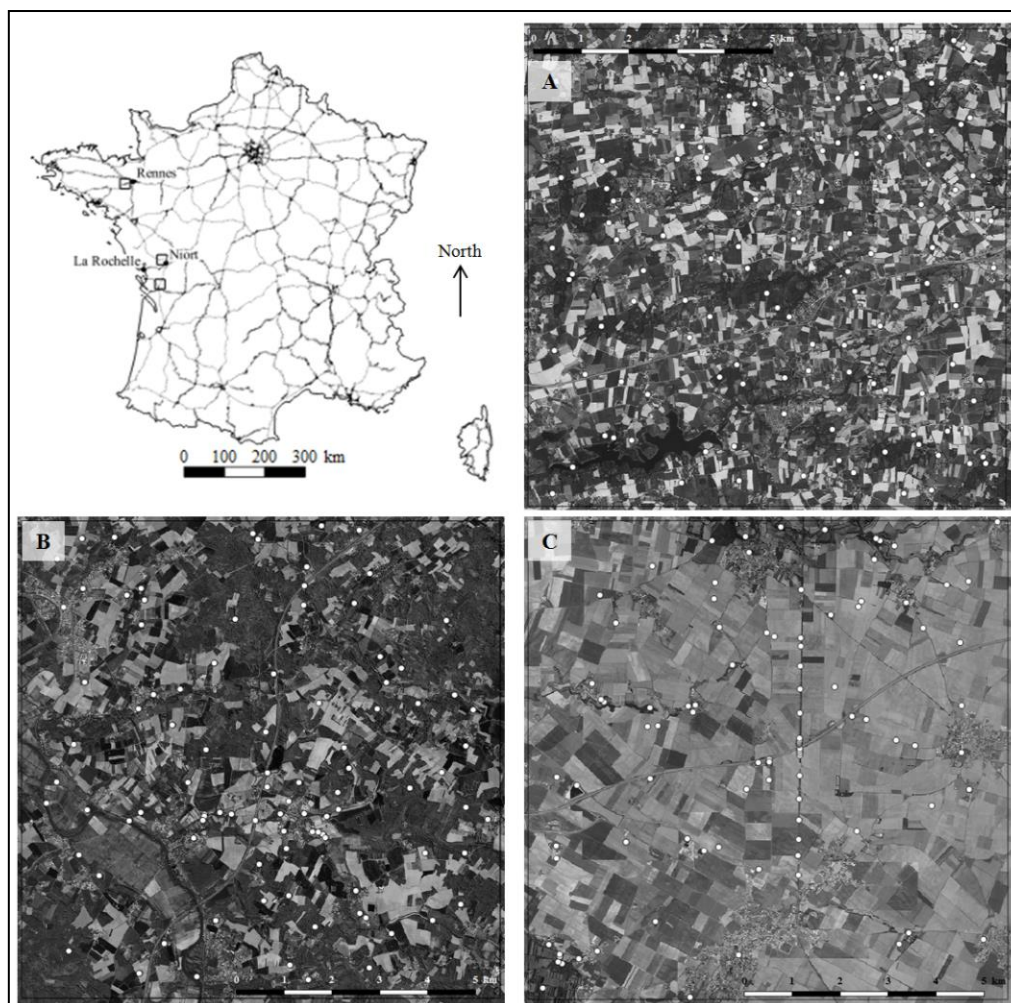


Figure 1 Study sites: N24 (A), A10 (B) and A83 (C). White points represent sample points of recordings.

2.2. Sampling design

With the aim to assess the influence of major roads on bat activity, we recorded in each site different acoustic sample points: for A83, $n = 100$; for A10 $n = 94$; and for N24, $n = 112$. Five main habitats in each site was sampled (wetlands, woodlands, agricultural lands, urban areas and hedgerows) at different distance from the road (from 25 to 5420 meters). Each habitat was sampled in average 61.2 ± 5.06 and for each twelve 400 m distance classes, each habitat was sampled 5.01 ± 2.16 (Table A.1). In order to homogenize the conditions of sampling in each

site, we sampled simultaneously the five main habitats during the same nights at different distance classes and over several consecutive nights by changing the points

2.3. Acoustic surveys

The fieldwork was carried out, during the seasonal peak of bat activity, between the 28th of May and the 17th of August 2016. Recordings were conducted during 9 successive nights for A83 (in May-June), 8 successive nights for A10 (in July) and 10 successive nights for N24 (in August).

Bat activity was assessed by recording bat calls using Song Meter SM2Bat+ detector (Wildlife Acoustics Inc., Concord, MA, USA) fitted with omnidirectional ultrasonic microphones: SMX-US (Wildlife Acoustics Inc., Concord, MA, USA) placed at a height of 1 m from the ground. We tested systematically microphone sensibility when we installed and removed each sample point. Recordings were performed during the whole night (from 30 min before civil sunset to 30 min after civil sunrise).

With such Passive Acoustic Monitoring (PAM), the detectors automatically recorded all sounds (> 8 KHz) while maintaining the characteristics of the original signals. We used a trigger level threshold of 6 dB signal-to-noise-ratio (SNR) for frequencies between 8 and 384 KHz following the triggering of the French Bat Monitoring Programme [FBMP, (Kerbiriou et al. 2018a)].

2.4 Species identification

To identify the species from acoustic recordings, we first used Kaleidoscope© software (Wildlife Acoustics Inc., Concord, MA, USA) to extract .wav files from the recorded .wac files.

A time expansion factor of 10 was specified, and we split channels using five seconds as a maximum duration.

Then, we analysed the ultrasound recordings with the software Tadarida in its latest version [(Bas, Bas & Julien 2017), online repository: <https://github.com/YvesBas>]. This software automatically detects and extracts sound feature parameters of the recorded echolocation calls and classifies them into known classes according to a probability value that a call is from a specific group/bat species using a random forest algorithm (Cutler et al. 2007).

Using a FBMP dataset of manually checked calls by the national Museum experts (17 531 sound events), we performed a logistic regression between the success/failure of automatic species assignation and the confidence index provided by the software for all species. Following the approach of Barré et al. (2018), we could hence associate each confidence index with an identification success probability and calculate the minimum confidence index required for a species to tolerate a given maximum error risk, i.e., confidence threshold (appendix B). We used the confidence threshold calculated on the national dataset to create subsets of this study's dataset. We performed all analysis on a subset with a 0.5 maximum error risk tolerance and on another subset more restrictive (i.e., a 0.1 maximum error risk tolerance).

First, we studied the activities for all the bats and then the activity of two sets of species based on their flying and foraging preferences. The set of aerial species is composed of five species which are medium to high-altitude fast-flying species: *E. serotinus*, *N. leisleri*, *N. noctula*, *P. kuhlii* and *P. pipistrellus* (Blake et al. 1994; Lacoëuilhe et al. 2014; Azam et al. 2015; Roemer et al. 2017). The set of clutter species is composed of low-altitude slow-flying species that generally forage in cluttered vegetation, i.e, *Barbastella barbastellus*, *R. ferrumequinum* and *R. hipposideros* and two groups: *Myotis spp.* and *Plecotus spp.* which cannot be identify at the species level with certainty (Obrist, Boesch & Flückiger 2004). In third time, we conducted analysis for these eight species and the two species groups.

Since it is impossible to determine the number of individual bats from their echolocation calls, we calculated a bat activity metric (bat passes), as the number of contacts per species and per night. Thus, a bat pass was defined as a single or more echolocation call within a 5-second interval. This interval is considered a good compromise according to bat pass duration among species (Millon et al. 2015; Kerbiriou et al. 2018b). Although it does not allow us to assess bat abundance, it can reflect the suitability of the habitat in terms of food resource.

2.5. Environmental variables

With the aim to assess the joint effect of major road distance on bat activity and accounting for surrounding habitat, at each sample point, we extracted 57 variables (Table A.2). These variables are: several distances (e.g., to the major road, hedgerow...) and variables taken within a buffer of 50, 200 and 500 m radius around each sample point (e.g., density of hedgerows, proportion of ponds, proportion of crops...). The choice of each variable corresponding to numerous studies that have identified these habitat can influenced bat activity (Verboom & Spoelstra 1999; Russo & Jones 2003; Kaňuch et al. 2008; Rainho & Palmeirim 2011; Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Kelm et al. 2014; Lacoeyuilhe et al. 2016). And we chose these three buffer because the landscape effect on bat activity could change according to the spatial scale considered (Grindal & Brigham 1999; Lacoeyuilhe et al. 2016; Kerbiriou et al. 2018a).

Landscape data come from a manual digitization by photo-interpretation (Fig. A.1); and distances, lengths and proportions were calculated using QGIS 2.18.14 (QGIS Development Team 2017).

2.6. Bat activity modelling

We assessed if bat activity (i.e. our response variable is the number of bat passes) could be influenced by the distance to road using Generalized Linear Mixed Model (GLMM) with the glmmTMB function (R package glmmTMB) with a negative binomial link to deal with overdispersion in the count data (Zuur et al. 2009). When occurrence of bat activity was recording under 50% of sampling points, we conducted models with zero-inflated.

According to the sampling design (i.e., simultaneous recordings of bat activity the same night in different habitat at different distance class in successive nights for each site), we included a two level random effect to take into account the spatial structure (sampling points nested within site) as recommended in Bates et al. 2014.

With the aim to assess the join effect of road distance on bat activity and accounting for surrounding habitat, we included in the modelling, landscape co variables as fixed effect. We also included interactions of the distance to the major road with hedgerows and wetlands in order to assess the landscape dependence.

All fixed effects were centred and standardized so that the regression coefficients were comparable in magnitude and their effects were biologically interpretable (Schielzeth 2010). With the aim to avoid over-parametrization, we selected the best scale of covariates (i.e., 50, 200 and 500 m) before including them in the full model, using hierarchical partitions (R package hier.part). Thus, this selection process led us to include the 5 best covariates in the full model. Thus, our full models included 8 environmental covariates (6 simple effects and 2 interactions) and were structured in the following way:

$$\text{Bat activity} \sim \text{Distance to major road} + \text{Landscape co-variables} + \text{Interaction terms} + 1|\text{Site/Point}$$

In order to avoid potential multicollinearity problem we ensured that all the variables used have a Spearman's rho under 0.7 (Dormann et al. 2013). In addition, we assess Variance Inflation Factor (VIF) following Chatterjee & Bose (2000) and Zuur, Ieno & Elphick (2010) approaches, while all variables showed a VIF value <3 and the mean of VIF values <2 there was no evidence of multicollinearity. We also checked the non-spatial autocorrelation of residuals of each selected model using Moran's I test (R package *ape*).

From the full model, we applied a stepwise selection with backward elimination by removing at each step the least significant variable while taking account to the model with lowest AIC. Furthermore, we aimed to evaluate whether the quality of our model was good by comparing it to the null model (including only the random effects) using Akaike's information criterion (AIC) (Burnham, Anderson & Huyvaert 2011; Mac Nally et al. 2017). In order to assess the influence of error link identification, we also ran selected models with a 0.1 maximum error risk tolerance and compare p-value and estimates provided by models with a 0.5 maximum error risk tolerance.

Finally, the potential non-linear effect of the distance to a major road was checked by visual inspection of the plot from Generalized Additive Mixed Models (GAMM, R package *mgcv*).

2.7. Road-effect zone

Following Forman & Deblinger (2000) approach, we assessed the potential cumulative effect of the "road-effect zone" at the scale of European Union. Depending results obtained by our models by species, we hence estimated the proportion of area which could be impacted by major roads in Europe and Natura 2000 areas on bat activity.

3. Results

3.1. Bat monitoring

In the dataset allowing for a maximum error risk of 0.5, there was a total of 223 601 bat passes for ten species in the three study sites. Bat activity for aerial species (n=89.4%; 200 072 bat passes) were higher than clutter species (n=10.6%; 23 729 bat passes). Among these 223 601 bat passes, the most abundant species was *Pipistrellus* species (n=85.6%; 191 546 bat passes) and *Myotis spp.* (n=8.2%; 18 282 bat passes) and least abundant species were *Nyctalus* species (n=1.5%; 3 383 bat passes), *Rhinolophus* species (n=0.6%; 1 354 bat passes) and *Plecotus* species (n=0.5%; 1 257 bat passes), (Table 1).

Table 1 Total of bat passes, occurrence, number of points recorded bat passes (%) and mean with standard error of bat passes per sample point for each sample point at 0.5 maximum error risk tolerance

Species	Total bat passes	Occurrence on 306 sample points	Occurrence (%)	Mean of bat passes per sample point	SE of bat passes per sample point
<i>B. barbastellus</i>	2 836	181	59.15	9.27	1.46
<i>E. serotinus</i>	5 143	167	54.58	16.81	3.78
<i>Myotis spp.</i>	18 282	244	79.74	59.75	12.53
<i>N. leisleri</i>	1 726	111	36.27	5.64	1.25
<i>N. noctula</i>	1 657	69	22.55	5.42	1.80
<i>P. kuhlii</i>	29 090	222	72.55	95.07	17.74
<i>P. pipistrellus</i>	162 456	299	97.71	530.90	53.75
<i>Plecotus spp</i>	1 257	141	46.08	4.11	0.80
<i>R. ferrumequinum</i>	319	53	17.32	1.04	0.30
<i>R. hipposideros</i>	1 035	105	34.31	3.38	1.25

3.2 Impact of major roads on bat activity

Species effects

At the species scale, our results showed a significant negative effect of major roads on bat activity for 4 species on the 10 studied i.e., for these 4 species, the bat activity increased with the distance to the major road. These 4 species were *E. serotinus* ($P < 0.05$), *Myotis spp.*

($P < 0.001$), *P. pipistrellus* ($P < 0.05$) and *R. hipposideros* ($P < 0.05$) (Table 2 & C.1). We also found a significant negative effect of the interaction between the distance from a major road and the distance to an hedgerow for *Myotis spp.* and *P. pipistrellus* ($P < 0.05$) and a significant negative interaction between distance from a major road and the density of hedgerow in buffer of 200 m for *E. serotinus* ($P < 0.05$) (Table 2 & C.1). All models showed a lower value of AIC than null models ($\Delta > 2$) (Table C.2).

Table 2 Estimates, standard errors and p-value of the distance from the major road variable for all bat, the two guilds, the two species group and the eight species studied according a maximum error risk of 0.5 in species identification. Legend: *, subsist spatial-correlation in the model even if we added the autocov_function; X, distance from the major road non-selected in the best model. Complete results of other covariates can be found in Table C.1.

	All bats	Aerial species	Clutter species	<i>B. barbastellus</i>	<i>E. serotinus</i>	<i>Myotis spp</i>	<i>N. leisleri</i>
β	0.13212	0.10848	0.28870	-0.11880	0.34200	0.41421	X
SE	0.07095	0.07703	0.08566	0.13490	0.15910	0.09659	X
p-value	0.06260	0.15900	0.00075	0.37853	0.03160	0.00002	X

	<i>N. noctula</i>	<i>P. kuhlii</i>	<i>P. pipistrellus</i>	<i>Plecotus spp</i>	<i>R. ferrumequinum*</i>	<i>R. hipposideros</i>
β	X	0.03277	0.18830	X	-0.02274	0.47630
SE	X	0.13775	0.08159	X	0.22713	0.20250
p-value	X	0.81190	0.02100	X	0.92030	0.01870

All bats, aerial and clutter species

According to a maximum error risk of 0.5 in species identification, our results showed a slight non-significant negative effect ($P < 0.062$) of major roads on bat activity for all species sampled in this study. We also found a slight non-significant effect of the interaction of the distance from a major road with the distance to a hedge ($P < 0.061$) (Table 2 & C.1).

Concerning the aerial species, we found no effect of the distance to a major road on their activity ($P = 0.159$). For clutter species, our results demonstrated a significant negative effect of major roads on their activity ($P < 0.001$) (Table 2). Moreover, we found an interaction of the

distance to a major road with the distance to an hedge ($P < 0.01$) (Table C.1). The interaction showed that clutter species are more commuting on hedgerows when they fly near a major road (Fig. C1).

3.3. Additional analyses with GAMM

For bat activity species impacted by the distance to a major road by GLMM, we did not detect non-linear effect for all taxa except clutter species and *Myotis spp.* where a weak change in slope was observed around 700-1300 m from the road (Fig 2).

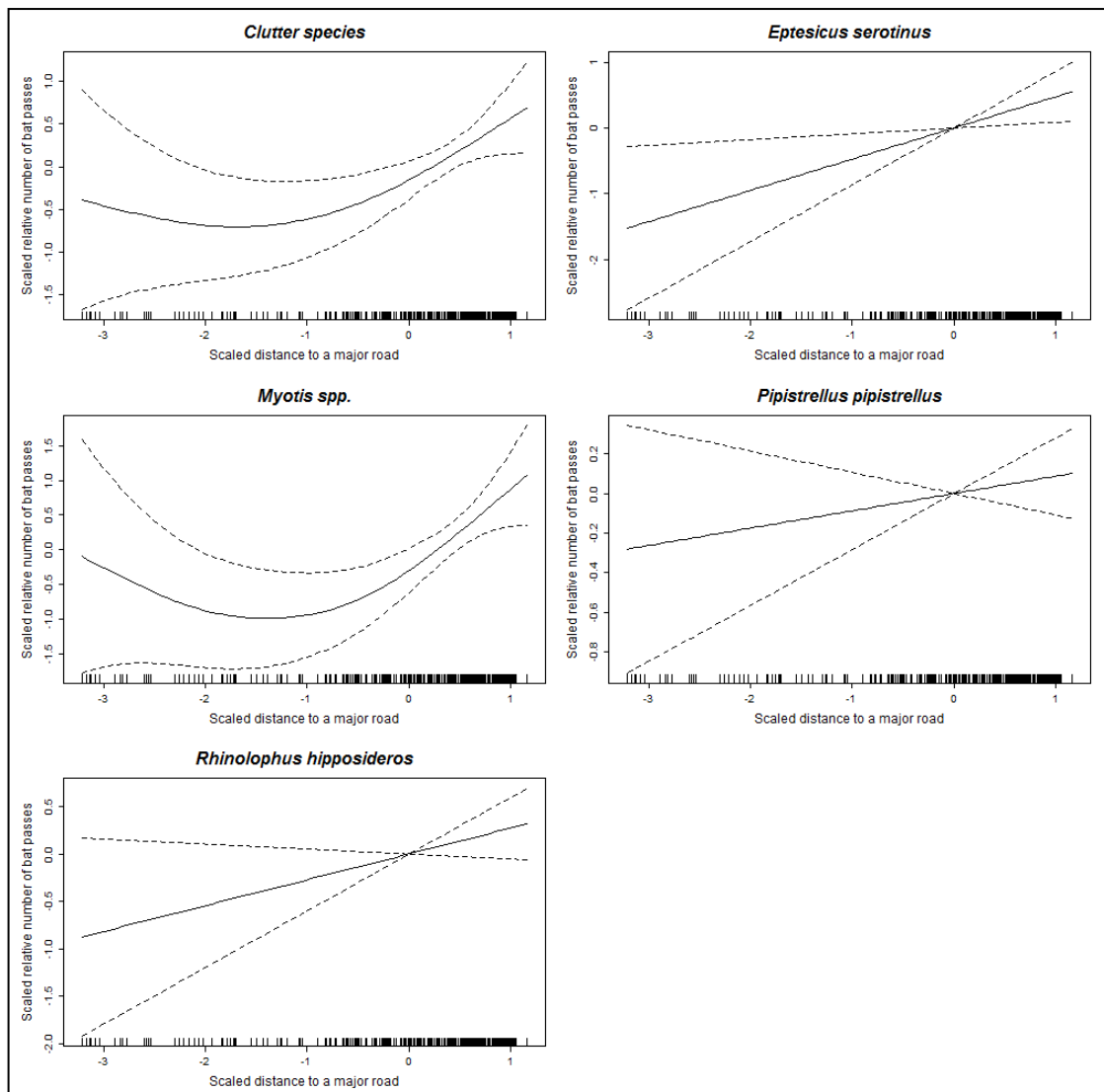


Figure 2 Generalized additive mixed model (GAMM) for species where a significant negative effect has been assessed. Scaled distance to a major road: -3, 0 m; -2, 110 m; -1, 370 m; 0, 1330 m; 1, 5000 m.

3.4 Influence of error risk

We ran again the analyses for species for which a significant negative effect had been found using the most restrictive tolerance of 0.1 maximum error risk in the data selection of the response variable (i.e., corresponding to an error rate between 2.9% to 5.3% of the total number of bat passes, Table B.1). We found qualitatively similar results for all taxa precluding for *P.pipistrellus* which was not significant for a 0.1 maximum error risk.

3.5 Road-effect zone

We assessed the potential cumulative effect of the "road-effect zone" on bat activity detected previously by our results (i.e., an impact of major road up to 5 km) and applied it at the Europe scale and on Natura 2000 areas. We found that, bat activities in 35,32 % of Europe and 5,19 % of Natura 2000 areas are potentially under the influence of major road (Fig. 3).

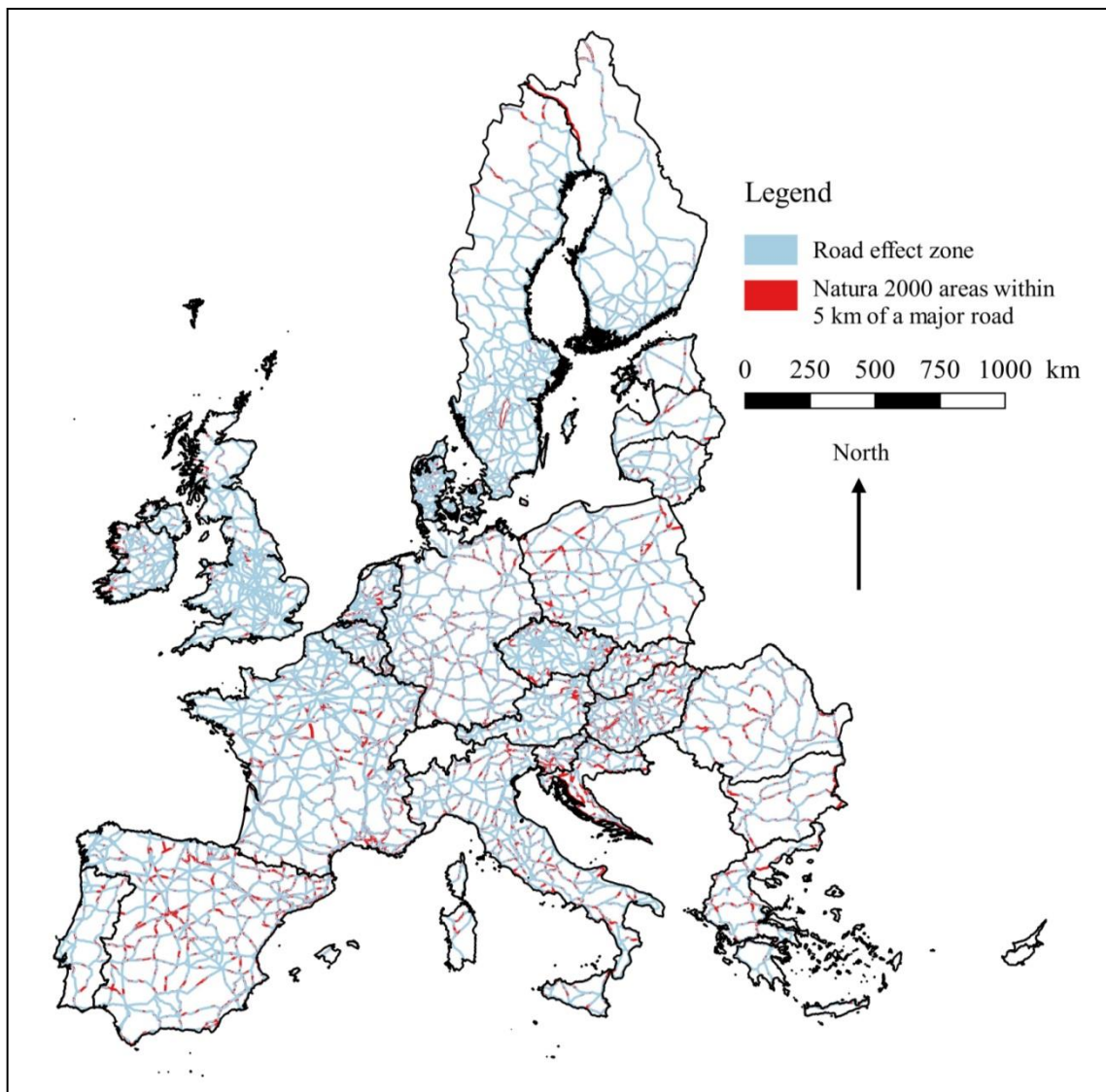


Figure 3 Mapping of areas impacted by major roads in Europe.

4. Discussion.

4.1. Road effects

Among the 13 bat taxa studied here, 5 taxa seemed to be significantly impacted by major roads, no one exhibited a positive effect of major roads. The five species were belonging to the clutter species group, *E. serotinus*, *Myotis spp.*, *P. pipistrellus* and *R. hipposideros*. Noticeably, no effect was found for *P. kuhlii* while it was the second species which used the most the bat

passes (13% of total bat passes). This result suggest that the activity of this species is not disturbed by major roads. At the opposite, for *R. hipposideros*, a species rarely contacted [0.46% of total bat passes, 34.31% of occurrence (Table 1)] we found a significant effect suggesting that this species could be very sensitive to major roads. We cannot exclude that for other species rarely contacted such as *R. ferrumequinum*, we did not detect an effect by lack of statistical power. To detect a potential effect, it would be essential to improve the sampling design for example in extend the sampling area.

The important sensitivity of the clutter species such as *R. hipposideros* and *Myotis spp* to roads can be explained by their ecology. Indeed, clutter species are more gleaner than aerial species, and thus forage more in woodlands and fly less in open space.

With the importance of the effect, we were able to compare the road effect to other well-known factors identified to substantially improve the accuracy of predictive model for bat occurrence or abundance such as distance from a hedge (Kelm et al. 2014; Pinaud et al. 2018; Lacoëuilhe et al. 2018). The effect size of distance to the major road is equivalent to 40% of the effect of the distance to an hedgerow for *P. pipistrellus* and 50% for *R. hipposideros*. *Myotis spp.* appeared more sensitive than other species because the effect size of the distance from a major road is of the same magnitude than the distance from an hedgerow (i.e., 100%).

We also found an interaction between the distance to major roads and the distance to an hedgerow. Clutter species appeared commuting and/or foraging more on hedgerows when they flied closer to a major road, suggesting a possible behavioural response - bats seeking refuge in the surrounding of hedgerows - when exposed to situation (the closer road zone) perceived at risks.

This differential response of bat according to their flying traits may be related to a perception of a real risk of road dangerousity. In Europe, Fensome & Mathews (2016) found that

low-flying species are more prone to collisions than high-flying species. Especially in France, *P. pipistrellus* and *Myotis spp.* are considered the species with the most fatalities (Capo, Chaut & Arthur 2006).

Another non-exclusive hypothesis to explain a lower bat activity close to major roads could be that bats avoid lit areas. Indeed, even if studies found that *P. pipistrellus* and *E. serotinus* were light-tolerant at a local scale (Azam et al. 2018), their movements are supposed to be negatively affected by light at a landscape scale (Hale et al. 2015; Azam et al. 2016). For species identified as light-avoider such as *R. hipposideros*, Stone, Jones & Harris (2009) have shown that light can have significant negative effect on commuting. Similarly for *Myotis spp* (light-avoider species), Azam et al. (2018) showed that light induced habitat loss.

A third non-exclusive hypothesis of the avoidance of bats close to major roads is the rupture of habitat connectivity. Although bats are able to cross large roads, involving cross gaps of 30–100 m (Claireau et al. in revision; Abbott, Butler & Harrison 2012), the probability of crossing gap can decrease with gap width (Entwistle et al. 2001; Bennett & Zurcher 2013; Pinaud et al. 2018). Overall, there is a consensus regarding the importance of the conservation of connected linear features to facilitate bat commuting within landscape (Hale et al. 2012).

Studies will have to be carried out to assess the relative part of these different hypotheses explaining the observed decrease of bat activity in the surrounding of roads. This avoidance could have negative impacts for bats to access to foraging areas, involving increase of paths length, decrease of home range quality and thus potentially their fitness and population dynamics. Indeed, a recent study in United Kingdom, found that *R. ferrumequinum* colony size was positively related to a range of landscape features (e.g. amount of broadleaf woodland and grassland, and density of linear features) surrounding the roost (Froidevaux et al. 2017).

4.2. Limitations and robustness of results

Our results showed an obvious avoidance of major roads by bats up to 5 km without drastic slope changes [i.e., only linear effects, (Fig. C.1)]. Beyond a certain distance, major roads are expected to no longer influence bat activity. With our study design that allowed to measure bat activity on points located several kilometre from the road (Table A.1), we expected to observe an attenuation of the road effect when the distance to the major road increased. Possibly changes in slope occurred but were too weak to be detected with our study design and important attenuation of the road effect was observed over 5 km.

These results are congruent with previous studies. Kitzes & Merenlender (2014) found in the USA that bat activity was twice higher 300 m from roads and Berthinussen & Altringham (2012b) found in the UK that bat activity was 3.5 times higher at a distance of 1600 m than at major roads. Finally, for the species and group for which we detected a significant effect of the road, our result showed that the effect of major roads was not limited to a few meters on both sides of the road but had an impact at the landscape scale (i.e., bat home range) highlighting possible impacts at population scales.

4.3. Road-effect zone

Actually, road designs do not take into account road zone effects whereas areas impacted are non-negligible: 35,32 % of the Europe territory and 5,19 % of Natura 2000 areas. These results could be develop considering other variables such as traffic and habitat type crossed by the roads. Considering that other taxa are also impacted by roads, e.g. Forman (2000) found a road effect zone about one-fifth of the USA land area on birds species, it seems urgent to consider the road zone effect on land uses policies and to implement conservation practices all the more for the species are of conservation concerned. Moreover, bats have to face other threats

such as agricultural practices in their home-range. A land use planning is necessary to manage conservation and development of bat species.

4.4. Recommendations

This study highlighted a major effect often neglected in mitigation hierarchy (Bigard, Pioch & Thompson 2017). It is necessary to think of alternatives such as road requalification, e.g., road widening, avoiding building new roads in habitats of good quality for bats, taking into account these effects on a large scale to maintain the good state of conservation of the spaces with stakes and preserving the commuting route as much as possible. .

If the avoidance of road impacts is impossible (i.e., major road impact bat foraging areas), it is necessary to reduce the barrier effect. Many mitigation measures have been proposed in order to restore habitat connectivity such as the implementation of overpasses (e.g., wildlife crossings), underpasses (e.g., viaducts), speed reduction, deterrence and diversion (e.g., planting hedges) and habitat improvement (Møller et al. 2016). Recent studies have suggested that wildlife crossings and underpasses could be the best solution to restore ecological continuity, whereas bat overpasses seem to be less effective (Claireau et al. in revision; Berthinussen & Altringham 2012a; Abbott, Butler & Harrison 2012; Abbott et al. 2015; Møller et al. 2016). When avoidance of impacts and mitigation measures are not sufficient, it is imperative to propose offset measures. These measures can be the restoration of foraging areas and habitat connectivity in the landscape around colonies over the "road-effect zone".

Finally, for future road construction, we advocate to assess the loss of connectivity due to the road effect zone with the aim to evaluate if the connectivity gains obtained by this bat overpasses fully mitigate or not and thus if other offsetting measures will have to be planned for a not net loss.

5. Conclusions

Major roads have a significant negative impact on bat activity, especially on clutter species. It is imperative for new road projects to think about alternatives and for existing ones to reduce their impact through mitigation and / or offset measures.

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ARTICLE 6

APPENDICES

Appendix A: Additional information about material and methods

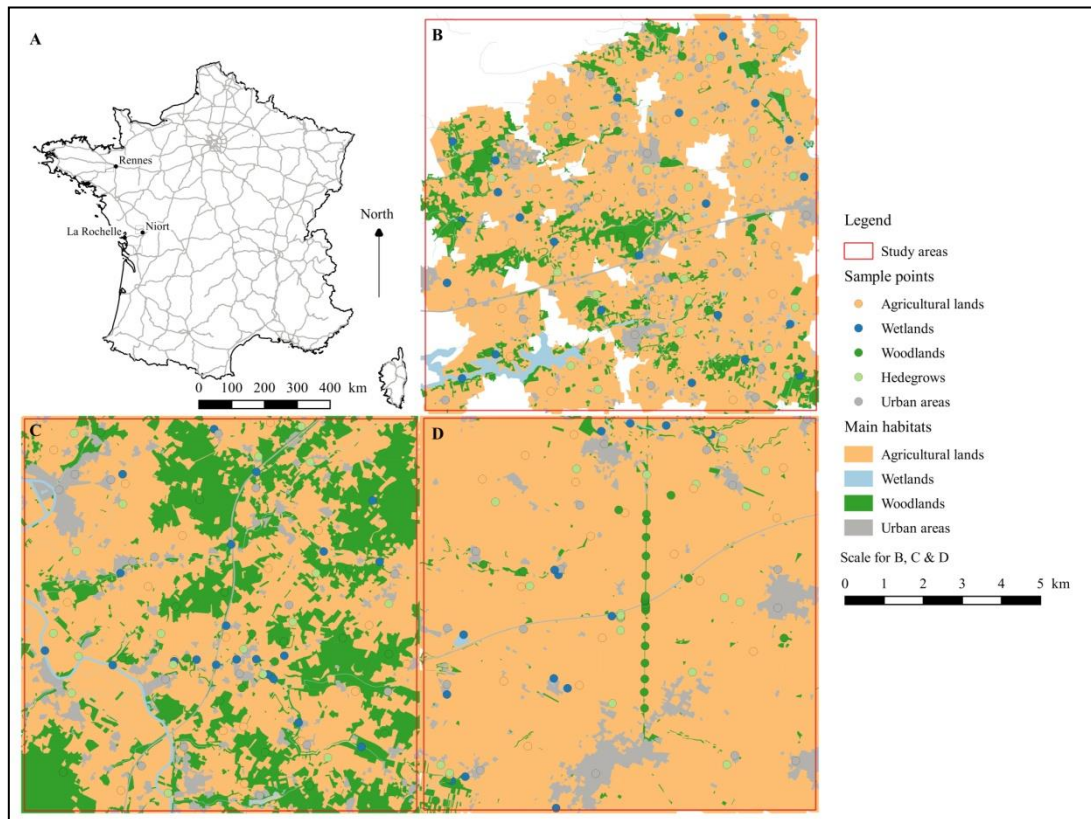


Figure A.1 Study sites: N24 (B), A10 (C) and A83 (D). Manual mapping of land use. Colour points represent sample points of recordings.

Table A.1 Distribution of the sample habitat types in several distance classes to the road.

Distance classes	Agricultural lands	Wetlands	Woodlands	Hedgerows	Urban areas	Total
[0-400 m[7	7	14	11	5	44
[400-800 m[4	5	7	5	6	27
[800-1200 m[6	6	5	8	4	29
[1200-1600 m[6	6	10	6	6	34
[1600-2000 m[5	4	5	4	3	21
[2000-2400 m[7	5	6	5	4	27
[2400-2800 m[2	5	3	7	6	23
[2800-3200 m[6	6	4	6	5	27
[3200-3600 m[5	4	3	3	3	18
[3600-4000 m[3	3	4	5	4	19
[4000-4400 m[6	4	4	2	5	21
[4400-4800 m[3	2	2	4	4	15
>4800 m	/	/	/	/	1	1
Total	60	57	67	66	56	306

Table A.2 Variables used to assess the effect of landscape characteristics on bat activity. Legend: *Italic text*, variables taken within a buffer of 50, 200 and 500 m radius around each sample point

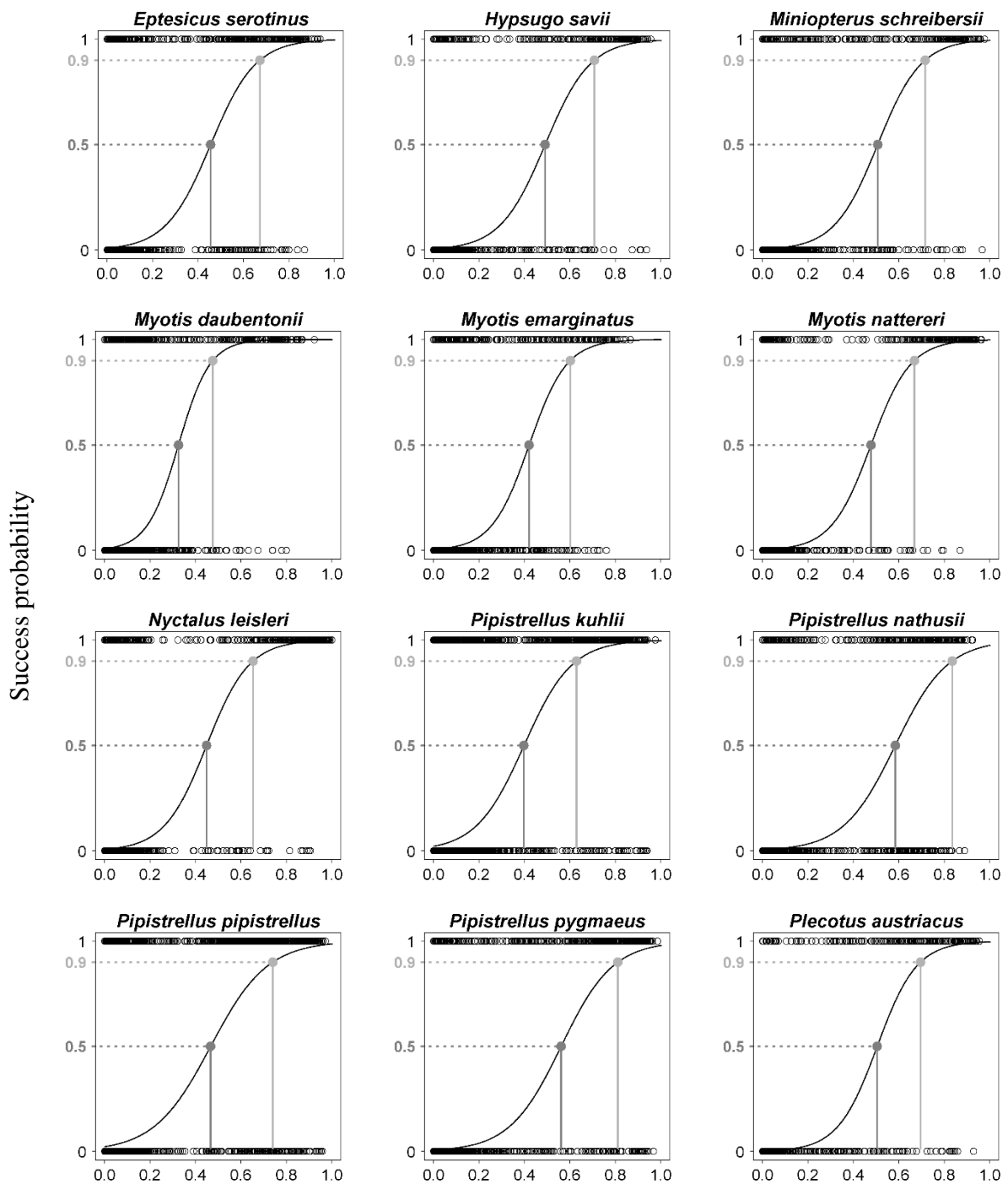
Category	Variable	Description	Unit	Total covariate
Hedgerows	<i>dist_hedge</i>	Distance to hedgerow	m	1
	<i>dist_edgeforest_agri</i>	Distance to edge forest or agricultural hedgerows	m	1
	<i>dist_riparianforest</i>	Distance to riparian forest	m	1
	<i>density_hedge</i>	Density of hedgerows	m	3
Wetlands	<i>dist_wetland</i>	Distance to a wetland	m	1
	<i>wetland</i>	Proportion of wetlands areas	%	3
	<i>hydrographic network</i>	Proportion of hydrographic network	%	3
	<i>pond</i>	Proportion of ponds, lakes, retention basins	%	3
Agricultural	<i>agri_land</i>	Proportion of agricultural areas	%	3
	<i>crop</i>	Proportion of crops	%	3
	<i>meadow</i>	Proportion of meadows	%	3
	<i>vines_orch</i>	Proportion of vines and orchards	%	3
	<i>wood</i>	Proportion of woods (deciduous woodlands and scrublands)	%	3
Wood	<i>dec_wood</i>	Proportion of deciduous woodlands	%	3
	<i>scrub</i>	Proportion of scrublands	%	3
Urban	<i>dist_road</i>	Distance to the major road	%	1
	<i>urban</i>	Proportion of urban areas	%	3
	<i>ALAN</i>	Proportion of lux (artificial light at night)	%	3
	<i>disp_urban</i>	Proportion of dispersed habitat areas	%	3
	<i>dense_urban</i>	Proportion of dense residential areas	%	3
	<i>inter_urban</i>	Proportion of intermediary of dispersed habitat areas and dense residential areas	%	3
	<i>major_road</i>	Proportion of major roads	%	3
	<i>dist_major_road</i>	Distance to the major road	m	1
Total covariates				57

Appendix B: Error risk modelling for bat species identification

A national dataset of 17 531 species occurrences (including 8405 bat passes) underwent automatic identification using the software Tadarida (Bas et al., 2017) (online repository: <https://github.com/YvesBas>) to be classified to the most accurate taxonomic level and assigned a confidence probability between 0 and 1. The same dataset was also manually checked using BatSound© (Pettersson Elektronik AB, Sweden) and Syrinx (John Burt, Seattle, WA, USA)

softwares. The dataset contained data for 28 out of the 34 bat species present in France and all species considered in this study.

For each species, we build a generalized linear model (R Core Team, 2017) using the success/failure of automatic identification as a binomial response variable and the probability given for that species by the random forest classifier as an explanatory variable. We selected the *probit* link which better fitted the binomial distribution of manual checking for all species. Reading the logistic regression curves produced, we could hence determine the needed confidence index to tolerate a given maximum error risk, i.e. confidence thresholds (Figure B.1).



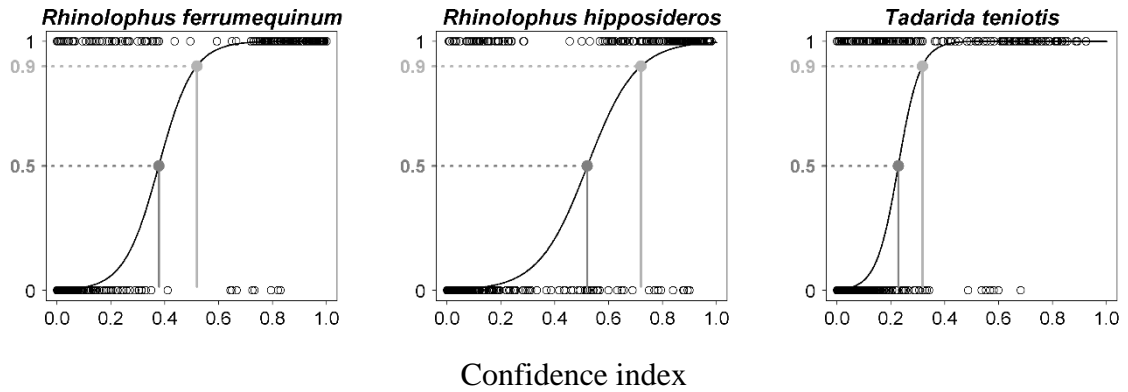


Figure B.1. Logistic regressions between the success probability and the confidence index of the automatic identification for the 15 bat species studied. Horizontal dotted lines show identification success probabilities (0.5 and 0.9) corresponding to the maximum error risk tolerance thresholds used in the analysis (respectively, 0.5 and 0.1) and corresponding confidence thresholds (vertical solid lines). Each open circle represent a bat pass taking an identification success probability value of 1 when correctly identified by Tadarida software and 0 otherwise.

Table B.1 Error rate per species and group for an 0.5 and 0.1 maximum risk tolerance

Species	Group	0.5 maximum error risk tolerance		0.1 maximum error risk tolerance	
		Per species	Group average	Per species	Group average
<i>Barbastella barbastellus</i>	/	2.27%	/	1.06%	/
<i>Eptesicus serotinus</i>	/	8.40%	/	3.73%	/
<i>Myotis alcathoe</i>	<i>Myotis spp.</i>	5.51%	13.28%	1.38%	3.11%
<i>Myotis capaccinii</i>		24.58%		6.86%	
<i>Myotis daubentonii</i>		3.02%		0.88%	
<i>Myotis emarginatus</i>		26.18%		5.99%	
<i>Myotis myotis/blythii</i>		19.03%		4.28%	
<i>Myotis mystacinus</i>		12.60%		1.94%	
<i>Myotis nattereri</i>		15.31%		3.54%	
<i>Nyctalus leisleri</i>	/	6.44%	/	1.78%	/
<i>Nyctalus noctula</i>	/	3.78%	/	0.67%	/
<i>Pipistrellus kuhlii</i>	/	8.83%	/	3.68%	/
<i>Pipistrellus pipistrellus</i>	/	9.49%	/	5.35%	/
<i>Plecotus auritus</i>	<i>Plecotus spp.</i>	23.19%	16.64%	2.22%	2.88%
<i>Plecotus austriacus</i>		10.09%		3.54%	
<i>Rhinolophus ferrumequinum</i>	/	0.20%	/	0.04%	/
<i>Rhinolophus hipposideros</i>	/	3.45%	/	2.88%	/

Appendix C: Additional information about results

Table C.1 Complete results from model selection according a maximum error risk of 0.5 in species identification. Table shows estimates (β), with the standard error (SE) and p-value (P) for all bats, guild and each species/group according to covariates. Legend: /, variable no-selected in full model; X, variable no-selected in selected model. Table A.2 refer the description of each variable.

For *R. ferrumequinum*, it remains in our model spatial autocorrelation even after having corrected it with the *autocov_dist* function (R package, *spdep*) (Table C.1). As we know the location of the only colony in A10 site (Pinaud et al., 2018) we ran models with the distance to the roosting bat. Spatial autocorrelation was corrected but we don't found effect of the major road on their activity. Moreover, according the number of bat passes detected in each site (A10=291 bat passes; A83=24 bat passes; N24: 4 bat passes), we ran model ran at the site scale only for A10 and without the distance to roost. No effect of the distance of the major and no spatial autocorrelation was found (Table C.2).

Table C.2 Additional and complete results from model selection according a maximum error risk of 0.5 in species identification for *R. ferrumequinum*. First model selection with the distance to the colony and the second for only A10 site. Table shows estimates (β), with the standard error (SE) and p-value (P) for all bats, guild and each species/group according to covariates. Legend: /, variable no-selected in full model; X, variable no-selected in selected model. Table A.2 refer the description of each variable.

Variables	<i>R. ferrumequinum</i> with distance to colony			<i>R. ferrumequinum</i> for A10 site		
	β	SE	P	β	SE	P
dist_colo_Rhifer	-0.606	0.205	0.003	/	/	/
dist_major_road:dist_wetland	X	X	X	X	X	X
dist_major_road:dist_hedge	X	X	X	X	X	X
dist_major_road	X	X	X	-0.451	0.355	0.203
dist_wetland	-0.779	0.188	0.000	-0.933	0.252	0.000
dist_hedge	X	X	X	-0.666	0.323	0.039
agri_land_50	X	X	X	/	/	/
wood_500	/	/	/	0.589	0.3024	0.051
urban_50	-0.671	0.313	0.032	X	X	X
crop_50	/	/	/	0.590	0.306	0.053
scrub_500	2.450	1.029	0.017	/	/	/

Table C.3 Full, best and null model with their AIC according a maximum error risk of 0.5 in species identification. Table A.2 refer the description of each variable. Table C.1 refer the estimate, standard error and p-value of selected models.

Table C.4 Estimates, standard errors and p-value of the distance from the major road variable for clutter species, one guild and three species affected by major roads according a maximum error risk of 0.1 in species identification.

Clutter species	<i>E. serotinus</i>	<i>Myotis spp</i>	<i>P. pipistrellus</i>	<i>R. hipposideros</i>
β	0.29293	0.7139	0.4926	0.1106
SE	0.09284	0.3296	0.1115	0.122
p-value	0.0016	0.03034	0.00001	0.364543

As a reminder, **Table 2.** Estimates, standard errors and p-value of the distance from the major road variable for clutter species, one guild and three species affected by major roads according a maximum error risk of 0.5 in species identification.

	Clutter species	<i>E. serotinus</i>	<i>Myotis spp</i>	<i>P. pipistrellus</i>	<i>R. hipposideros</i>
β	0.28870	0.34200	0.41421	0.18830	0.47630
SE	0.08566	0.15910	0.09659	0.08159	0.20250
p-value	0.00075	0.03160	0.00002	0.02100	0.01870