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Oral presentations

Barbaro, L., Andrieu, E., Brockerhoff, E.G., Charbonnier, Y., **Laforge**, **A**., Halder, I.V., & Deconchat, M. (2018) Forest edges as keystone structures for animal biodiversity in mosaic landscapes. *SFE², International conference on Ecological Sciences*, Rennes (France).
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Posters

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Latgé Thomas – Licence professionnelle Etude et Développement des Espaces Naturels (Montpellier) – 3 mois – Evaluation de l'influence du paysage sur l'utilisation des passages inférieurs par les chiroptères (2018) – Encadrement principal.

Fresse Emeline – Master Expertise Ecologique et Gestion de la Biodiversité (Marseille) – 6 mois - Elaboration d'une Trame Sombre par la mise en place d'un protocole sur les chiroptères au sein du Parc national des Pyrénées (65) - *Etude de la tolérance de deux espèces (Rhinolophus hipposideros et Rhinolophus ferrumequinum) et d'un groupe d'espèces (les Myotis) de chiroptères lucifuges à la pollution lumineuse* (2018) – Encadrement en partenariat avec le Parc National des Pyrénées (Eloïse Deutsch).

ABSTRACT

Landscape anthropization through habitat loss and fragmentation is one of the main threats to biodiversity. This PhD (CIFRE funding) was carried out in at INRAE Toulouse (Dynafor lab) in collaboration with the Conservatoire des Espaces Naturels de Midi-Pyrénées (CENMP). It aimed at a better understanding of the impacts of light pollution and road expansion on bats, two major and inevitable elements of anthropization, using a landscape ecology framework applied to bat conservation. This work is structured in 4 sections: (i) by means of an exhaustive review of bat telemetry studies in Europe and North America, I explored how landscape anthropization influenced bat mobility through mean home range sizes and commuting distances; (ii) using simultaneous acoustic sampling of bat communities at both edge and interior forest patches in 172 landscapes varying in terms of forest amount and road density, I analyzed how forest fragmentation and road network shaped the taxonomic, functional and phylogenetic diversity of bat communities at multiple spatial scales; (iii) by developing models of species distribution and connectivity (least-cost path) at the scale of a large urban area, I assessed the effect of different street lighting extinction scenarios on landscape connectivity for three bat species; and (iv) using a field experiment, I tested the influence of landscape context around road underpasses on their use by bats and the efficiency of these structures in maintaining landscape connectivity while reducing the risk of collision with vehicles. While the first two sections of the PhD seek to better understand the mechanisms underlying the effects of landscape anthropization on bats, the last two axes are applied to their direct conservation by demonstrating how landscape ecology can contribute to improve existing measures.

RÉSUMÉ

L'anthropisation des paysages à travers la perte des habitats naturels et leur fragmentation est une des premières menaces sur la biodiversité. Cette thèse Cifre effectuée à l'INRA Dynafor de Toulouse en collaboration avec le Conservatoire des Espaces Naturels de Midi-Pyrénées a pour fondement de mieux comprendre les impacts de la pollution lumineuse et du réseau routier, deux éléments majeurs et inévitables de cette anthropisation, sur les chauves-souris. Les approches, concepts et méthodologies provenant de l'écologie du paysage ont été mobilisés à des fins appliquées à la conservation des chiroptères. La thèse se structure en 4 axes de recherche: (i) à travers une revue exhaustive des études de télémétrie en zone tempérée, nous avons cherché à comprendre comment l'anthropisation des paysages influence la mobilité des chiroptères via la taille des domaines vitaux et les distances de déplacement; (ii) grâce à un échantillonnage simultané des communautés de chiroptères en lisière et à l'intérieur de fragments forestiers dans 172 paysages variant en termes de proportion de forêt et de densité du réseau routier, nous avons étudié comment la configuration forestière, la composition de la matrice paysagère et le réseau routier façonnent la diversité taxonomique, fonctionnelle et phylogénétique des communautés de chiroptères à différentes échelles spatiales; (iii) en développant des modèles de distribution d'espèces et de connectivité (chemins de moindre de coût) à l'échelle d'une grande agglomération nous avons pu évaluer l'effet de différents scénarios d'extinction de l'éclairage public sur la connectivité du paysage en faveur de trois espèces de chiroptères; et (iv) par une expérimentation in situ, nous avons testé l'influence du contexte paysager autour des passages routiers inférieurs sur leur usage par les chiroptères et l'utilité de ces ouvrages à maintenir une connectivité du paysage tout en réduisant le risque de collision avec les véhicules. Alors que les deux premiers axes de la thèse cherchent à mieux appréhender les mécanismes sous-jacents aux effets de l'anthropisation du paysage sur les chiroptères, les deux derniers axes sont appliqués à leur conservation en cherchant à montrer les apports de l'écologie du paysage pour améliorer des mesures déjà existantes.

FOREWORD

This PhD thesis began in January 2017 thanks to the funding of the Direction Régionale de l'Environnement, de l'Aménagement et du logement d'Occitanie (DREAL) and the Association Nationale de la Recherche et de la Technologie (ANRT), under the supervision of the Conservatoire d'espaces naturels de Midi-Pyrénées (CENMP) and the DYNAFOR laboratory of the French National Institute of the Agricultural Research (INRA). The starting point of this project followed difficulties encountered during the construction of the RN88 – circumvention of Baraqueville lead by road constructor service of DREAL to adapt project already launch to new recommendations for bat conservation measures. This case of study highlights difficulties to CENMP and DREAL, partners in several road construction projects, for the implementation of biodiversity offsetting measures for bat conservation on road project.

This statement followed also several years of solicitation for consultancy mission of the CENMP from the biodiversity instructor service of DREAL in the numerous road development projects in the region formely known as "Midi-Pyrénées" into the Environmental Impact Assessment (EIA) process by integrating potential impacts into the mitigation hierarchy of avoidance, reduction, and offset measures. Facing with often different situations and needs for responses from the DREAL but also from road project planners, the CENMP and their bat experts realized that their knowledge on the impacts of roads on bats but also on the effectiveness of their proposed conservation measures remained too limited to be fully satisfactory for conservation purpose. However, this situation does not come necesarrily because the knowledge does not exist but also because bat experts rely almost exclusively on their intuitions and can rarely base their reflexion on the scientific literature to build their survey protocols and propose mitigation measures (language constraint and lack of time). Moreover, the recommendations that the CENMP can provide in the framework of these road projects can represent heavy technical constraints and important financial costs reminding them of the responsibility for effective proposals and decisions. It is indeed important to remember that the funding allocated to biodiversity and therefore to bat conservation remains very limited.

In this context and on the strength of his past experience in the funding and supervision of research work within the framework of CIFRE thesis (four previous CIFRE thesis were already supervised on other taxa such as odonates and the desman of the Pyrenees), the CENMP proposed the initial idea of using the funding provided for a road project offsetting measures to finance a new PhD Thesis on the impact of road network on bats and on how to improve existing conservation measure. Idea that has been accepted from the DREAL of Occitanie in 2016. Finally, the CENMP elaborated a research proposal in collaboration with Luc Barbaro from DYNAFOR (INRA) and Frederic Archaux (IRSTEA) and successfully applied to the CIFRE program (ANRT), which funds PhD thesis in the framework of collaborations between research laboratories and private companies, governmental organisations or NGOs.

GENERAL INTRODUCTION

1. Multiple land use changes and biodiversity loss

1.1. Biodiversity loss

Among the many alterations humans have imposed on our planet, some of the most severe appear to be (1) the addition of more than 550 billion metric tons of carbon to the atmosphere, which is the main driver of global climate change and ocean acidification (Ciais et al., 2013; Gray, 2007), (2) the global nitrogen cycle alteration through the widespread use of artificial fertilizers across many ecosystems (Canfield, Glazer, & Falkowski, 2010), (3) the routing of more than one third of global primary production to human consumption through intensive agriculture (Krausmann et al., 2013), (4) the mechanization of natural resources management leading to the homogenization of landscapes (Gámez-Virués et al., 2015), and (5) the globalization of transport infrastructures, which has resulted in the spread of invasive species and pathogens (Lewis & Maslin, 2015). Altogether, this large-scale anthropization of most ecosystems worldwide have led to an unprecedented ongoing mass extinction of species (Barnosky et al., 2011; Díaz et al., 2019). This well-documented global biodiversity loss (Ceballos, Ehrlich, & Dirzo, 2017; Régnier et al., 2015) is such that it is widely considered as the beginning of the Earth's sixth mass extinction (Ceballos et al., 2015). Indeed, species are becoming extinct at a rate of 100 to 1,000 times the normal rate of extinction (Chivian & Bernstein, 2010). The work of millions of years of evolution is therefore now at stake, as well as the stability of food systems, economy and human health, which depend in many ways on the stability, as well as the multifunctionality of ecosystems (Young, McCauley, Galetti, & Dirzo, 2016). Following the recognition of the biodiversity crisis, conservation ecology has rapidly become a major discipline in ecological research; it investigates the influence of natural processes and human activities on biodiversity dynamics with the aim to maintain both species diversity and associated ecosystem functions (Soulé, 1985).

The main causes of biodiversity loss are: the removal of individuals and overexploitation, land-use change (habitat loss and fragmentation), biological invasions and diseases, pollution and climate change (Maxwell, Fuller, Brooks, & Watson, 2016; Young et al., 2016). Human activities have modified over 77 % of terrestrial land. Over 40 % of terrestrial land has been converted for agriculture or settlements (i.e. habitat loss; Ellis et al., 2010). An extra 37 % are natural (e.g., primary or mature forest) or semi-natural (e.g., secondary forest) habitats embedded within a mosaic of land converted for human use (i.e. habitat fragmentation). Pristine areas (i.e., landscapes with no human impact) represent only 23 % of terrestrial land

but much less in lowlands temperate regions. This explains why habitat loss and fragmentation are together one of the largest driver of biodiversity loss (Betts et al., 2017; Newbold et al., 2015). Furthermore, these two processes have also altered both biogeographical and ecological patterns of species distributions, most often acting alongside climate change (Brown et al., 2016; Chen, 2012). As a result, understanding the consequences of habitat loss, habitat fragmentation and landscape homogenization on biodiversity has become even more critical since their synergistic effects with the ones of climate change has become more prominent (Chazdon et al., 2009; Van De Perre et al., 2018). Consequently, investigating how changing landscapes affect populations, communities, and metacommunities is a key challenge of the 21st century (NRC, 2001).

1.2. Landscape ecology: a key discipline for conservation

Landscape ecology is a relatively recent discipline (emerged in the late 20th century as a new paradigm for the study of biodiversity) that investigates the influence and properties of spatial heterogeneity on ecological systems (Presley, Cisneros, Klingbeil, & Willig, 2019). A landscape is defined as a set of interacting ecosystems; it corresponds to the upper ecological organization level, i.e., above ecosystems (Forman & Godron, 1986). Thus, the discipline focuses on spatial and temporal extents that are wider than those typically studied in ecology (e.g., ecosystems or habitats). It explicitly addresses the importance of landscape composition, defined as the relative proportions of different land cover types within a focal area, and configuration, defined as the spatial arrangement of land cover types within a focal area, in determining ecological patterns and processes (Dunning et al., 1992; Fahrig et al., 2011; Turner, 1989). Landscape changes can affect either or both the landscape composition (e.g., habitat loss) and configuration (e.g., habitat fragmentation *per se*). The concept of "habitat patch" is thus central to landscape ecology, defined as a relatively homogeneous area (e.g., forest patch, agricultural patch) that ecologically differs from its surroundings. Many metrics of landscape composition and configuration use this discrete definition of a patch as the focal unit of measure, at least in terrestrial ecology (Presley et al., 2019).

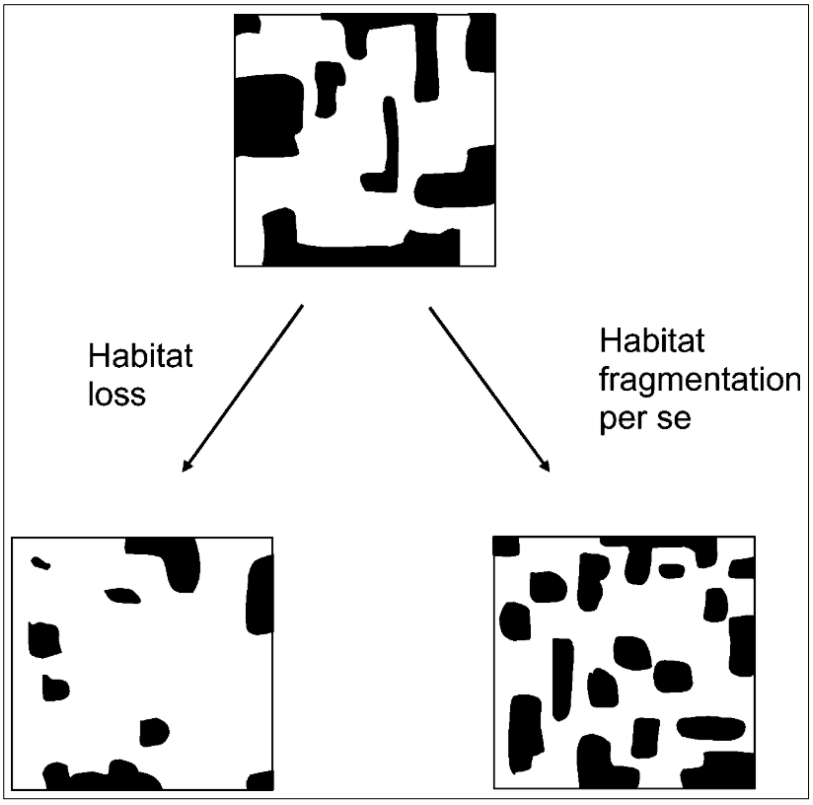

Figure 1: Both habitat loss (habitat amount reduction) and habitat fragmentation per se (independent of habitat amount) may result in smaller patches. Therefore, patch size itself is ambiguous as a measure of either habitat loss or habitat fragmentation per se from (Fahrig, 2003).

Three landscape-level processes can respectively or jointly affect patterns in the abundance and distribution of species: 1) habitat loss, 2) habitat fragmentation per se (i.e., formation of isolated patches of habitat) and 3) matrix permeability or utility (i.e., types of habitat that surround a patch; Tscharntke et al., 2012). The habitat loss and matrix effects are associated with the presence and proportion of natural and anthropogenically-modified land cover types, independent of their spatial arrangement (i.e., landscape composition), whereas fragmentation per se affects spatial arrangement (i.e., landscape configuration) of resource patches (Bennett et al., 2006; Fahrig, 2003). Comprehensive understanding of the effects of habitat loss and fragmentation, as well as the effects of matrix quality on biodiversity requires explicit consideration of compositional and configurational characteristics of landscapes. Although patch area and isolation are important drivers of the distribution of animals, the quality of the matrix is of primary importance in determining both patch occupancy and inter-patch dispersal (Prugh, Hodges, Sinclair, & Brashares, 2008). Species can be splitted in two main types: 1) those for which individuals primarily live within a single patch, and 2) those for which individuals have large home ranges that include multiple patches of the same land cover

type or multiple patches of distinct land cover types (Sanderson, Redford, Vedder, Coppolillo, & Ward, 2002). However, both types of species are affected by the composition and configuration of landscapes, either for their dispersal or daily movements in search of critical resources (Presley et al., 2019). Thus, anthropogenic landscape modifications can perturb landscape connectivity which is the degree to which the landscape facilitates or impedes movements among resource patches (Tischendorf & Fahrig, 2000), metapopulation dynamics and landscape supplementation and complementation processes that facilitate access to different types of substitutable and non-substitutable resources respectively in different habitats (Dunning et al., 1992). The popularity of investigating the relative importance of landscape composition versus configuration is largely due to the empirical proposition that the amount of land cover types in an area has a stronger influence on the abundance and distribution of species than the spatial arrangement of those land cover types (Andrén, 1994). Moreover, species perceive their environment at different spatio-temporal scales due to differences in habitat requirements and movement ability with direct consequences on home range sizes (Betts et al.,2006; Ewers & Didham, 2006; Gorresen & Willig, 2004; Gorresen, Willig, & Strauss, 2005; Klingbeil & Willig, 2016; Smith et al., 2011). Consequently, the multiscale approach has become more and more widespread in landscape ecology, especially to ensure that landscape structure is measured at the 'right' extent for the target organisms studied (Miguet et al., 2016). The spatial extent within which a landscape metric has its strongest effect on a particular species' response has been called the *scale of effect* (Jackson & Fahrig, 2012).

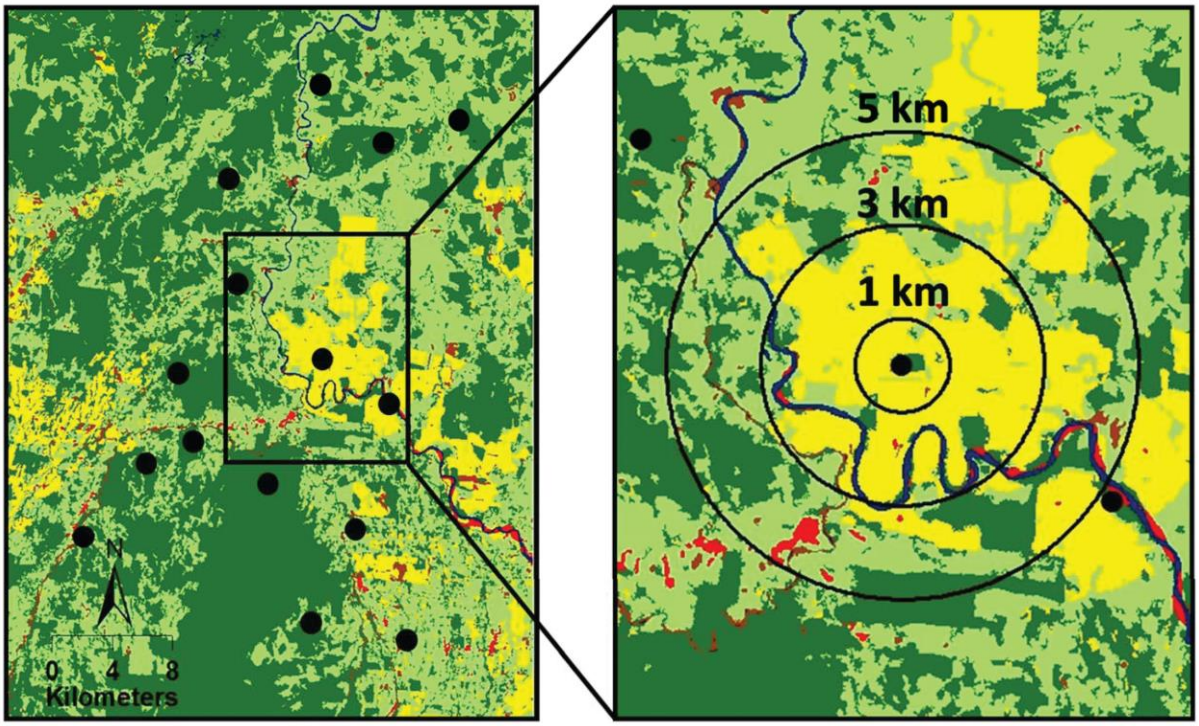

Figure 2: An example of sites distributed in a heterogeneous landscape with various types of land cover (left), and an example of multiple scales used to evaluate the effects of landscape structure on animals in a focal patch (right). Black dots represent sampling locations, dark green is forest, light green is pasture, yellow is agriculture, blue is water, and red is urban (Presley et al., 2019).

A recent meta-analysis has shown that the response of biodiversity to habitat loss tends to be almost always negative whereas its response to habitat fragmentation per se tends to be more often positive than negative, contrarily to former assumptions (Fahrig, 2017). However, the direction of effects vary both among taxa and geographical areas. Many authors have suggested that variations observed among studies could be due to variations in the quality of the matrix (portion of the landscape covered with non-habitat) surrounding the habitat patches studied (mainly forests). As a result, they advocate for studies using a more holistic view of landscapes, including all land cover types, rather than studies focusing only on the amount versus the spatial configuration of a given habitat (Fahrig, 2017; Presley et al., 2019).

1.3. Impacts of road expansion on biodiversity

Road expansion has been described as an important driver of landscape dynamics (Noss, 1993) and its ecological effects are considered "the sleeping giant of biological conservation" (Forman, 2002). Roads affect landscape composition through habitat loss, habitat creation (e.g., road verges) and changes in habitat quality (Carr, Fahrig, & Pope, 2002). For instance, the

construction of a 7m-wide road destroys 7 ha of habitat for every 10 km of road, without taking into consideration roadside hard shoulders, verges, junctions, service areas and other structures (Altringham & Kerth, 2015). In wooded areas, roads increase the amount of forest edges, resulting in additional loss of habitat for forest interior species but also in the creation of potential new habitats for edge species (Ranney, Bruner, & Levenson, 1981). Roads also affect landscape configuration and connectivity by introducing barriers and corridors for animal movement into the landscape that may alter landscape processes previously mentioned (Carr et al., 2002).

Road expansion directly or indirectly contributes to biodiversity loss through several processes. Roads increase rates of wildlife mortality during the construction phase (Trombulak & Frissell, 2000) and afterwards due to collision with vehicles (Forman & Alexander, 1998). They facilitate the overexploitation of resources by extending the road network leading to extractive industries (van der Ree, Smith, & Grilo, 2015). They ease the spread of invasive species by disrupting indigenous communities and altering habitats (Brown et al., 2006; Trombulak & Frissell, 2000; van der Ree et al., 2015). They spread different pollutions beyond road surfaces such as artificial lights (lightings at road verges and vehicle headlights), noise pollution from the traffic, chemical pollution of soil and water by runoff and contribute to climate change through greenhouse gas (CO_2) emissions (Chapman, 2007). The combination of all those impacts increases the extinction risk of populations (Figure 4) and makes ecosystems more sensitive to other threats (Selva et al., 2011). There has been a growing literature on the impact of roads on biodiversity, especially on vertebrate animals over the last 20 years. This field of research is now referred to as ‘road ecology’. This abundant literature has been synthetized in several in-deep reviews including Bennett (1991), Forman & Alexander (1998), Spellerberg (1998), Trombulak & Frissell (2000), Coffin (2007), Fahrig & Rytwinski (2009), Laurance et al. (2009), (Benítez-López et al. (2010), and Rytwinski & Fahrig (2012).

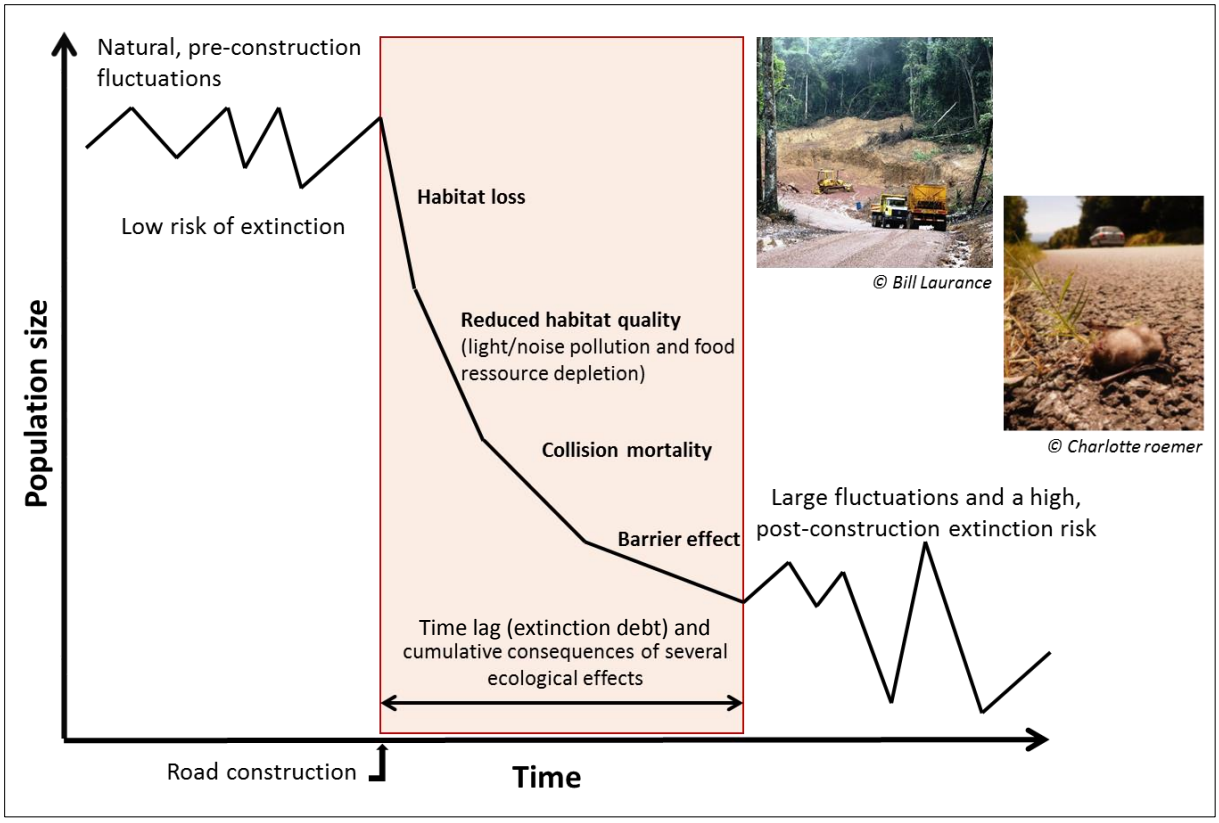

Figure 4: Theoretical graph representing multiple impacts of road expansion on populations and their delayed response (extinction debt). We note that those impacts are both temporally and spatially cumulative. Adapted from Forman et al. (2003).

Europe is the continent with the highest road density (Selva et al., 2011) and France is among the leaders at European level in terms of network length and density per million inhabitants (MEEM, 2017; Figure 5). In France, the road network represents one million kilometers in 2015, including 21,232 km for main roads (motorways and national roads), with an increase by 12 % in total and 40 % for main roads between 1995 and 2015 (MEEM, 2017).

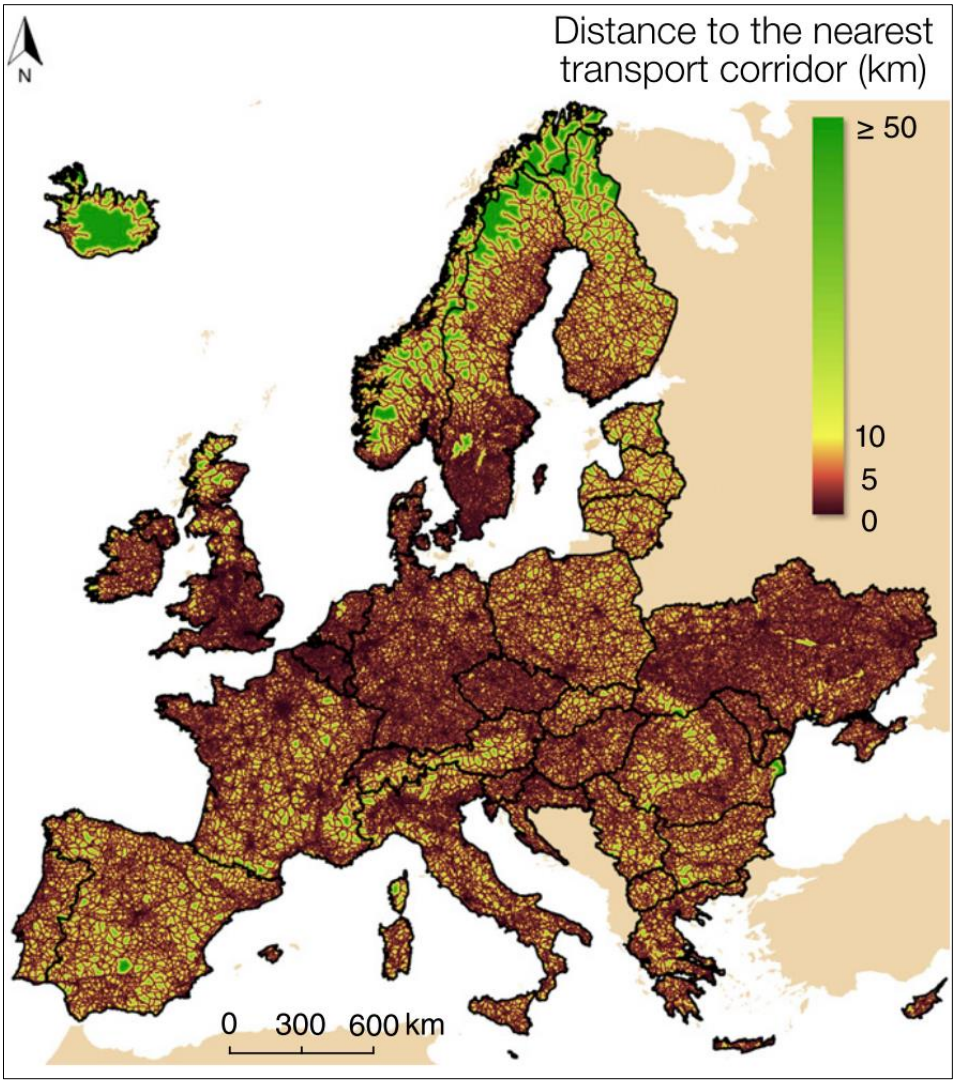

Figure 5: Mapped distances to the nearest transport infrastructure (paved roads and railways in Europe. Distances were quantified at a resolution of 50 m and ranged from 0 to 83.5 km (Torres et al., 2016).

Roads are moreover expected to increase by nearly 25 million kilometers by 2050 worldwide (Dulac, 2013). The road network is likely to get longer, wider and more complex with existing road systems being upgraded and new roads being built. Despite the widely acknowledged need to reduce our dependency on fossil fuel and despite growing concerns about the environmental impact of roads, improved communication by road remained perceived as a key driver of our economy (Altringham & Kerth, 2015). It is therefore critical to reduce the negative effects of roads on biodiversity, including indirect effects through light pollution, noise pollution and 'interior' habitat loss (i.e., unaffected by edges).

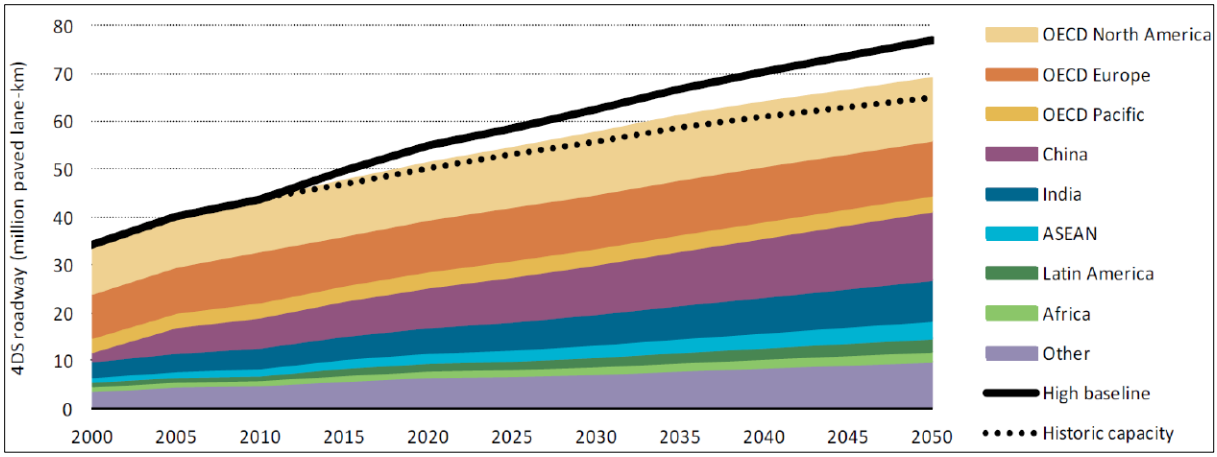

Figure 6: Global projection: roads are likely to grow by nearly 25 million paved lane-km by 2050 (Dulac, 2013).

1.4. Light pollution as an emerging issue

Road expansion and urbanization are generally associated with an increase in outdoor Artificial Light At Night (ALAN). ALAN has grown by between 3 and 6 % per year during the second half of the 20th century (Hölker et al., 2010). Between 2012 and 2016, Earth's artificially lit outdoor area have increased by 2.2 % per year, with a radiance growth of 1.8 % per year, and the brightness of continuously illuminated areas has increased by 2.2% per year (Kyba et al., 2017). Light pollution affects 23% of the global terrestrial area, including 88% of the European terrestrial area (Falchi et al., 2016).

ALAN causes many ecological disturbances (Rich & Longcore, 2013) and represents one of the least explored sources of perturbation affecting biodiversity (Gaston et al., 2015). Altering the natural day/night rhythm within ecosystems (Gaston et al., 2017; Longcore & Rich, 2004; Navara & Nelson, 2007), ALAN impacts a wide range of taxa, interactions between species and their regulatory processes (Bennie et al., 2018; Hölker et al., 2010; Knop et al., 2017). Indeed, 30% of all vertebrates and more than 60% of all invertebrates are nocturnal (Hölker et al., 2010). ALAN influences species metabolism (Touzot et al., 2019; Welbers et al., 2017), their fitness (Touzot et al., 2019), the ability of animals to move into and out of artificially lit areas (Hale et al., 2015), genetic processes (Hopkins et al., 2018) and predator-prey relationships (Becker et al., 2013; Buchanan, 1993; Heiling, 1999). The effects of ALAN on species are also likely to impact ecosystem functions and services (Gaston et al., 2014; Hölker et al., 2010). For example, it was suggested that ALAN may affect natural forest succession and connectivity of forest patches through a reduction in the activity of obligate

nocturnal mammals such as bats (Lewanzik & Voigt, 2014). In summary, the loss of darkness has a potentially important, albeit almost completely neglected, impact on biodiversity (Hölker et al., 2010). ALAN constitutes a threat for some taxa that is more and more considered as potentially equivalent to other threats such as urbanization and agricultural intensification (Azam et al., 2016).

Landscape ecology is likely to play a key role to understand the effects of ALAN on biodiversity. First, the response of species to ALAN strongly depends on spatial scale, with e.g. positive effects on some bat species activity at the lamp scale but strong negative effects at landscape scale (Azam et al., 2015, 2018; Blake et al., 1994). Second, it is critical to disentangle the effects of ALAN from the effects of landscape structure and to assess their interactive effects on biodiversity. Finally, it is also urgent to better take light pollution into account in landscape planning tools (Azam et al., 2016, 2018; Pauwels et al., 2019). Indeed, even most recent approaches of landscape planning, such as ecological networks consisting in core areas, corridors, restoration areas and buffer zones, implemented by the Pan-European Biological and Landscape Diversity Strategy (Jongman et al., 2011; Jongman & Pungetti, 2004), do not explicitly integrate this dimension of landscape quality. These planning tools need to evolve in order to take into account all dimensions of landscape structure, including its nocturnal dimension (Azam et al., 2016; Hale et al., 2015; Hölker et al., 2010).

2. Bats as ideal model organisms to study the effects of multiple land use changes

2.1. Bats are sensitive species to landscape structure

Bats are nocturnal, mobile and most often multi-habitat species, which makes them highly sensitive to multiple land-use changes presented above (Presley et al., 2019). The evolution of true, i.e., active powered flight more than 50 million years ago, as wells as the acquirement of echolocation and the ability to see well in dim light, allowed bats to adapt to a variety of niches largely unoccupied at night (Erkert, 2000). Nocturnality for the bats entailed the benefit of minimizing the predator pressure by diurnal birds of prey while bats seems to not constitute a major part of the diet of most owls (Fenton & Fleming, 1976). It also provided access to important food resources otherwise scarcely exploited because most insectivorous birds are diurnal with approximately only 2.5 percent of the species being mainly nocturnal (Van Tyne & Berger, 1959). Because bats and birds are the only groups of vertebrates capable of powered flight, they occupy similar trophic roles (Lein, 1972; Wilson, 1973), with bats acting

in many cases as the nocturnal counterparts of birds (Erkert, 2000; Fenton & Fleming, 1976). Thus, while many mammals became nocturnal to deal with human pressures, bats are fully adapted and linked to the nights and represent great bio-indicators to the quality of nocturnal dimensions of ecosystems and landscapes. Bats are highly mobile for their size and may travel nightly long distances between roosts and foraging sites (Altringham et al., 1996; Findley, 1993). Bats need a wide range of diversified habitats for roosting, commuting, foraging, mating and breeding and thus for accomplishing both their daily and annual life-cycle. As a consequence, most bats' individual home ranges are expected to include ecologically heterogeneous areas, i.e., individuals are likely to use multiple patch types in a given landscape).

Bats also represent an extraordinary ecologically diversified order, which makes them ideal to study the effects of global changes on community structuration and ecosystem functioning. There are more than 1300 species (forming the second largest mammalian order), with many foraging guilds (frugivores, nectarivores, carnivores, insectivores, sanguinivores, and omnivores), providing many ecosystem functions and services such as arthropod regulation, forest regeneration and maintenance via seed dispersal and pollination of a wide variety of ecologically and economically important plants, biological pest control, nutrient redistribution and fertilization through the landscape (i.e., high concentrations of nitrogen and phosphorous in the guano that both are primary limiting nutrients of most plant life) (Jones et al., 2009; Kunz et al., 2011). Among the 1300 bat species worldwide, over two thirds are either obligate or facultative insectivores and European species are almost exclusively insectivores (Dietz, Nill, & von Helversen, 2009). Bats are commonly recognizes for their voracious appetites for nocturnal and crepuscular insects and for their important role in arthropod suppression/regulation in a very wide range of habitats from vegetation and water in cluttered forests to those that feed in open space above forests, grasslands, croplands but also directly on the ground, meaning that bats have a very large diet composing of flying and non-flying arthropods (Jones et al., 2009; Kunz et al., 2011; Figure 3). Insectivorous bat communities can be divided into three main guilds: open-space species, edge-space species and narrow-space species (Schnitzler & Kalko, 2001). These three guilds are defined according to species ability to fly in clutter (i.e. in dense vegetation) or open spaces, which depends on the physical features of their sonar (Budenz et al., 2018; Fenton, 1990; Fenton et al., 2016; Neuweiler, 1989) and on the wing morphology, playing a role in maneuverability and being correlated to sonar frequency (Aldridge & Rautenbach, 1987). Physical properties of sound constrain bats to keep a certain distance from obstacles to perceive the returning echo and thus their surrounding environment.

Indeed, sound energy greatly attenuates with distance, especially for high frequencies (Pye, 1979). Thus, while open-space species, emitting low frequencies, can keep contact with landscape structure further away from it, clutter-space species, emitting higher frequencies, have to stay closer to landscape elements to keep a good mental map of their environment (Goerlitz, 2018). These diversified behavioral, morphological and sensory adaptations are associated with strong diet and habitat partitioning (Siemers & Schnitzler, 2004). For instance, *Myotis bechsteinii* forages almost exclusively within canopy thanks to its high flight maneuverability (e.g., short and large wings) and its large bandwidth enhancing discrimination between prey and vegetation while *Nyctalus noctula* feeds on aerial plankton in open-scape thanks to its fast flight (e.g., long and narrow wings) and its long distance echolocation ability (e.g., low frequencies ultrasound). Bat guilds are associated with different habitat requirements, different movements and therefore different perception of landscape structure. These among-species differences explain contrasted bat responses to changes in landscape structure (Ducci et al., 2015; Olden et al., 2004). However, bat echolocation have not only co-evolved due to habitat structure and morphological constraints but also due to a specific predator–prey interactions system with antipredator adaptations and predator counter-adaptations including calls at frequencies outside the sensitivity range of most eared prey, changes in the pattern and frequency of echolocation calls during prey pursuit, and quiet, or 'stealth', echolocation (Goerlitz et al., 2010; Ter Hofstede & Ratcliffe, 2016).

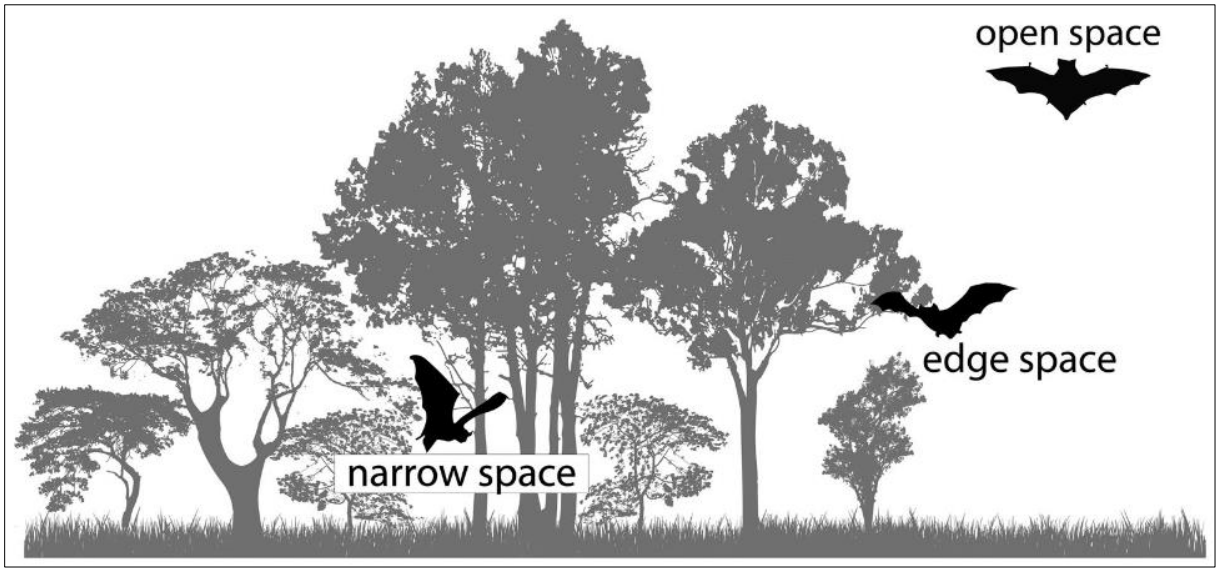

Figure 3: Air-space used by bats. Open-space species are aerial hawkers flying higher and further from vegetation and ground in uncluttered space; edge-space species are aerial hawkers in background-cluttered space flying along the vegetation edge; and, narrow-space species are either aerial hawkers or gleaners in highly cluttered space flying within the vegetation (Peixoto et al., 2018; Schnitzler & Kalko, 2001).

Bats are very long-lived considering their size, which makes them very sensitive to changes in landscape structure, with potentially long time-lags between these changes and bat responses to landscape dynamics and land use changes. Indeed, most bats live more than 10 years and some up to 20 years or more (Altringham, 2011; Barclay & Harder, 2003). This survival strategy allow bats to develop a very good large-scale mental map of their home ranges through the years and a very routine behavior (e.g., long distance flight path), making them very sensitive to landscape modifications (Yovel & Ulanvosky, 2017) either through their density (e.g., survival) or through their movement because they know how to find alternative resources in case of destruction of usual resources. High sensitivity of bats to landscape structure and its modifications has deep consequences for landscape conservation and management, not only because bats provide important ecosystem services and functions but also because bats have a low fecundity (1-2 offspring per year; Barclay et al., 2004) and an elevated juvenile mortality (Dietz et al., 2009; Culina et al., 2019). Despite their low reproductive rate and long life-span, small-sized bats have relatively high metabolic rates leading to rather high food requirements (Speakman et al., 2003; Voigt & Kingston, 2016). In addition, many species live at low densities and have a patchy distribution (i.e., highly gregarious and dependent on patchily distributed roosts), making them vulnerable to local extinction (Fensome & Mathews, 2016; Kerth, 2008). Any external factor that even moderately reduces reproductive success, increases mortality, or both, can lead to severe population declines, while demographic recovery will be slow (Schorcht et al., 2009; Sendor & Simon, 2003). Finally, bats typically have large summer home ranges compared to other similarly-sized mammals and many bats migrate over considerable distances between winter and summer roosts (Altringham, 2011). As a result, changes in landscape structure can affect large numbers of individuals simultaneously, typically at the colony scale (Froidevaux, Boughey, Barlow, & Jones, 2017). In conclusion, because of their particular life history, bats are susceptible to a wider range of environmental disturbances than many other small mammals (Altringham & Kerth, 2015). Moreover, as it has been demonstrated that habitat fragmentation reduces individuals' movements in terrestrial mammals (Tucker et al., 2018), similar studies on bats are highly needed to assess whether this trend also holds for these aerial mammals.

2.2. Bat conservation status

The IUCN Bat Specialist Group assessed that 15 % of 1150 evaluated bat species worldwide are threatened (i.e. either critically endangered, endangered or vulnerable) and 7 % are Near Threatened. Populations are considered stable for 21 % of species, increasing for less than 1 %, decreasing for 23 %, and associated with an unknown trend for 55 % of species (Voigt & Kingston, 2016). In developed countries, major threats are forest loss and fragmentation, expanding urbanization (e.g., artificial lights, transport infrastructures, light pollution), massive use of pesticides and vermifuges (that have dramatically modified insect prey communities), perturbations and destructions of roosting habitats (O'Shea et al., 2016; Russo et al., 2007; Voigt & Kingston, 2016). Dramatic declines of bat populations as well as local extinctions have been documented in Europe (Van der Meij et al., 2015), where all bats have been strictly protected for the last two decades by law. All European bat species are listed in Annex 4 of the Habitats Directive, and several species are also listed in the Annex 2 of the Habitats Directive (Council Directive 92/43/EEC). In France, 31 % of bat species are listed as threatened (IUCN France, 2017) and bat activity has been reduced by 46 % from 2006 to 2014 (ONB, 2017). Consequently, environmental impact assessments are now mandatory (Bigard et al., 2017) and mitigation measures are often required for projects on infrastructure development such as road construction (Kerth & Melber, 2009). These environmental impact assessments and associated mitigation measures have become key for the conservation of bat species (Altringham & Kerth, 2015).

3. Thesis aims and methodological approaches

3.1. Scope and general objectives

So far, literature on the effects of habitat loss and habitat fragmentation on bat species have mainly been conducted in tropical zones with few studies in temperate landscapes, typically composed of heterogeneous mosaics of cultivated and semi-natural habitats. Furthermore, previous works showed that these effects on bat diversity and abundance vary greatly between studies and bioclimatic regions, found to be either positive or negative or both (Ethier & Fahrig, 2011; Gorresen & Willig, 2004). For instance, the responses of bats to forest fragmentation depend on a combination of factors: landscape context, species traits and spatial scale (Fuentes-Montemayor et al., 2017; Klingbeil & Willig, 2009). As a consequence, recent studies argue

that a more holistic perspective is needed, including investigating matrix 'quality' such as road network and light pollution along with habitat loss/fragmentation, as well as the potential role of the former in mediating responses to the latter (Fahrig, 2017; Presley et al., 2019).

In parallel, there is a growing literature on the impacts of roads and ALAN for bat conservation but so far few studies investigated landscape-scale effects of these cumulated drivers. As a result, mitigation measures have largely been applied at local levels (e.g., dimensions of wildlife crossings, type and duration of lightings) largely ignoring infrastructure planning at larger scales. To date, there has been no consideration for landscape-level processes in the design of road networks or outdoor lightning planning as well as in the design of their mitigations (Carr et al., 2002). In their research agenda for road ecology, Roedenbeck et al. (2007) identify the most pressing research question as: "Under what circumstances do roads affect population persistence?"

The foundations and purposes of this PhD were to assess the effects on bat diversity of multiple components of land-use changes, namely habitat loss, habitat fragmentation, road expansion and ALAN that have so far been studied in isolation. This work lies at the interface between landscape ecology and conservation biology. Its fundamental aim is to better understand mechanisms underlying the effects of multiple land-use changes on bats. Its more applied aim is to mobilize landscape ecology concepts and methodologies to improve future conservation measures to mitigate roads and artificial lights effects on bats. This thesis is composed of four chapters with complementary aims:

- ⇨ The first objective was to better understand the interactive and/or cumulative impacts of road network, forest amount and forest fragmentation on bat communities (chapter 1).
- ⇨ The second objective was to review relationships between landscape structure, species traits, individual bat movements and space use at the global level (chapter 2).
- ⇨ The third objective was to demonstrate the importance of landscape-level consideration in improving the efficiency of two common conservation measures for bats, light extinction schemes and road underpasses (chapters 3 and 4).

3.2. Collection of field and literature data

Studying bat distribution and movement has long time be challenging due to their cryptic nocturnal behavior and their high mobility. The last decade has seen a fast development of automatic methods of recording and location of foraging bats, either by GPS, telemetry or

Passive Acoustic Monitoring. The latter methods have been recently expanding for their easy-to-use, standardized and non-invasive way of sampling bat communities (Sugai et al., 2019). This PhD made use of two types of data: ultrasonic emissions recorded at a fixed location (passive acoustic method) and 'real' movements of radio-tracked bats (Millspaugh & Marzluff, 2001; Tomkiewicz et al., 2010).

For the first and third chapters, I used passive acoustic method, which allows recording all ultrasonic emissions emitted by bats during their foraging and commuting behaviors. This method provides a large quantity of data, temporally and spatially replicated simultaneously in a standard way (i.e. no observer bias). In this case, the response variable was the activity of each bat species as a proxy of bat local density (Froidevaux et al., 2014).

For the second chapter, I gathered individual (or colony-level) bat movement data from published telemetry studies in regular, standard scientific journals using a systematic literature search. This method provides an estimation of two key parameters of animal movements: home range size and mean daily distances travelled between roosts and foraging areas.

When using a fixed location approach to study the impact of roads on bats, two sampling designs can be used: habitat-centered or road-centered. In the habitat-centered design, a habitat type of interest (i.e., forest) is the focal point of the study. The bat community is assessed within the habitat patch, and the predictor variable is the road density in the landscape surrounding the patch. In the road-centered design, the road is the focal point of study and the bat community is sampled both at the road and in the surrounding landscape. In this thesis, I used a habitat-centered design in chapter one and a road-centered design in chapter four to study the interactive effects of roads and landscape context.

Finally, to respond to the third objective of the thesis I used a fixed location sampling protocol to predict bat movements through two different approaches, resulting in 'pseudo-movement' patterns. First, to evaluate the influence of landscape structure on the efficiency of road underpasses for bats, we deployed synchronised ultrasound recorders to analyze bat movements using a post-hoc ratio of activity recorded at the different locations. Second, to evaluate the influence of landscape context on the efficiency of different scenarios of light reduction to maintain landscape connectivity for bats, activity from fixed locations were used to predict the spatial distribution of bats (e.g., species distribution modelling), the landscape resistance to movements and ultimately the least-cost movements of bats in a suburban matrix.

CHAPTER 1

Interactive effects of forest fragmentation and road density on temperate bat communities

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ABSTRACT

Context: The respective effects of forest amount and configuration on bat communities are not well understood, especially when the landscape matrix is fragmented by road networks that decrease habitat quality. Worldwide, road construction is expanding, yet roads are known to have negative effects on bats. Understanding how this affects bat communities in fragmented landscapes is therefore critical.

Aim: We sampled bat communities in 172 landscapes in southern France along gradients of forest amount and road density to: (i) disentangle the relative and interacting effects of forest fragmentation and road density on the activity of temperate bat communities, (ii) investigate how road density affects different components of bat diversity (taxonomic, functional and phylogenetic) in various landscape contexts, and (iii) assess whether road density affects bats depending on the level of forest amount, forest configuration, and edge effects.

Results: Forest amount and configuration were more important predictors shaping bat diversity than road density, except for functional evenness. The three components of diversity peaked in landscapes with an intermediate forest amount or number of forest patches, while road density had negative effects on functional and phylogenetic diversity. Road density affected bat species differently depending on their traits. The activity of *R. ferrumequinum*, *R. hipposideros* and *N. leisleri* decreased significantly with increasing road density only in landscapes with a low forest amount or number of forest patches. Conversely, *P. pipistrellus* responded positively to road density, but only in landscapes with the highest number of forest patches.

Conclusion: By favouring high-flying or non-forest specialists at the expense of low-flying forest-dwelling species, roads act as an environmental filter and contribute, together with forest fragmentation, to changing the composition of bat communities. Maintaining a large number of forest patches may reduce the impact of road expansion and favour a landscape complementation process by increasing short-distance movements and decreasing road-crossing events (i.e., mortality risk). Our findings show that landscape-scale interactions between habitat loss, fragmentation and matrix quality are complex, indicating the need for a more holistic view in fragmentation studies to inform conservation policy.

1. INTRODUCTION

While the negative impact of habitat loss has been largely documented for a wide range of taxa, habitat fragmentation (independent of amount) can have positive, negative or neutral effects on biodiversity (Fahrig, 2003; Fletcher et al., 2018). The positive effect of fragmentation observed when the amount of habitat is kept constant suggests that several small patches or a large patch of a given habitat can have the same conservation value. This may result from one or several of the following mechanisms: higher landscape connectivity, higher habitat diversity, positive edge effects and/or landscape complementation/supplementation (Fahrig, 2017).

Forest fragmentation is a widespread phenomenon, with nearly 20% of the world's remaining forests now found within 100 m of an edge, 50% within 500 m, and 70% within 1 km (Haddad et al., 2015). Understanding and managing the impacts of forest fragmentation have therefore become critical for effective conservation (Pfeifer et al., 2017). In Europe and other temperate regions, forests are key roosting and foraging habitats for bats (Charbonnier et al., 2016; Dietz et al., 2009; Plank et al., 2012). To date, the effects on bats of the amount of forest and its fragmentation at the landscape scale have been studied mostly in tropical zones (Presley et al., 2019). Previous studies have found that the amount of forest in a landscape is a more important predictor of bat diversity and activity than forest fragmentation per se (Arroyo-Rodríguez et al., 2016; Ethier & Fahrig, 2011). Accordingly, landscapes with moderately fragmented forests often host the highest functional diversity, species richness or abundance in bats (Fuentes-Montemayor et al., 2013; Klingbeil & Willig, 2009).

The relative importance of forest amount and fragmentation depends on bat life-history traits. For instance, forest amount plays a greater role for frugivorous bat species, while fragmentation has a higher impact on animal-eating bat species (Klingbeil & Willig, 2009). Bat species with low mobility are more affected by fragmentation, whereas for more mobile species, the amount of a given habitat in a landscape generally outweighs the pure fragmentation effect (Fuentes-Montemayor et al., 2017). However, these effects on bat diversity and abundance vary greatly between studies and bioclimatic regions, found to be either positive or negative or both (Ethier & Fahrig, 2011; Gorresen & Willig, 2004). The responses of bat species to forest fragmentation depend on a combination of factors: landscape context, species traits and spatial scale (Fuentes-Montemayor et al., 2017; Klingbeil & Willig, 2009). Recent studies argue that a more holistic perspective is needed, including investigating matrix quality along with habitat loss/fragmentation, as well as the potential role of the former in mediating responses to the latter (Fahrig, 2017; Presley et al., 2019).

Edge effects are an unavoidable result of increasing forest fragmentation (Ries et al., 2004). They affect the majority of vertebrate species worldwide, especially the most specialized and threatened forest-interior species of immediate conservation concern (Fletcher et al., 2018; Pfeifer et al., 2017). Consequently, there is high turnover in the composition of vertebrate communities at forest edges, which likely reflects pronounced changes in the ecological functioning of fragmented versus continuous forest habitats (Pfeifer et al., 2017). This seems also true for temperate insectivorous bats, in which edge effects appear to favour generalist aerial-hawkers over gleaners and clutter-adapted species, which are more specialized to forest interiors (Morris et al., 2010).

One of the main driver of forest fragmentation across the globe is the unceasing expansion of roads and vehicle traffic (Carr et al., 2002). Road networks have expanded by 12 million km worldwide since 2000, and 25 million km of additional roads are expected by 2050 (Laurance et al., 2014). A dense road network in forested landscapes leads to increased forest edges (Carr et al., 2002), resulting in habitat loss for forest-interior species, but also potentially new habitats for generalists or edge specialists. One of the few studies to specifically examine the effect of road density on forest edge communities found both negative and positive effects on several insectivorous birds (Khamcha et al., 2018), but the effect on bats has not been previously studied. Road expansion is a complex phenomenon with cumulative negative impacts on bats beyond pure habitat loss and fragmentation, including a barrier effect (Claireau et al., 2019), mortality due to collisions with vehicles (Fensome & Mathews, 2016), and light and noise pollution, which disturb bats while commuting and foraging (Bennett & Zurcher, 2013; Schaub et al., 2008; Stone et al., 2015). In light of the rapid increase in road infrastructure, a better understanding of how this affects bat communities is required. Breaking down bat diversity to investigate its different dimensions, including its functional components, should help to better predict how these changes may affect bat communities (Cisneros et al., 2015). To this end, this aim of this study was to: (i) disentangle the relative and interacting effects of forest fragmentation and road density on the activity of bat communities, (ii) investigate how road density affects different aspects of bat diversity (taxonomic, functional and phylogenetic), (iii) assess whether road density affects bats differently depending on the level of forest amount, configuration, and edge effects.

2. MATERIALS AND METHODS

2.1. Study area

The study was carried out in the region of Occitanie in southwestern France in an area spanning 19 583 km² (N 43.70, E 1.56) (Fig 1). The region has a predominantly temperate climate, lying at the intersection of the Atlantic, Mediterranean and Continental climatic zones, with the additional influence of the Pyrenees Mountains to the south (Fig. 1). The study area is below 400 m a.s.l. and is dominated by agriculture (crops, vineyards, pastures), with patches of grasslands and forests of various sizes (mainly mixed woods and deciduous stands), tree-lined hedgerows, rivers, and a large network of both major and minor roads (Fig. 1). Urban areas range from scattered rural housing to large conurbations. The area hosts high bat diversity, with a total of 27 bat species (Bodin et al., 2011). The study was conducted between June and October 2017, with a mean air temperature of 20.8°C (oscillating between 38.3°C in June and 1.5°C in October) and average monthly precipitation of 38.6 mm (varying between 55.2 mm in July and 11.6 mm in October).

2.2. Landscape and site selection

We selected landscapes along a gradient of road density and forest amount in three sub-regions: the Lot (5217 km²), Tarn and Tarn-et-Garonne (9476 km²) and Ariege districts (4890 km²) (Fig. 1). We excluded landscapes with elevations above 1000 m to keep climatic conditions comparable and limit bias due to the complex impacts of elevation on bat activity and richness (McCain, 2006). Within each sub-region, we defined selected 'landscapes' with a square area of 1 km x 1 km. This spatial scale broadly corresponds to the mean daily movements of bat species occurring in the study area (about 1–3 km). To limit the effect of possible confounding variables, we excluded landscapes with more than 20% coverage by impervious surfaces (buildings and parking lots) and/or wetlands (lakes, ponds and watercourses). We then calculated the amount of forest and road density in each 1-km² landscape and categorized them according to 8 classes (forest amount in %: 0–12.5, 12.5–25, 25–37.5, 37.5–50, 50–62.5, 62.5–75, 75–87.5, 87.5–100; road density in km/km²: 0–5.5, 5.5–11, 11–16.5, 16.5–22, 22–27.5, 27.5–33, 33–38.5, 38.5–44). This resulted in 64 potential combinations of road density and forest amount for which we selected three replicates, one in each sub-region. As a few combinations were not represented in some sub-regions, the final set included 172 landscapes (Fig. 1).

Overall, 94% of forest patches in the selected landscapes were dominated by deciduous trees (80.2% by *Quercus* spp.) and only 6% by conifers (47.6% by mixed fir and spruce trees and 38.1% by pines). All landscape variables were calculated with ArcGis 10 (ESRI, Redlands, CA) based on land cover data obtained at the same year of bat sampling from the French Theia Land Data Centre (www.theia-land.fr/) and the French National Institute for Geographic and Forestry Information (www.ign.fr/). This data was obtained by systematic acquisitions of high-resolution multi-spectral images from Sentinel-2 time series updated in 2016 with a spatial resolution of 10 m (Inglada et al., 2017).

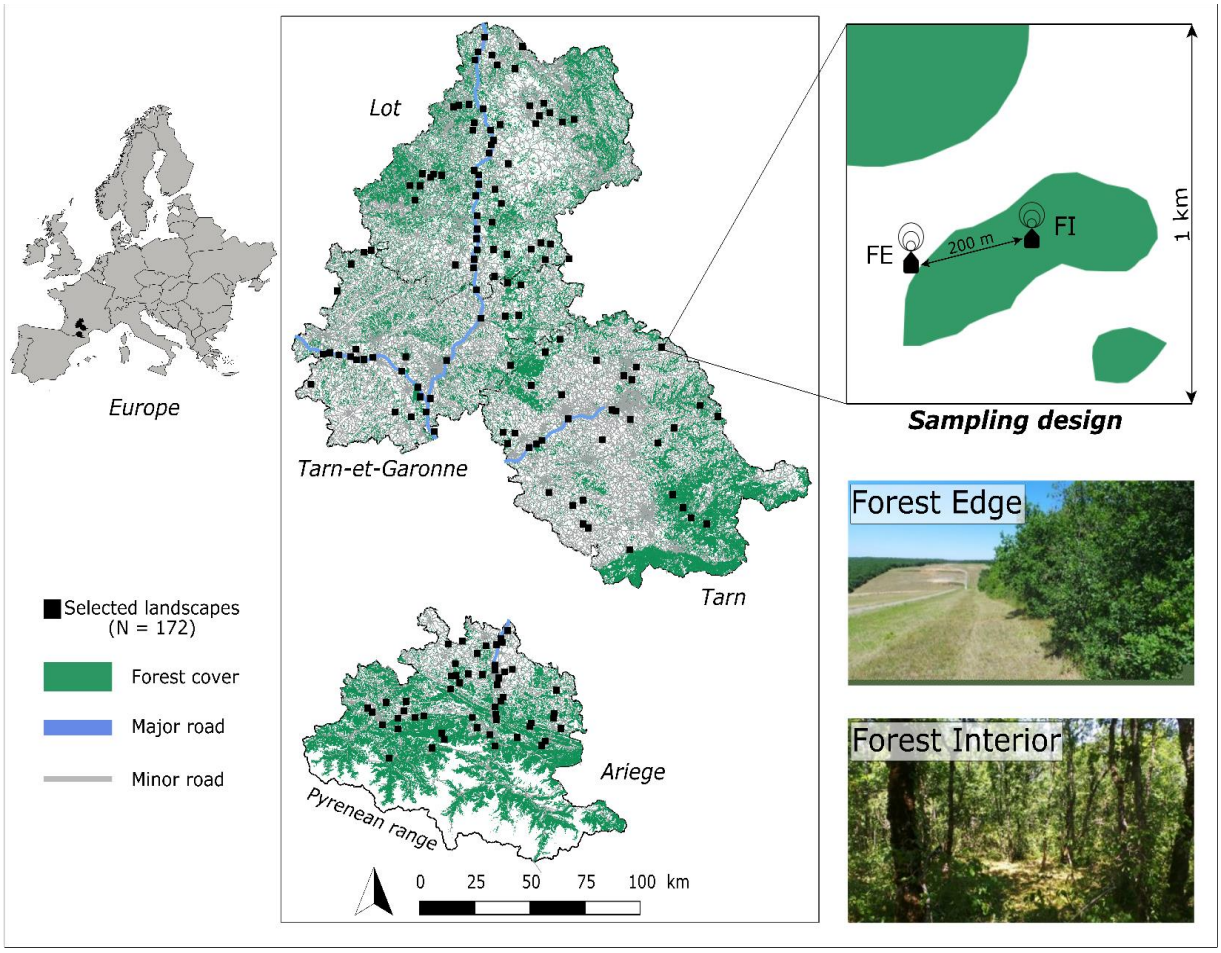

Figure 1 - Land cover map and location of selected landscapes in the study area, showing sampling design with simultaneous recordings of bat activity over one night at the forest edge and interior within each landscape.

2.3. Bat community sampling

Within each of the 172 landscapes, we selected the forest patch closest to the landscape centroid for bat sampling. We deployed two automatic bat ultrasound recorders (Batlogger A, Elekon AG, Lucerne, Switzerland), one in the centre of the forest patch and the second at the interface

between the forest and the semi-natural agricultural matrix (i.e. forest edge). We did not study forest edges created by roads, but mainly those created by land cover change. The recorders were at least 200 m away from each other (mean distance: 412.3 ± 183.8 m; see Fig. 1) to avoid simultaneous recordings of the same bat calls. In a few landscapes, the most central forest patch was too small to respect this minimum distance between recorders. In such cases, the 'edge' recorder was set up at the border of a different forest patch. In the six landscapes with no forest patch (i.e. 0% forest), the two recorders were placed along hedgerows surrounded by agricultural land.

Each landscape was surveyed twice, at two key periods in the annual bat life-cycle: parturition (sampled between 19 June and 27 July) and the dispersion and mating period (sampled between 23 August and 14 October) (Dietz et al., 2009). We simultaneously surveyed eight landscapes at a time (16 deployed detectors) during one full night. The order in which we surveyed landscapes was chosen to limit correlations between landscape variables (forest amount and road density) and the date (Ethier & Fahrig, 2011). Each recorder was calibrated to automatically trigger in reaction to any sound with a signal-to-noise ratio above 6 dB. The recorders were set to start recording ultrasound calls from half an hour before sunset to half an hour after sunrise. Surveys were conducted only when there was no rain, the wind speed was below 30 km/h, and the ambient temperature was above 12°C, as these factors are known to substantially reduce bat activity (Erickson & West, 2002). Microphones were placed 1.50 m above the ground and oriented upwards on a vertical axis.

2.4. Bat call identification and response variables

As it is currently impossible to determine the actual number of individual bats using acoustic data from passive ultrasound recorders, we calculated bat activity as the number of bat passes per night and per species. A bat pass was defined as one or several echolocation calls during a given 5-second interval. This time interval is considered to be the best trade-off to optimize bat pass duration among species with different call lengths and frequencies (Millon et al., 2015). In a first step, echolocation calls were detected and classified to the most accurate taxonomic level, allowing a confidence index to be assigned to each bat pass using the software Tadarida (Bas et al., 2017). The raw data was then divided into two subsets using two confidence index thresholds, corresponding to a predicted maximum error risk of 0.5 (a 0–50% probability of misidentifying a bat pass) or 0.1 (a 0–10% probability). The 0.5 confidence index threshold represented the best trade-off to retain a good quantity of data (in terms of number of bat passes and species occurrences), while the 0.1 threshold limited the number of false positives. To

ensure robustness, we performed analyses on these two subsets to verify the consistency of the results (Barré et al., 2019).

We conducted analyses at the species level for *Pipistrellus pipistrellus, P. kuhlii, Barbastella barbastellus, Myotis crypticus, Rhinolophus ferrumequinum, R. hipposideros, Nyctalus leisleri* and *N. noctula*, which all produce very distinctive calls (Obrist et al., 2004). We assigned all automatic identifications of *Myotis nattereri* to *M. crypticus*, which has recently been split genetically and geographically from the *M. nattereri* species complex, as our study area is within the range of this newly described species (Juste et al., 2018).

We measured four diversity indices: species richness, functional dispersion, functional evenness and phylogenetic diversity. Species richness (i.e. taxonomic diversity) considers species as distinct and is insensitive to ecological and evolutionary attributes. Functional dispersion (FDis) and functional evenness (FEve) measure the variability in ecological attributes between species and provide a mechanistic link to ecosystem resistance, resilience and functioning (Petchey & Gaston, 2006). Functional dispersion measures the mean abundance-weighted distance of an individual species to the centroid of the more abundant species in a multidimensional trait space (Laliberté & Legendre, 2010). Functional evenness measures the regularity of the distribution of species abundance and dissimilarities in the functional space; it represents the proportion of dominant species in the community, ranging between 1, when the community is perfectly even, to 0, when the community is dominated by one species (Villéger et al., 2008). These functional indices are complementary (respectively measuring dispersion and regularity in trait space) yet independent, representing two different facets of functional diversity (Laliberté & Legendre, 2010). Lastly, we calculated the mean nearest taxon distance (MNTD), a phylogenetic diversity index that indicates the mean distance between each species in the phylogeny and its most closely related species in the sampled community (Vamosi et al., 2009). The MNTD measures the evolutionary difference between species based on the time since the divergence from a common ancestor (Faith, 1992) and may represent the long-term evolutionary potential of a community in response to current and future landscape modifications (Cisneros et al., 2015). We calculated FDis and FEve using the dbFD function in R (R package 'FD'; Laliberté and Legendre, 2010), based on a dataset of 11 traits that we are confident to influence bat responses to forest fragmentation and road density (Santos et al., 2016; see Appendix A). We computed MNTD using a tree-based method implemented in the *ses.mntd* function (R package 'Picante') and a phylogenetic tree obtained from https://www.treebase.org/. Finally, we integrated species abundance variations in the

phylogenetic and functional diversity calculations to better reflect finer variations in community structure and composition (Devictor et al., 2010).

2.5. Calculation of local and landscape-level variables

We calculated, as variables of interest, road density, the proportion of forest, and the number of forest patches (see Table 1). At the landscape scale, we also calculated a set of covariates: the Euclidean distance to the nearest paved road (whatever its width) and the Shannon diversity index calculated from all types of land cover (n = 9) in the landscape matrix (another proxy of matrix quality; see Appendix B.1). As different bat species respond to the landscape at different spatial scales (Ethier & Fahrig, 2011), we quantified landscape variables at six spatial scales (a radius of 0.5, 1, 2, 3, 4 and 5 km from each landscape centroid) to identify the strongest biologically relevant 'scale of effect' (Jackson & Fahrig, 2012). The mean spatial overlap of our landscapes for each scale was 1% for 0.5 km, 3% for 1 km, 11.2% for 2 km, 23% for 3 km, 34.4% for 4 km and 44% for 5 km.

To statistically control for local habitat quality effects known to influence bat activity (Langridge et al., 2019), for each forest edge we measured the width, height and proportion of space between understory and canopy levels relative to the total height (Andrieu et al., 2018). For forest interiors, we measured the basal area (using a relascope), canopy height (mean height of the ten highest trees) and mean vegetation clutter (proportion in four vertical height bands: 0–2 m, 2–10 m, 10–20 m and > 20 m; see Table 1). To avoid collinearity in model predictors, we used a principal component analysis (PCA) to aggregate into axes local edge (PCA1) and forest interior (PCA2) attributes as two new variables (see details in Appendix B.2).

Table 1 - Mean, standard deviation, minimum and maximum of the raw (not scaled) environmental covariates used in the analysis, according to the buffer size considered for landscape-scale variables.

Predictors	Local	Nearest element	Buffer (0.5 km)	Buffer (1 km)	Buffer (2 km)	Buffer (3 km)	Buffer (4 km)	Buffer (5 km)
Local								
Basal area (m²/ha)	129.8 ± 137.6 (10 - 535)	-	-	-	-	-	-	-
Mean vegetation clutter (%)	28.2 ± 13.5 (2.5 - 62.5)	-	-	-	-	-	-	-
Edge height (m)	14.2 ± 4.7 (6.0 - 35.0)	-	-	-	-	-	-	-
Edge width (m)	3.8 ± 3.4 (0.0 - 20.0)	-	-	-	-	-	-	-
Edge gap (%)	17.2 ± 12.2 (0.0 - 65.0)	-	-	-	-	-	-	-
Landscape composition								
Forest proportion (%)	-	-	30.6 ± 23.6 (0.0 - 99.2)	28.5 ± 23.4 (0.0 - 97.6)	28.4 ± 19.9 (0.0 - 83.4)	26.9 ± 20.3 (0.0 - 95.1)	27.0 ± 18.7 (1.2 - 87.8)	28.3 ± 18.8 (2.0 - 77.5)
Road density (km/km²)	-	-	3.7 ± 2.4 (0.0 - 14.8)	3.8 ± 1.9 (0.7 - 10.3)	3.5 ± 1.4 (1.4 - 9.2)	3.4 ± 1.2 (1.4 - 8.2)	3.3 ± 1.0 (1.2 - 7.2)	3.2 ± 0.9 (1.2 - 6.9)
Matrix Shannon diversity	-	-	0.8 ± 0.3 (0.1 - 1.4)	0.8 ± 0.3 (0.1 - 1.7)	0.9 ± 0.3 (0.3 - 1.6)	0.9 ± 0.3 (0.3 - 1.6)	0.9 ± 0.3 (0.3 - 1.5)	0.9 ± 0.3 (0.4 - 1.5)
Landscape configuration								
Number of forest patches	-	-	17.9 ± 11.4 (0.0 - 69.0)	57.5 ± 32.0 (0.0 - 197.0)	206.8 ± 94.1 (19.0 - 540.0)	470.3 ± 190.3 (57.0 - 1113.0)	838.1 ± 320.7 (116.0 - 1937.0)	1235.9 ± 484.1 (5.0 - 3012.0)
Distance								
Dist. to road (m)	-	133.5 ± 119.5 (1.1 - 701.6)	-	-	-	-	-	-

2.6. Statistical analysis

To assess how road density, forest amount and forest fragmentation influenced bat activity and diversity, we used generalized linear mixed models (GLMM, R package 'glmmTMB'). Models were fitted using a Gaussian distribution for the bat diversity variables (richness, FDis, FEve and MNTD) and a negative binomial error distribution for bat activity (the number of bat passes per night for each species) with a log link function to take into account overdispersion in our data (Zuur et al., 2009).

We included the first two PCA axes (the local predictors) and the five landscape covariates (Table 1) as fixed effects in the full models, while 'landscape' and 'date' were included as random effects to account for spatial correlation between the two recorders and the correlation in weather conditions between all landscapes sampled during the same night.

To assess differences in bat activity and diversity between forest edges and interiors, we used a two-level factor: forest interior (FI) versus forest edge (FE). We also included the interaction terms between this edge/interior factor and road density, forest amount and configuration, as follows:

$$Bat\ Activity/Diversity \sim PCA1 + PCA2 + Road_dens + Forest_prop + Numb_forestp + Dist_road + Matrix_div + FI/FE + FI/FE{:}Road_dens + Road_dens{:}Forest_prop + Road_dens{:}Number_forestp + 1|Date + 1|Landscape$$

Potential non-linear effects of each landscape predictor were visually checked on biplots from generalized additive mixed models (GAMM, R package 'mgcv').We detected non-linear relationships for richness, FDis, FEve and MNTD with forest amount, and for FDis and MNTD with the number of patches (see Appendix C). In those cases, we added a quadratic effect for these two predictors in the models (see Fig. 2 - Appendix C). The eight continuous fixed effects were scaled so that the associated regression coefficients were comparable in magnitude and their effects were biologically interpretable (Schielzeth, 2010). For each of our 12 response variables, six full single-scale models were built with all 11 predictors. We calculated multivariate regressions (R-package 'MuMIn') for all possible combinations of predictor variables and performed AICc-based model averaging using only the best models within ΔAICc ≤2. Model averaging calculates the averaged coefficients and relative variable importance (RVI) for each predictor as the sum of AICc weights of all top models containing that variable (Burnham & Anderson, 2002). The RVI of a predictor (the maximum importance is 1 if it is present in all top models) can be interpreted as its contribution to the explanatory power of the models in which it is present (Braaker et al., 2017). This procedure was conducted at all six spatial scales for each response variable. The best spatial scales were identified according to

the highest R^2 among the six best models (one per scale; Appendix D). We show detailed results only from the best model of the best scale. We checked for multicollinearity on each of the best models: all variables showed a Spearman's correlation value of < 0.7 and a VIF value of < 4, indicating no strong multicollinearity between explanatory variables (Zuur et al., 2009; see Appendix E). We also checked for spatial autocorrelation in the residuals of the best models using the dnearneigh and sp.correlogram functions (R package 'spatial', Moran, 1950) and found no significant Moran's I values. We did not detect any overdispersion in the best models (ratio < 1). Models were also validated by visual examination of residual plots (Zuur et al., 2009). We performed all analyses in R version 3.3.1. (R Core Team, 2018). The results were largely similar at both confidence thresholds (Table 2), so we only present outcomes from the 0.5 threshold of maximum error risk tolerance (Barré et al., 2019).

Despite using an urban filter during landscape selection, the road network was still correlated (Spearman's correlation > 0.7) with urban cover and average radiance (i.e. light pollution). Consequently, we carried out a complementary analysis (see Appendix F) to test whether urban cover or light pollution better explained the data compared to road density at the best scale for each response variable. For 11 out of the 14 response variables, we found that road density was the most selected urban-related predictor with highest RVI. Only for *N. leisleri* was urban cover more important than road density, while for FDis, road density and average radiance were equally important, with an RVI of 1 (Appendix F).

3. RESULTS

In total, 263 463 passes of 21 bat species were recorded at the 672 recording points spread over 172 landscapes (Table 2). The best models from multi-model averaging showed model fits (R^2) of 0.19–0.48 for bat activity (with the highest variance for *P. kuhlii;* see Fig. 3) and of 0.07–0.29 for bat diversity (with the highest variance for species richness; see Figs 2-3-Appendix D). Overall, forest amount or number of forest patches were always more important than road density for bat diversity, except for functional evenness (Fig. 2). At the species level, forest amount or its fragmentation were more important than road density for only two of the eight studied species, while it was equally important for six of the species (Fig. 3).

Road density had a significant effect (RVI > 0.6) on all bat species and diversity indices, except for *B. barbastellus*, which responded more to the distance to the nearest road (Figs 2-3). The effect of road density was negative for the functional and phylogenetic diversity of *M. crypticus* and *R. hipposideros*, but positive for *N. leisleri*, *N. noctula*, *P. kuhlii*, *P. pipistrellus* and *R. ferrumequinum* (Figs 2-3). In four of these five species, we found significantly different

responses to road density between forest edges and interiors (Fig. 4). The effect of road density was positive in forest interiors, but negative for *R. ferrumequinum* and neutral for *P. pipistrellus* at forest edges. For *P. kuhlii*, road density was positive at both forest locations, although this effect was stronger in interiors than at edges (Fig. 4). In *N. noctula*, activity increased with road density at forest edges, but decreased in interiors. For phylogenetic diversity, we found that road density had no effect at forest edges, but was negative in interiors (Fig. 4).

Table 2 - Number of bat passes per species and the corresponding percentage of total passes and occurrences (percentage of points with presence from all the recording points) according to the applied maximum error risk tolerance for data selection (raw data, maximum error risk tolerance of 0.5 and 0.1).

	Number of passes recorded			% of total passes			Occurrences (%)		
Species	Raw	0.5	0.1	Raw	0.5	0.1	Raw	0.5	0.1
Pipistrellus pipistrellus	164387	161944	119122	54.7	61.5	62.6	98.2	97.0	62.9
Pipistrellus kuhlii	79968	72917	59428	26.6	27.7	31.2	88.3	62.9	31.4
Pipistrellus pygmaeus	14940	7273	1061	5.0	2.8	<1	62.2	12.5	<1
Pipistrellus nathusii	6986	480	-	2.3	0.2	-	57.3	11.2	-
Nyctalus leisleri	5784	4611	3101	1.9	1.8	1.6	71.0	53.1	28.5
Barbastella barbastellus	5237	4886	4122	1.7	1.9	2.2	57.8	53.1	48.9
Eptesicus serotinus	3971	2357	-	1.3	0.9	-	47.6	11.9	-
Rhinolophus hipposideros	3144	2783	254	1.0	1.1	<1	47.1	45.1	16.7
Miniopterus schreibersii	2978	627	-	1.0	<1	-	45.2	14.0	-
Myotis alcathoe	1815	1209	651	<1	<1	<1	7.6	4.3	1.8
Rhinolophus ferrumequinum	1603	1590	1570	<1	<1	<1	22.2	22.2	23.2
Tadarida teniotis	1529	254	171	<1	<1	<1	24.6	4.5	1.9
Myotis crypticus	1502	1204	456	<1	<1	<1	43.6	36.2	15.4
Plecotus austriacus	1326	247	-	<1	<1	-	40.7	4.3	-
Hypsugo savii	1162	584	-	<1	<1	-	29.2	6.0	-
Myotis mystacinus	1152	3	-	<1	<1	-	36.3	<1	-
Myotis emarginatus	936	14	-	<1	<1	-	38.2	1.2	-
Nyctalus noctula	871	386	298	<1	<1	<1	33.8	13.5	9.2
Myotis daubentonii	583	37	3	<1	<1	<1	29.9	4.0	<1
Plecotus auritus	253	17	-	<1	<1	-	11.3	1.8	-
Rhinolophus euryale	74	40	17	<1	<1	<1	5.2	1.8	1.1
Myotis capaccinii	72	-	-	<1	-	-	4.7	-	-
Myotis myotis/blythii	66	-	-	<1	-	-	5.8	-	-
Nyctalus lasiopterus	1	-	-	<1	-	-	<1	-	-
Species richness	24	21	13						
n landscapes	172	172	171						
n recording points	675	672	617						

The effect of road density on bats also depended on forest fragmentation (amount and configuration) (Fig. 5). A significant positive effect of road density on *P. pipistrellus* occurred

only in landscapes with higher numbers of forest patches at the 0.5 km scale. For *R. ferrumequinum* and *R. hipposideros*, the negative effect of road density was significant only in landscapes with lower, or both lower and intermediate numbers of patches, respectively. Finally, road density had a significant negative impact on *N. leisleri* only in landscapes with a low amount of forest.

For five bat species activity, the number of patches was more important than forest amount, while the reverse was true only for *N. noctula* (Fig. 3). For *M. crypticus* and *P. pipistrellus*, both factors were equally important. More precisely, a higher number of patches could have opposite effects depending on species identity. This effect was positive for the activity of five species, but negative for the two *Pipistrellus* species. In contrast, no positive effects of forest amount were found on bat activity (negative effects for four species and no effect for the others). The effect of forest amount on functional diversity (FDis) was also negative, whereas species richness showed a hump-shaped response (quadratic term), with maximum taxonomic diversity in landscapes with 40–50% of forest cover (Fig. 6). The effect of forest fragmentation on functional and phylogenetic diversity also showed a hump-shaped response, with a maximum occurring at an intermediate number of patches (Fig. 6).

Of the eight species activity and four diversity indices, six species and two diversity indices were significantly higher at forest edges compared to interiors, while no significant differences were found for *M. crypticus*, *N. noctula* or phylogenetic diversity. In contrast, functional evenness was significantly higher in interiors (Appendix G). Local forest edge structure (PCA1; see Appendix B.2.) was important for three species, with a positive relationship for *P. kuhlii* and *P. pipistrellus*, but negative for *R. ferrumequinum*. Local forest interior structure (PCA2; see Appendix B.2.) was positive for two species (*B. barbastellus* and *R. ferrumequinum*; see Fig. 3). PCA1 was the only important local predictor for bat diversity, with a positive relationship for taxonomic diversity, but a negative one for functional and phylogenetic diversity (Fig. 3). Finally, landscape matrix diversity was important (RVI > 0.6) for three species (*N. noctula*, *P. kuhlii* and *R. ferrumequinum*) and for phylogenetic diversity (MNTD), with both positive and negative effects (Figs 2-3; see Appendix B.1. for interpretation).

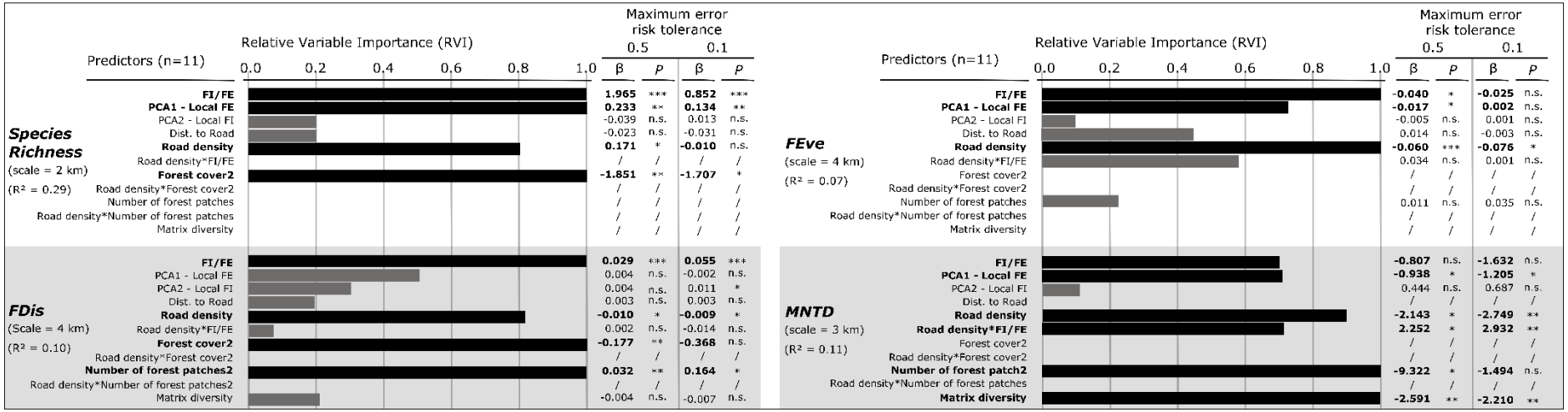

Figure 2 - Relative importance (bar length), estimates (β) and significance (*P < 0·05; **P < 0·01; ***P < 0·001; n.s. = not significant) of model-averaged multiple regressions for the four bat diversity indices at their best scale (highest R^2 of the best model). The relative importance of predictor variables indicates the individual contribution of the variable to the explanatory power of the models (a value of 1 indicates its presence in all top models; bar is black if >0·6). *P*-values are only provided for comparison of the model averaging approach with null hypothesis testing. Forest interiors were used as the reference (i.e. intercept) in each model. A predictor followed by the number 2 indicates quadratic terms.

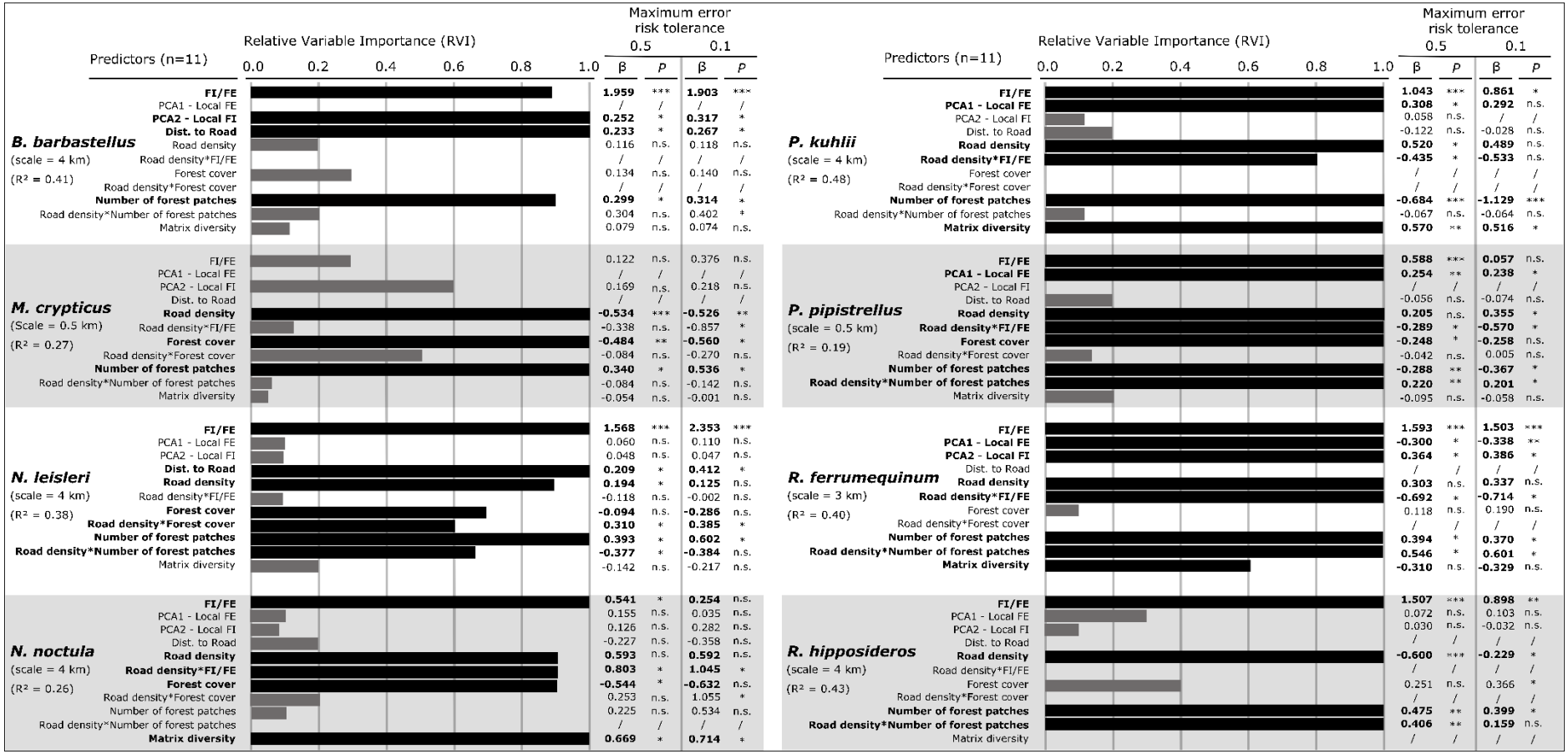

Figure 3 - Results from model-averaged multiple regressions for the activity of 8 bat species (i.e. number of bat passes per night). See details in caption of Fig. 2.

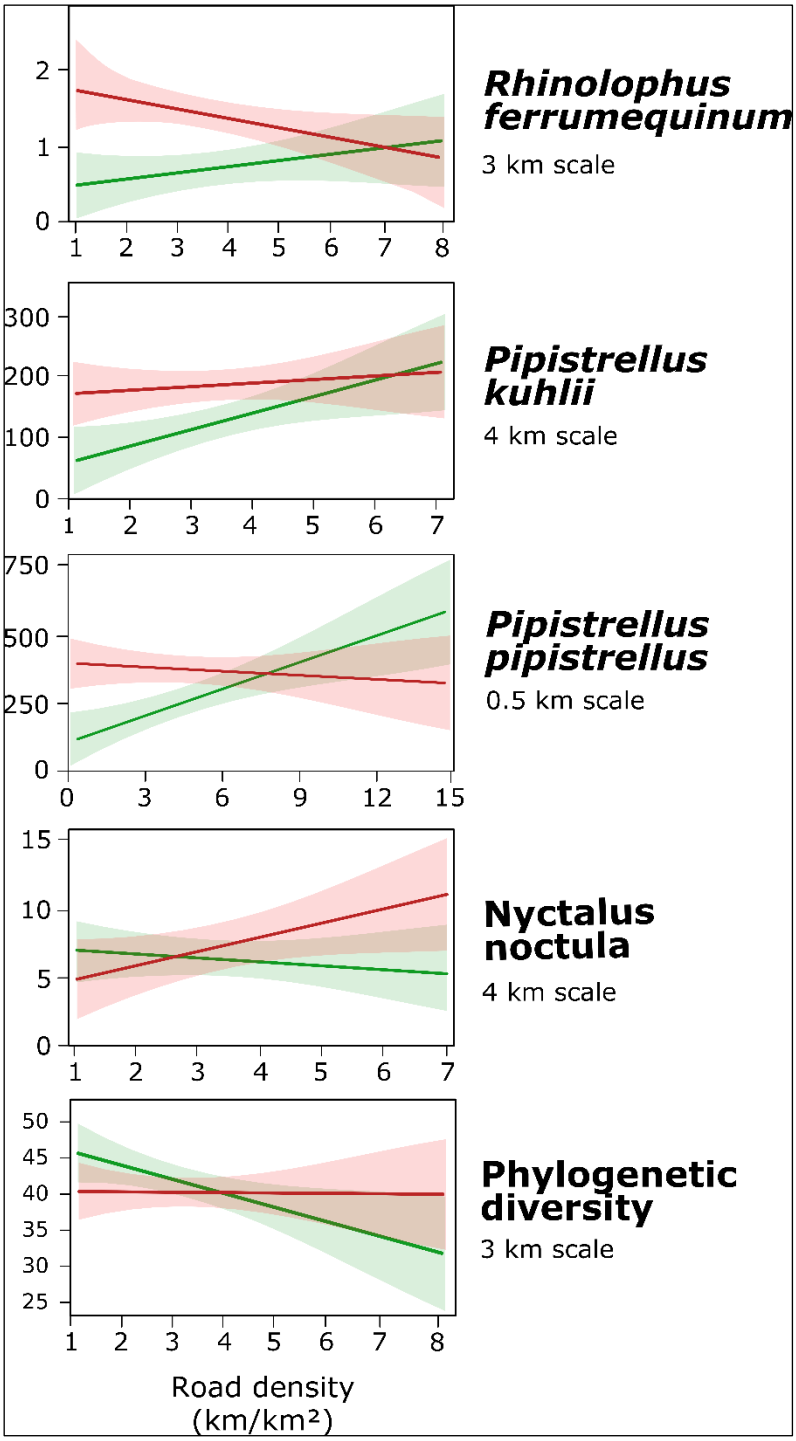

Figure 4 - Predicted bat responses to road density at forest edges versus forest interiors from the best model at the best scale. Values on the y-axis are the number of bat passes per night (i.e. activity). The red and green bands represent the 95% confidence interval for the predicted values at the forest edges and interiors respectively.

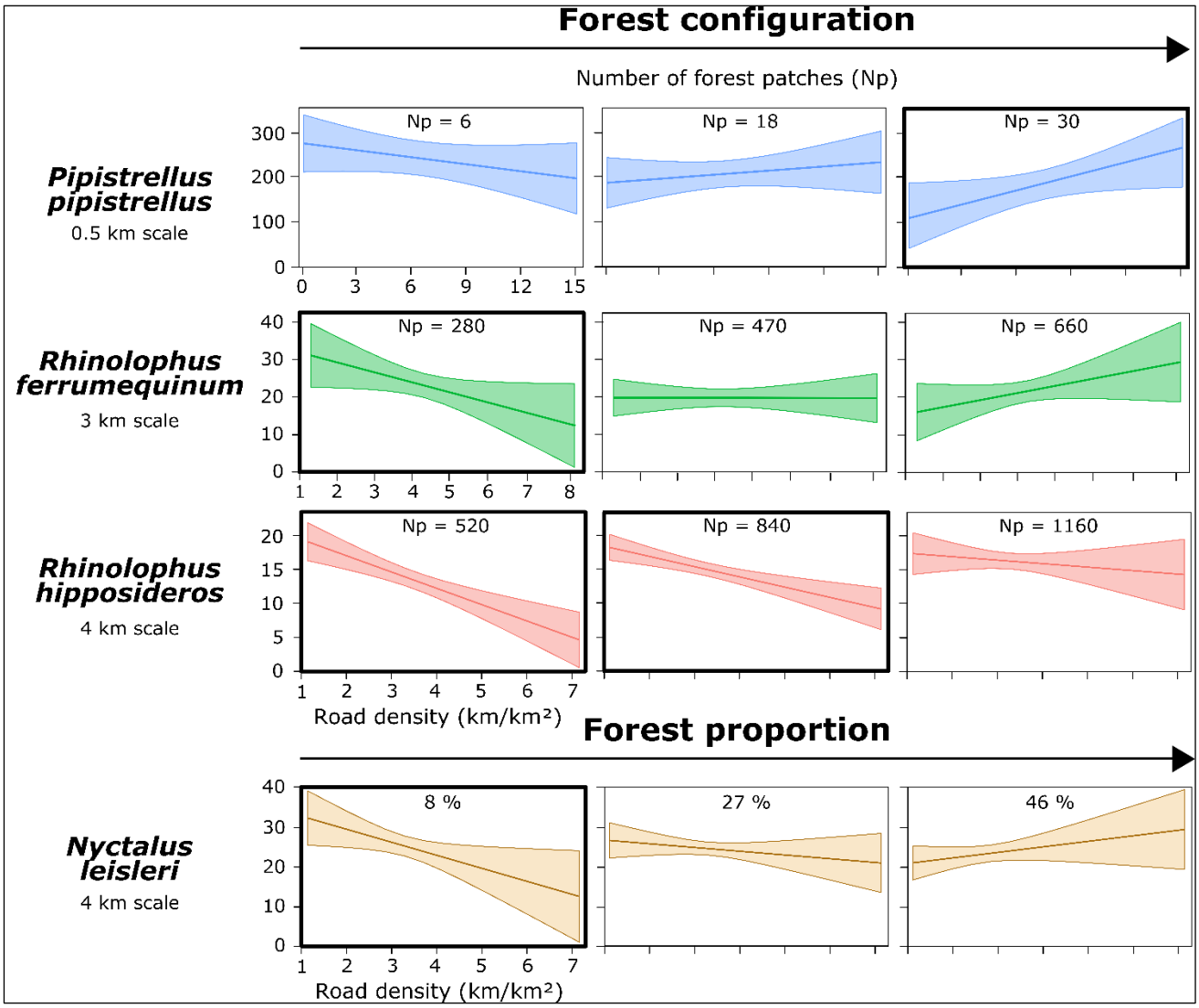

Figure 5 - Predicted bat responses to road density (with the 95% confidence interval) at three different levels of forest amount and configuration from the best models. The three levels have been calculated according to the standard 'spotlight analysis' as follows: mean - SE; mean; mean + SE (Aiken et al., 1991). Values on the y-axis are the number of bat passes per night (i.e. activity). Bold frames represent significant slopes (i.e. 95% confidence interval not containing zero).

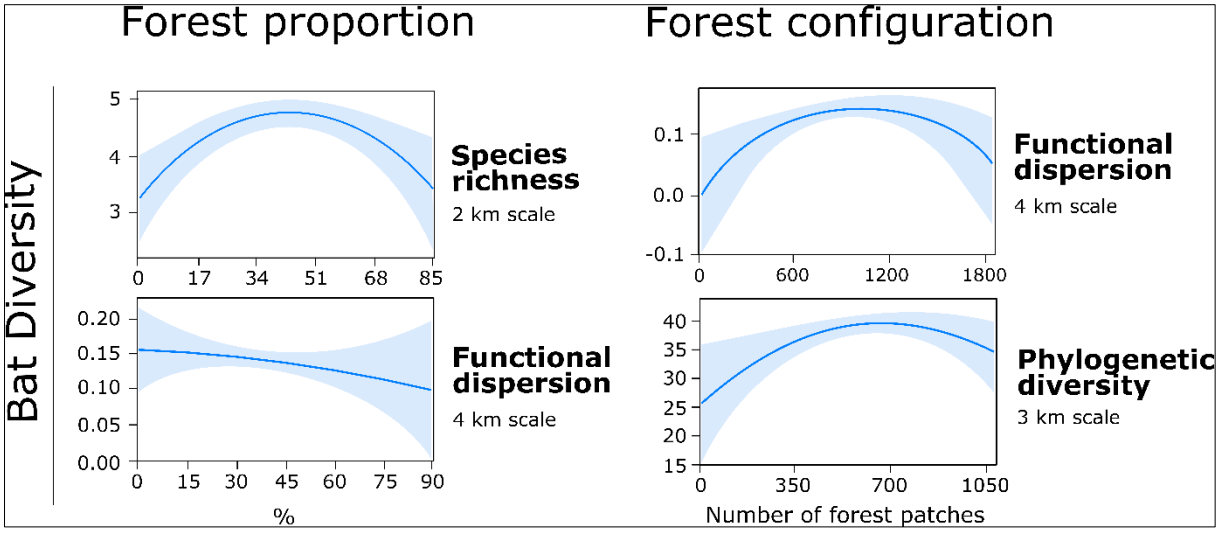

Figure 6 - Variation in the three dimensions of bat diversity predicted (with the 95% confidence interval) in response to forest amount and configuration from the best model at the best scale.

4. DISCUSSION

4.1. Disentangling the landscape-scale drivers of bat diversity

To our knowledge, this study is the first to simultaneously assess the taxonomic, functional and phylogenetic dimensions of bat diversity in human-modified landscapes of a temperate region. We found that taxonomic variation was best accounted for by the amount of forested area, whereas variation in functional and phylogenetic diversity was best accounted for by a combination of forest amount and configuration (i.e. number of patches). In line with studies in tropical regions (Cisneros et al., 2015), these findings demonstrate the complex interactions between habitat loss and fragmentation on the different dimensions of bat community diversity. In our temperate study area, forest amount and fragmentation were more important drivers for bat communities than road density for taxonomic, phylogenetic and functional diversity. Only functional evenness was more affected by road density than by forest amount and fragmentation. Species richness peaked at an intermediate forest amount, while the highest functional and phylogenetic diversity occurred at intermediate fragmentation level. This suggests that large areas of continuous forest or numerous patches mixed with other land cover would produce the best environmental trade-off for maintaining the highest diversity, in which the most species, functional groups and phylogenetic histories are represented (Klingbeil & Willig, 2009). At the landscape scale, this environmental trade-off may provide sufficient resources for both foraging and roosting for a wider range of bat species and life traits.

Beyond pure effects of forest amount and fragmentation, the density of the road network had a significant negative influence on bat functional and phylogenetic diversity, but not on taxonomic diversity. Thus, an increase in road density seems to alter species interactions, ecosystem functioning and the evolutionary history of bat communities regardless of any related changes in species richness. Our multi-dimensional approach investigating the different aspects of diversity was valuable, as we found relative asynchrony in the responses. An investigation solely on species richness would be limited for conservation purposes, as it could mask losses of key ecological or evolutionary attributes of bat assemblages involving decreased resilience to landscape modification (Cisneros et al., 2014; Devictor et al., 2010). Moreover, positive or non-significant effects of roads on taxonomic diversity may be coupled with significant decreases in functional and phylogenetic diversity, which would suggest that roads act as environmental filters, leading to a biotic homogenization of bat communities at landscape scale (Monnet et al., 2014).

We also found that road density had the weakest influence on functional diversity. This seems to be a common phenomenon, as fewer changes in functional diversity (compared to other aspects of diversity) along environmental gradients have been documented in a variety of taxa, including tropical bats (Cisneros et al., 2014). Several assembly mechanisms may differently influence the set of bat traits that we used to calculate functional diversity. For instance, a given mechanism could favour one trait and discriminate against another, leading to no change in functional diversity. An increase in functional and phylogenetic diversity could come either from adding more ecological or evolutionary attributes to a bat community, or from the loss of abundant and/or redundant species, both of which would enhance the distribution dispersion and/or regularity of traits in the functional space (Cisneros et al., 2014). Ultimately, the changes in functional and phylogenetic diversity observed in our study may reflect interactions between multiple mechanisms for which the species-specific responses can provide further insights.

4.2. Species-specific responses to forest amount and fragmentation

Our results showed that the pure effect of forest fragmentation (i.e. the number of patches) was more important than the pure effect of forest amount (7 vs 4 bat species respectively). In addition, the number of patches was a more important predictor than forest amount for *N. leisleri*, while they were of equal importance for *M. crypticus* and *P. pipistrellus*. Bat activity responded predominantly and positively to forest fragmentation but negatively to forest

amount. These findings may be due to three non-mutually exclusive mechanisms. First, the results are consistent with both landscape supplementation and complementation processes that facilitate access to different types of substitutable and non-substitutable resources in different habitats (Dunning et al., 1992). Previous telemetry studies have revealed that the studied bat species forage in a wide range of habitats and most often roost outside their preferential foraging habitat, as they depend on the availability of potential roosting structures (trees or buildings) in the landscape (Ancillotto et al., 2014; Downs et al., 2016; Fonderflick et al., 2015; Parsons & Jones, 2003; Shiel et al., 1999). Consequently, bats may be more likely to occur in landscapes in which both roosting and foraging areas are available. For instance, while a loss of forest cover reduces the overall number of potential roosting sites for tree-dwelling bats such as *N. noctula*, these rare roosting sites may become more optimal, with increased proximity to a diversified range of foraging habitats. However, the quality of foraging habitats surrounding roosts plays a decisive role in roost choice for insectivorous bats (Boughey et al., 2011; Fonderflick et al., 2015). An increase in the number of forest patches with constant forest amount decreases the mean distance between foraging and/or roosting sites, and therefore the landscape complementation and/or supplementation processes (Fahrig, 2017).

Secondly, it has been suggested that a positive influence of habitat fragmentation could arise from positive edge effects (Fahrig, 2017). Forest edges are key habitats for foraging and commuting for a wide range of insectivorous bat species (see Appendix G): acting as a navigational reference, a source of insect prey, a shelter from wind, and as protection from predators (Morris et al., 2010). At the landscape level, an increase in the number of forest patches necessarily results in an increase in forest edge density (Fletcher et al., 2007), thus improving overall landscape connectivity for bats. In our study, edge density was positively correlated with forest amount ($r > 0.7$), but bats systematically responded negatively to the latter. We argue that this is because access to foraging sites from roosting sites (i.e. connectivity) would only affect bat persistence when combined with the availability of quality roosting and foraging areas. The negative responses of several species to forest amount were likely driven by landscape complementation/supplementation processes that may have outweighed the increase in landscape connectivity, especially when roosting or foraging resources were limited.

Thirdly, some authors have suggested that a positive response to fragmentation can result from higher habitat diversity at the landscape scale, offering more diverse and abundant prey resources (Fahrig, 2017). However, our results did not support this hypothesis, as the number of forest patches was independent from matrix diversity. Here again, landscape

complementation/supplementation processes are likely among the key mechanisms driving bat responses to forest fragmentation in complex landscapes (Ethier & Fahrig, 2011). The results did not validate the prediction that less mobile species (in our case, *M. crypticus, P. pipistrellus, P. kuhlii* and *R. hipposideros*) would have a more marked response to forest configuration, while more mobile species (*N. leisleri, N. noctula, B. barbastellus* and *R. ferrumequinum*) would respond more to forest amount. Instead, the findings suggest that for most bat species, quantifying the amount of forest alone is not sufficient for analysing real habitat availability in heterogeneous landscapes (Fahrig, 2017). In line with a recent global meta-analysis (Keinath et al., 2017), our results also suggest that the response of bats to habitat loss and fragmentation depends more on foraging and roosting habitat requirements than on their movement capacity.

4.3. Bats respond to road expansion according to life traits

As road density and the number of forest patches were not correlated in our dataset, we did not directly studied fragmentation created by road expansion, but by land use conversion to agriculture. Our findings indicate that, beyond pure forest fragmentation effects, roads act as environmental filters for the diversity of bat communities. Road density had a positive effect on the highest-flying species (*Pipistrellus* and *Nyctalus* spp.) and non-forest interior specialists (*R. ferrumequinum*), while it had a negative effect on the lowest-flying species (*M. crypticus*) and on forest interior specialists (*R. hipposideros*). The activity of *R. ferrumequinum*, *P. kuhlii* and *P. pipistrellus* in forest interiors increased with road density, while it tended to decrease at edges. In landscapes with higher road density, the probability that forest edges are closer to roads is higher. Thus, this could be a behavioural adjustment induced by the risk of vehicle collision and by disturbance due to light and noise pollution from road traffic (Fensome & Mathews, 2016; Laforge et al., 2019b; Schaub et al., 2008). Landscapes with higher road density make the overall matrix less permeable to bat movements, leading to more time spent in forest patches than in the matrix (Carr et al., 2002; Fahrig, 2003). In contrast, the activity of *N. noctula* at forest edges increased with road density, while it tended to decrease in interiors. As a high-flying species, *N. noctula* is less vulnerable to road effects (Claireau et al., 2019; Medinas et al., 2019) and less concerned by road collisions compared to lower-flying species (Fensome & Mathews, 2016). Consequently, *N. noctula* may use roads as foraging areas that provide an insect biomass concentrated by road traffic (due to light and higher dusk temperature of paved surfaces). *N. noctula* may also benefit from less heterospecific competition with other insectivorous bat species more sensitive to the 'road-effect zone' (i.e. the cumulative ecological

effects of roads on biodiversity at the landscape scale) (Bhardwaj et al., 2019; Claireau et al., 2019; Medinas et al., 2019). In addition to pure edge effects, these contrasting effects of road density at forest edges vs interiors may contribute to significant turnover in bat community composition at both forest edges and interiors, and thus to the overall effect of forest fragmentation on bat communities.

4.4. Road density effects depend on forest amount and fragmentation

For at least four of the bat species studied, we found significant interactions of road density with forest fragmentation, indicating that landscape context can significantly mediate road density effects. For instance, *R. ferrumequinum* and *R. hipposideros* activity decreased with increasing road density only in the more fragmented landscapes. Similarly, road density negatively affected *N. leisleri* in landscapes with a low amount of forest (< 8 %), but not in more forested landscapes (> 27 %). In less forested landscapes, bats and birds may actually need to increase their home range to meet their ecological requirements (Kerth et al., 2002; Tucker et al., 2019). Consequently, the probability of mortality by crossing roads during nightly movements increases, reducing population density and bat activity (Carr et al., 2002; Fahrig, 2003; Gibbs & Shriver, 2005). Also, light and noise effects from traffic, which disturbs bats while commuting and foraging (Bennett & Zurcher, 2013; Schaub et al., 2008; Stone et al., 2015), are likely higher in open areas than in forest-dominated landscapes, potentially resulting in a wider 'road-effect zone' (Medinas et al., 2019).

The distance from major roads has a positive effect on bat activity, up to 5 km (Claireau et al., 2019). In our study, the probability of being closer to a major road was highest in the least forested landscapes. The weaker or neutral effects of road density in the most forested landscapes were also likely caused by a dominance of minor roads. This suggests that avoiding the construction of major roads in forested landscapes would aid bat conservation (Laforge et al., 2019a). Landscape complementation/supplementation processes may also be enhanced in more forested landscapes and may lead to better productivity and fitness within populations, offsetting the negative impact of road mortality on bats. This latter hypothesis may be particularly true for *P. pipistrellus*, which responded positively to road density where forest patches were numerous, but showed no responses to roads in more open landscapes. *P. pipistrellus* actually roosts almost exclusively in buildings and forages in synanthropic habitats (Dietz et al., 2009). Since road density is correlated with urban cover, this would affect roost availability for this species, that also prefers to roost closer to woodlands, probably to reduce

the cost of commuting to forest edges (Boughey et al., 2011). The probability that a forest edge is closer to a road increases with the number of patches and road density. Thus, landscapes with more forest patches and a denser road network may improve the foraging and commuting habitats surrounding roosts, and ultimately the complementation or supplementation processes, for such synanthropic species. However, further studies are needed to quantify the impact of road-related mortality on bat population dynamics and persistence (Fensome & Mathews, 2016).

4.5. Intertwined effects of forest amount and configuration

In our study, forest configuration (i.e., number of forest patches) was not fully independent from forest amount (i.e., forest proportion) in our sampling design (see Appendix H), that was instead focused on orthogonal gradients of forest amount and road density at the landscape scale. However, Ethier & Fahrig (2011), by controlling for independence of forest amount with forest fragmentation in their sampling design, found that bat activity responded only positively to forest fragmentation *per se* but negatively to forest amount. Although forest amount and fragmentation were not highly correlated among our landscapes ($r < 0.7$ and VIF < 4), the scatter plots representing the relationships between forest proportion and the number of forest patches revealed a typical hump-shaped relationship (Fahrig 2003) at 0.5 and 1 km scale but a strict positive relationship at the largest scales considered in our study (Appendix H). This means that our study did not include the less common combinations of low forest amount with high fragmentation and high forest amount with low fragmentation, being naturally the rarest landscape contexts because of intertwined patterns of forest loss and fragmentation (Fahrig, 2003, Smith et al., 2009). Here, we chose to include both forest proportion and number of forest patches in our models because they represent distinct ecological processes and/or mechanisms related to bat responses to fragmentation (Smith et al., 2009; Ethier and Fahrig, 2011, Fahrig 2017). Understanding the important ecological processes and mechanisms is essential if statistical modeling is to advance ecological science (MacNally 2000). Furthermore, Smith et al. (2009) found, by simulations that if forest amount and fragmentation are controlled, as potential confounding predictors, then standardized partial regression coefficients are unbiased estimates, even when predictors are highly correlated. Because forest proportion and number of forest patches have a suppressor relationship in our study (i.e., opposite qualitative effects and a positive correlation), removing one would underestimate the effects of our remaining predictors and would decrease the explanatory power of our models (Smith et al., 2009).

5. CONCLUSION

To our knowledge, this study is the first to attempt to disentangle the effects of forest fragmentation from road expansion on both bat activity and diversity. The results suggest that roads act as environmental filters, with cumulative negative effects to overall forest fragmentation on bats. Landscapes with 25–50% forest cover and/or moderately fragmented forest seem to maintain the highest bat diversity and reduce the magnitude of road effects by promoting short-distance landscape complementation processes and reducing road-crossing events (i.e. mortality risk). These findings are potentially useful to inform landscape-scale conservation planning for insectivorous bats. Although further research is needed to clarify the impact of these interactions on long-term population persistence, ongoing road expansion could alter long-term species interactions and ecosystem function, generating a loss of future options in evolutionary history for bat communities. Our study thus contribute to an improved understanding of the complex interactions between habitat loss, fragmentation per se and matrix quality in complex landscapes, showing the value of a more holistic approach in fragmentation studies.

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Appendix 1

Appendix A.

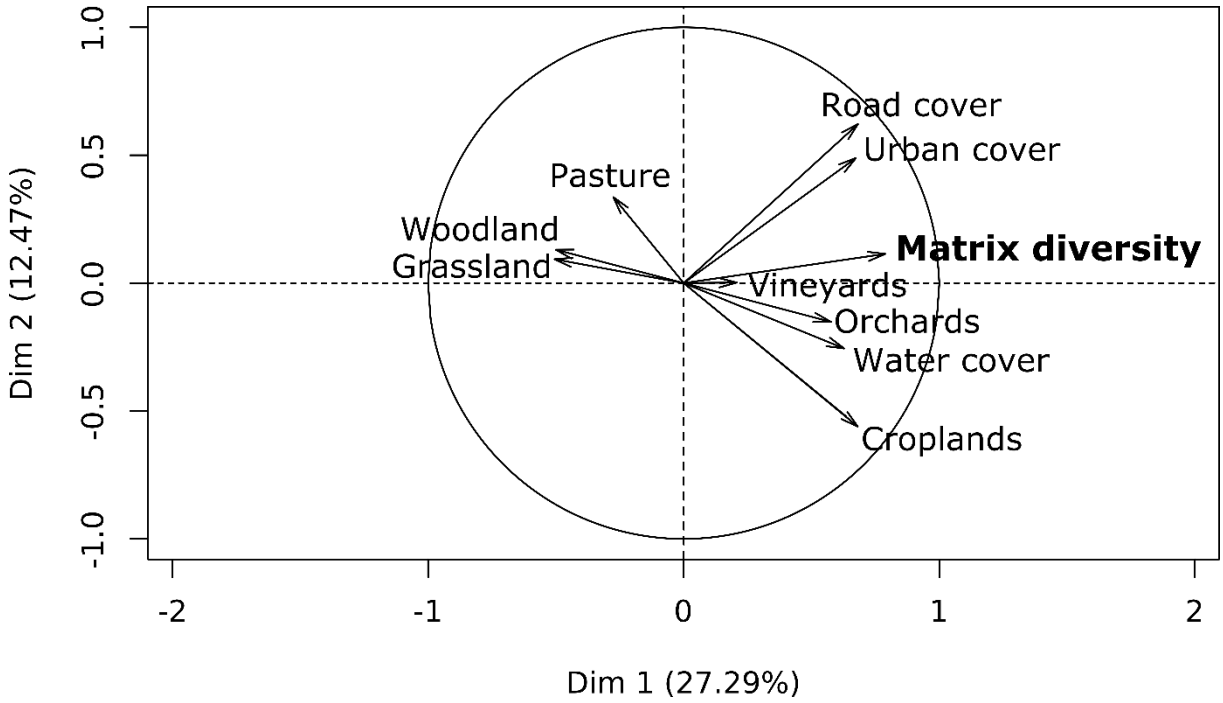
Description of the life traits used to calculate the functional diversity indices with R-package FD (FDis and FEve, see Methods).

Species	**Foraging**	**Diet**	**Roost type for nursing**	**Migrant**	**Parturition period**	**Home range size**	**Mass (g)**	**Species Thermal Index (STI)**	**Species Specialization Index (SSI)**	**Time spent at Height (%)**	**Distance detection (m)**
Reference	*Dietz et al. (2009)*	*Dietz et al. (2009)*	*Dietz et al. (2009)*	*Dietz et al. (2009)*	*Dietz et al. (2009)*	*Laforge et al. (In prep)*	*Dietz et al. (2009)*	*Dubos et al. (In prep)*	*Dubos et al. (In prep)*	*Roemer, et al. (2017)*	*Barataud, et al. (2015)*
Barbastella barbastellus	edge	specialist	tree	resid	may	large	8.50	21.43	2.18	0.00	15
Eptesicus serotinus	edge	generalist	build	resid	july	large	21.50	21.99	0.94	0.06	40
Hypsugo savii	open	generalist	cave	short	july	mid	7.00	23.81	1.55	0.23	40
Miniopterus schreibersii	open	intermediate	cave	short	june	verylarge	12.00	25.48	1.64	0.01	30
Myotis alcathoe	mixed	generalist	tree	resid	june	small	4.50	21.66	1.74	0.00	10
Myotis capaccinii	open	generalist	cave	resid	may	small	8.14	27.19	5.36	0.00	15
Myotis daubentonii	open	generalist	tree	resid	june	large	8.00	20.35	4.09	0.00	15
Myotis emarginatus	gleaning	specialist	build	resid	july	mid	7.50	23.01	2.32	0.00	10
Myotis myotis/Myotis blythii	mixed	intermediate	build	short	july	small	24.00	22.74	1.03	0.02	20
Myotis mystacinus	mixed	generalist	build	resid	june	mid	6.00	20.15	2.67	0.00	10
Myotis nattereri	glean	generalist	tree	resid	july	small	8.50	20.94	0.84	0.00	15
Nyctalus lasiopterus	open	generalist	tree	long	june	verylarge	44.00	23.41	2.24	0.72	150
Nyctalus leisleri	open	generalist	tree	long	june	large	15.50	21.76	1.55	0.49	80
Nyctalus noctula	open	generalist	tree	long	july	verylarge	25.50	20.32	2.22	0.31	100
Pipistrellus kuhlii	edge	generalist	build	resid	may	mid	6.50	24.76	1.23	0.10	25
Pipipistrelus nathusii	edge	intermediate	tree	long	may	large	8.00	20.76	2.55	0.19	25
Pipistrellus pipistrellus	edge	generalist	build	resid	june	mid	5.00	20.86	0.90	0.08	25
Pipistrellus pygmaeus	edge	generalist	build	short	june	small	5.50	20.97	2.15	0.04	25
Plecotus auritus	glean	specialist	tree	resid	july	small	7.50	19.85	3.50	0.00	20
Plecotus austriacus	mixed	specialist	build	resid	june	mid	8.00	23.41	1.06	0.00	20
Rhinolophus euryale	mixed	specialist	cave	resid	july	mid	9.18	25.69	3.59	0.00	10
Rhinolophus ferrrumequinum	mixed	intermediate	build	resid	july	large	21.00	23.63	2.12	0.00	10
Rhinolophus hipposideros	mixed	generalist	build	resid	july	small	5.50	22.78	7.10	0.00	5
Tadarida teniotis	open	intermediate	cave	resid	july	verylarge	25.00	25.74	1.31	0.48	150

Appendix B.1

To avoid collinearity in landscape predictors, we analyzed the correlations between landscape matrix diversity and the amount of each habitat used to calculate it through a PCA. Landscape matrix diversity was associated with a gradient of 'naturality' similarly at all spatial scales: the first axis (accounting for 27.3 % of the total variance) varied negatively with the proportion of natural or semi-natural open habitats (i.e., woodland, grassland and pasture) and positively with urban and crop lands (see figure below).

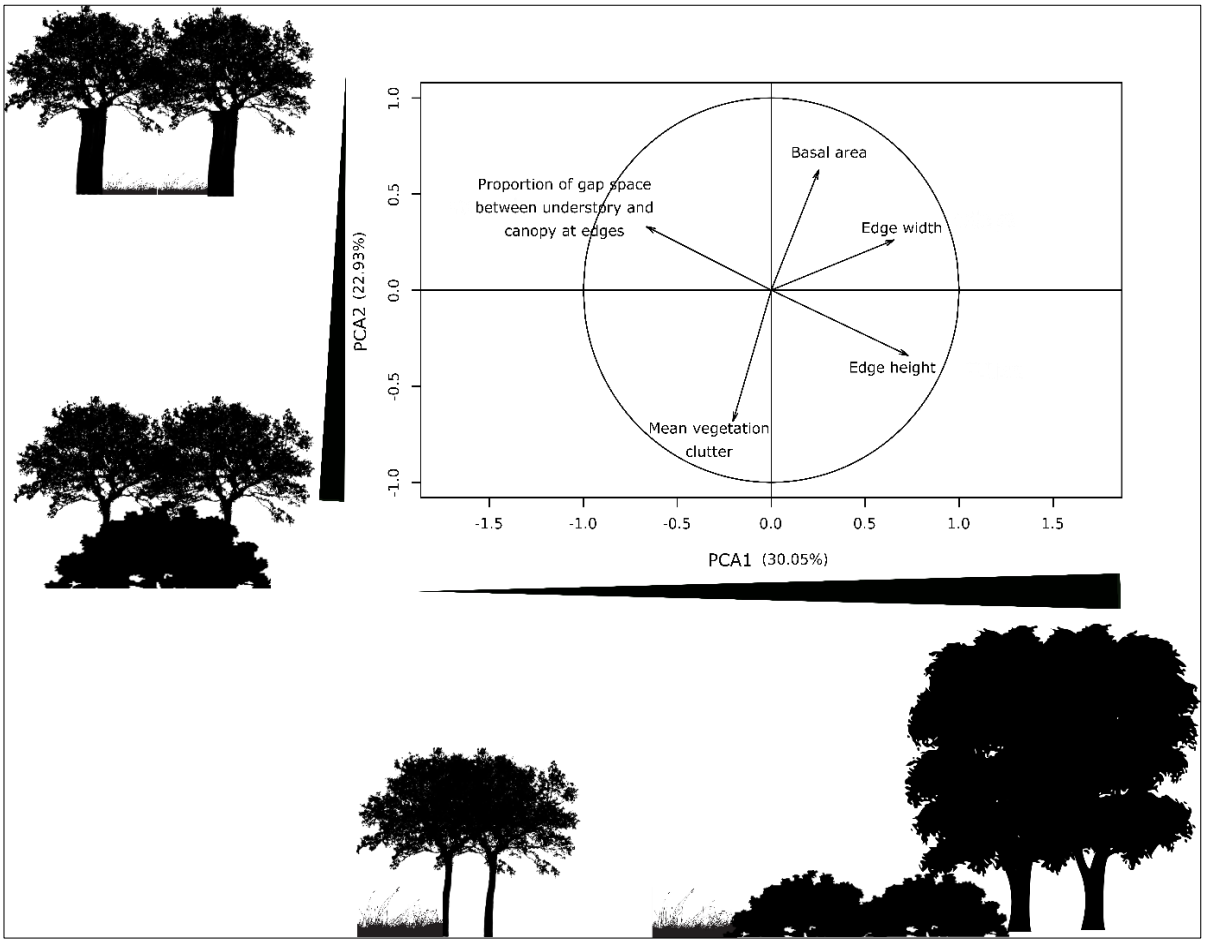
Figure B1 - PCA ordination biplot of all habitats cover and Shannon diversity of the landscape matrix calculated for 172 landscapes.



Appendix B.2

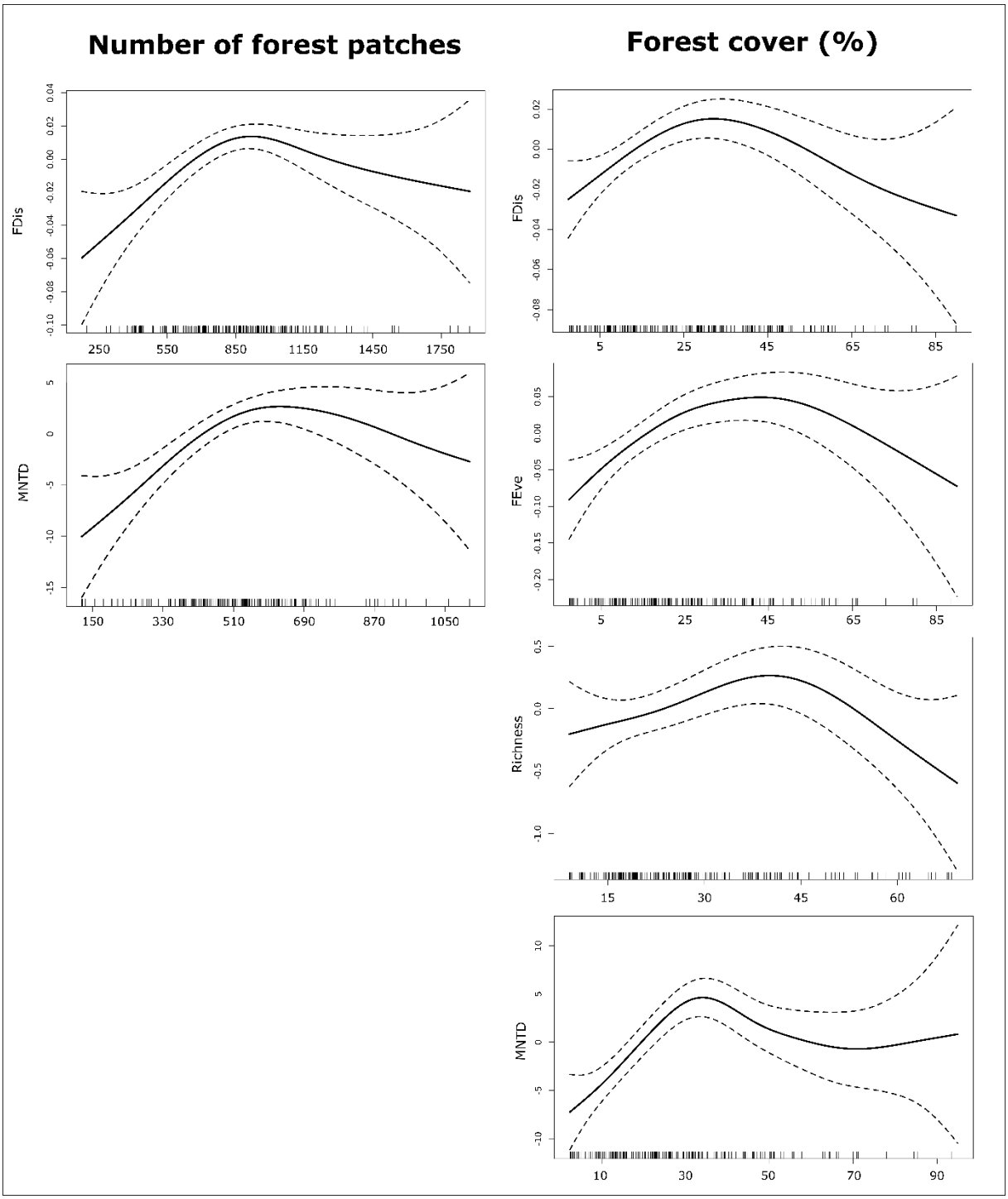
To reduce the number of predictors to be included in the models, we first explored the relationships of the local variables through a principal component analysis (PCA) using the *pca* function (R package *FactoMineR;* Lê et al., 2008). The first axis (PCA1, accounting for 30.0 % of total variance) was associated with edge variables: it varied negatively with the proportion of gap space between understory and canopy levels and positively with the edge width and height (see figure below). The second axis (PCA2, accounting for 22.9 % of total variance) matched a gradient of forest interior variables, from sites with high vegetation clutter values (on the negative side) to sites with high basal area values (on the positive side). We checked the absence of correlations between landscape-scale variables and the first two PCA axes and found no correlations above 0.3, which allowed us to use the two PCA axes as local variables in the same model.

Figure B2 - PCA ordination biplot of three edge local variables and two forest interior local variables recorded in the 172 forest patches. PCA1 is related to edge structures and PCA2 to forest interior variables. Up-right eigenvalues histogram.



Appendix C.

Figure C1 - Non-linear relationships between landscape attributes and bat activity or diversity detected with Generalized Additive Mixed Models (GAMM) fitted with Gaussian and negative binomial error distribution respectively.



Appendix D.

R-squared values (R^2) for the 12 response variables calculated from the best model at the six spatial scales. The values in bold represent the best spatial scale (highest R^2) selected for best models (see Results).

Scales (km)	Species richness	Fdis	Feve	MNTD	B. barbastellus	M. nattereri	N. leisleri	N. noctula	P. kuhlii	P. pipistrellus	R. ferrumequinum	R. hipposideros
0.5	0.27	0.05	0.06	0.06	0.39	**0.27**	0.28	0.24	0.42	**0.19**	0.34	0.28
1	0.27	0.07	0.05	0.08	0.39	0.20	0.28	0.22	0.41	0.18	0.38	0.37
2	**0.29**	0.09	0.06	0.08	0.39	0.18	0.29	0.21	0.46	0.14	0.36	0.38
3	0.28	0.09	0.06	**0.11**	0.40	0.19	0.32	0.21	0.47	0.16	**0.40**	0.41
4	0.28	**0.10**	**0.07**	0.10	**0.41**	0.21	**0.38**	**0.26**	**0.48**	0.16	0.36	**0.43**
5	0.28	0.09	0.06	0.08	0.40	0.16	0.34	0.25	0.45	0.17	0.36	0.41

Appendix E.

VIF values for the 11 predictors used in the full models at the best spatial scale for each response variable.

Predictors	Species richness 2km	FDis 4km	FEve 4km	MNTD 3km	Barbastella barbastellus 4km	Myotis nattereri 0.5km	Nyctalus leisleri 4km	Nyctalus noctula 4km	Pipistrellus kuhlii 4km	Pipistrellus pipistrellus 0.5km	Rhinolophus ferrumequinum 1km	Rhinolophus hipposideros 4km
FI/FE	1.02	1.01	1.02	1.02	1.05	1.09	1.09	1.06	1.03	1.05	1.08	1.11
ACP1	1.12	1.11	1.11	1.10	1.07	1.09	1.04	1.03	1.04	1.10	1.08	1.06
ACP2	1.12	1.12	1.07	1.16	1.10	1.31	1.09	1.10	1.07	1.09	1.08	1.09
Dist. to road	1.12	1.14	1.13	1.14	1.14	1.55	1.19	1.08	1.09	1.41	1.13	1.11
Road density	2.48	3.35	3.49	3.04	2.80	3.53	3.27	3.45	3.06	3.65	2.74	2.58
Forest proportion	1.37	3.04	2.49	1.99	2.80	1.92	2.90	2.81	3.03	1.51	1.84	2.76
Number of forest patch	2.03	1.64	2.53	1.37	2.18	1.56	2.10	2.40	2.24	1.53	1.71	2.04
Road density*FI/FE	1.74	1.85	2.13	1.85	1.66	2.45	1.79	2.16	1.66	2.31	2.21	1.86
Road density*Forest proportion	1.44	2.43	2.29	2.06	1.94	1.91	2.29	2.22	2.21	1.74	1.68	1.87
Road density*Number of forest patch	2.34	2.53	3.41	3.72	1.83	1.39	2.19	2.49	2.29	1.43	1.59	1.54
Matrix Shannon diversity	1.37	1.53	1.48	1.38	1.45	1.31	1.45	1.42	1.42	1.31	1.30	1.37

Appendix F.

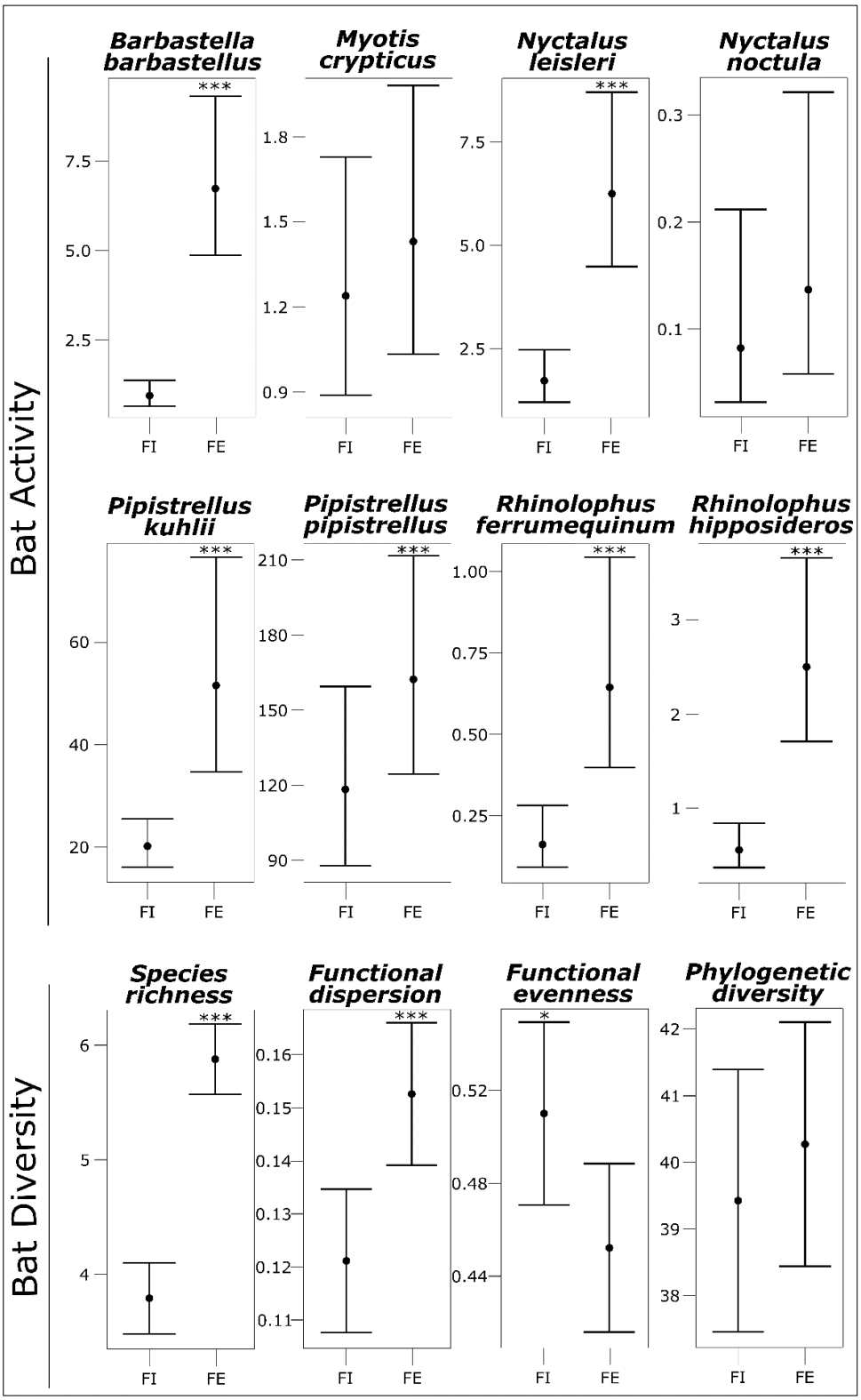
To test if urban cover or light pollution better explained our bat data in comparison with road density, we added urban cover and average radiance variables in the full model and perfrmed multi-model averaging to obtain the Relative Variable Importance (RVI) of each predictor at the best scale for each response variable (see Table below). We parametrized the *dredge* function (R package *MuMIn*, Barton, 2015) so that models did not include simultaneously the correlated variables urban cover, average radiance and road density (Azam et al., 2016). Average radiance is a metric of light pollution obtained from the Earth Observation Group, NOAA National Geophysical Data Centre (http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html).

Table F1 - Relative Variable Importance (RVI) of each urban-related predictors for each response variable obtained from multi-model inference averaging.

Predictor	Richsp	FDis	FEve	MNTD	Barbar	Myocry	Rhihip	Rhifer	Nyclei	Nycnoc	Pippip	Pipkuh
Road	**0.91**	1.00	**1.00**	**0.88**	**0.42**	**1.00**	**0.83**	**0.79**	0.06	**0.95**	**1.00**	**0.88**
Urban	0.26	0.00	0.00	0.00	0.11	0.20	0.00	0.08	**0.78**	0.16	0.66	0.09
Light	0.00	1.00	0.04	0.11	0.10	0.33	0.44	0.09	0.22	0.89	0.33	0.23

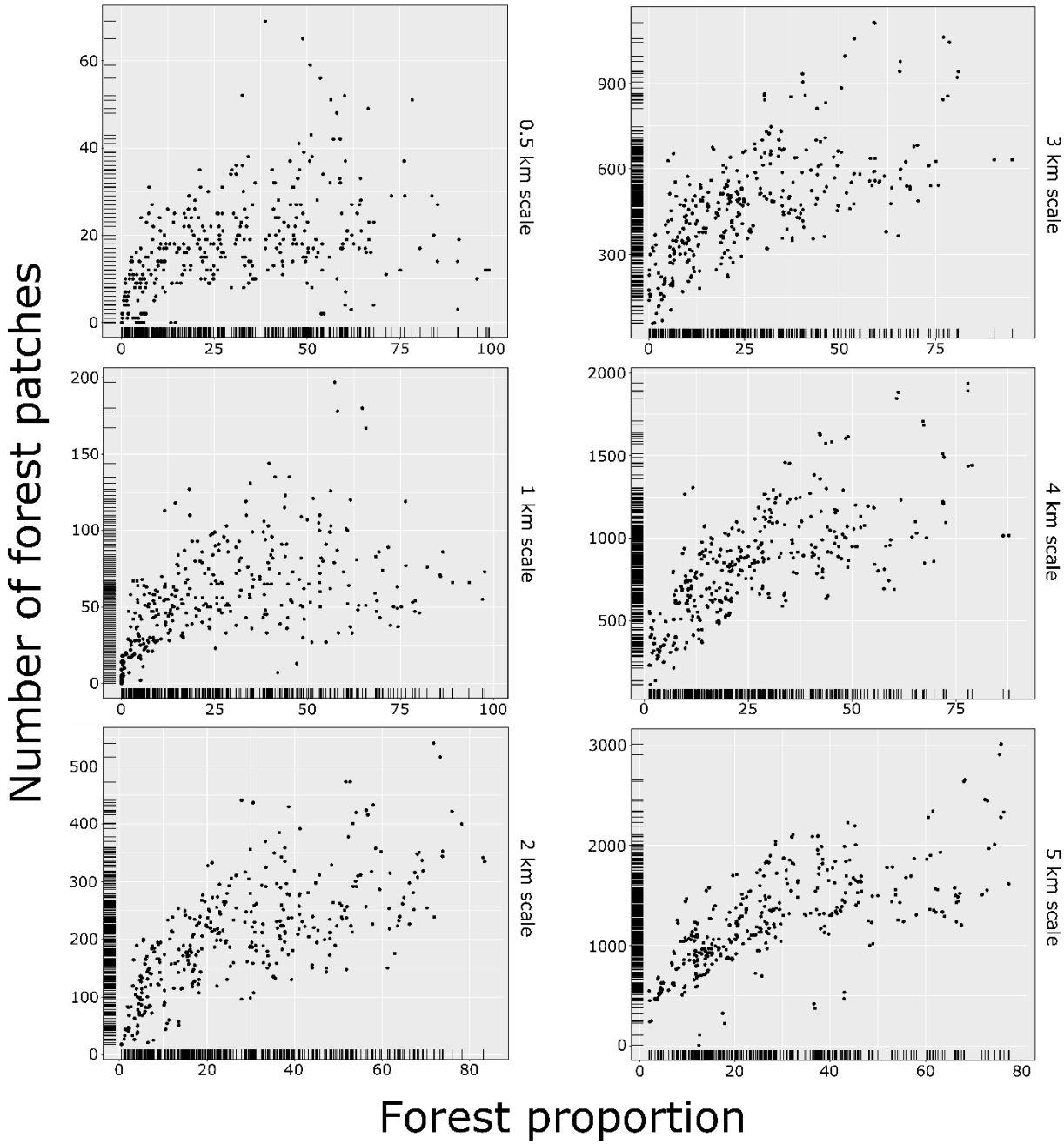
Appendix G.

Figure G1 - Boxplots of predicted bat activity and diversity for one night at forest edge versus forest interior. Dots represent means and error bars show 95% confidence intervals. FI = Forest Interior and FE = Forest Edge. Forest interior were used as the reference (i.e. intercept) in each model (***P < 0.001; *P < 0.05).



Appendix H.

Scatter plots representing the relationships between forest proportion and forest configuration (i.e. number of forest patches) in the studied landscapes (n=172) at the six spatial scales.



CHAPTER 2

Landscape composition and life-traits influence bat movement and space use

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This chapter, although presented in the form of a scientific article, is the least accomplished and further analysis are planned to be carried out prior to any submission/publication.

ABSTRACT

Aim: Individual animal movement is an important determinant of fitness, survival, and population dynamics. Movements have important consequences for species conservation, ecosystem structure and function, but it is often unclear how local and daily movements are related to the availability and spatial arrangement of resources (e.g., foraging habitats). Using temperate bats as central-place foragers, we examined how landscape structure affects their non-migratory daily movement patterns by re-analysing exhaustively published telemetry studies.

Location: North-America and Europe

Time period of survey: 1988 – 2016

Methods: We extracted radio-tracking data for 2072 individuals of 51 temperate bat species from 166 studies. We re-located the original 165 roosts within each studied areas and calculated multi-scale landscape metrics around these roots using standardized GIS data. For each colony and individual, we compiled the home-range size and mean daily distance between roosts and foraging areas. We used linear mixed-effects models to examine (i) the effects of the availability and spatial arrangement of resources, measured as Shannon diversity of the landscape matrix, number of forest patches and forest proportion; (ii) the influence of potential barriers to movement based on road density and Human Footprint Index on bat movements; and (iii) the relationship between bat movements and life-traits (i.e., body mass, aspect ratio, wing loading and habitat specialization) in interactions with the landscape.

Results: We found a significant effect of spatial arrangement of resource availability at the inter- and intra-colony level. On average, home-range sizes were up to 42% smaller in the most habitat-diversified landscapes compared to the least and mean daily distances up to 30% shorter in the most forested landscapes compared to the least. As expected, we also found significant positive effects of body mass, aspect ratio and wing loading and a negative effect of habitat specialization on the non-migratory movements of bats.

Conclusions: Using a unique dataset compiling all published home range studies for 51 temperate bats, we demonstrate the importance of resource diversity and spatial distribution on bat movements. We highlight the negative effects of landscape homogenization and forest loss on habitat quality, which make individual bats needing to fly farther to meet their ecological requirements and complete their life cycle by increasing home range sizes and daily foraging distances. It also implies that the key process of resource complementation for bats at the landscape scale is more difficult to achieve with increasing anthropization and distances to travel, and this contributes to a large-scale biotic homogenization of bat communities.

KEYWORDS

Bat conservation, central place forager, home range ecology, landscape complementation, Minimum Convex Polygon, movement ecology, spatial behaviour, radiotracking

1. INTRODUCTION

Animal movement plays important roles in shaping a wide range of ecological processes, from species survival to ecosystem functioning and large-scale biodiversity patterns of biodiversity (Nathan et al., 2008). As animals move across the landscape, they interact with individuals of the same or different species (e.g., predator–prey interactions, social facilitation), perform various ecological functions (e.g., pest regulation, seed dispersal) and mediate key processes (e.g., disease dynamics and gene flow) (Bauer and Hoye, 2014; Breed et al., 2010; Lundberg and Moberg, 2003). Previous studies have shown the severe effects of reduced movement on these processes (Allan et al., 2003; Hanski and Ovaskainen, 2000). As mobile species can provide important ecosystem functions (e.g., regulating prey abundance), conserving movement as a process may be just as important as conserving the species themselves (Runge et al., 2014).

The search for resources is one among the most important drivers of animal movements (Almenar et al., 2011; Arlettaz, 1996; Richter and Cumming, 2006; Rolando, 2002), where resources can be food, water, cover, suitable breeding habitat and access to mates (Figure 1). The link between resource abundance and movement has been found in animal home-range patterns, where home-range size, or the area used by an animal to reproduce and survive, decreases with increasing density of food resources (Anthony and Kunz, 1977; Henry et al., 2002; Herfindal et al., 2005; Kouba et al., 2017; Racey and Swift, 1985). The spatial arrangement of resources and the proximity of habitats containing vital resources (i.e., landscape complementation) are also important factors affecting animal movements (Figure 1; Fahrig, 2017). For example, changes in resource distributions (e.g., habitat loss and fragmentation) can lead to shifts between movement strategies and affect the search behaviors of individuals while foraging, depending on how heterogeneously distributed the resource patches are (Spiegel et al., 2017). Thus, with approximately 50 to 70% of Earth's land surface currently modified for human activities (Barnosky et al., 2012), the expanding human footprint is not only causing the loss of habitat and biodiversity, but is also affecting how animals move through landscapes (Tucker et al., 2018). For instance, large birds move farther in comparatively more homogeneous landscapes (Tucker et al., 2019) and non-flying terrestrial

mammals are forced to reduce their movements in high human-modified landscapes (Tucker et al., 2018).

Bats represent an ideal taxa for studying consequences of habitat loss and fragmentation (Presley et al., 2019). They are highly mobile and, as central-place foragers (Daniel et al., 2008), may travel daily long distances between roosts and foraging sites (Voigt et al., 2017), making them efficient seed dispersers, pollinators, and predators of insects and small vertebrates (Altringham et al., 1996; Kunz et al., 2011; Russo et al., 2018). Individual bats home ranges are generally ecologically heterogeneous areas because they use several habitats to meet their needs, i.e. for roosting, commuting and foraging (i.e., individuals use multiple patch types in a landscape) (Presley et al., 2019). Examining the link between bat movement and landscape (e.g., resources distribution) is important not only for contributing to a better understanding of the underlying drivers of animal movement (Nathan et al., 2008), but also for understanding how landscape modification will impact bat movement patterns (Voigt and Kingston, 2016). Previous research on the link between bat movement and landscapes has largely focused upon single populations (Borkin and Parsons, 2014; Knight, 2006; Reiter et al., 2013), with less attention on how daily movements and home-range size are impacted by resources distribution across multiple species (but see Dietz et al., 2013). Here, we aim to examine how different landscape gradients affects daily non-migratory movement patterns at four spatial scales (1, 5, 10 and 20 km radii) across 51 temperate bat species spread over 22 countries and two continents (Europe and North-America; Figure 2).

We predict shorter daily movements (and shorter home-range size) when landscapes are heterogeneous (i.e., resources more diverse and more heterogeneously distributed), because it provides a diverse range of habitats of diverse resources within a smaller area (Da Silveira et al., 2016; Popa-Lisseanu et al., 2009). This means that individuals do not need to travel long distances to fulfil complementary resource needs (e.g., roosting versus foraging). Consequently, we expected that the Shannon diversity of the landscape matrix and forest fragmentation (i.e., number of forest patches) would reduce bat movements by allowing landscape complementation processes at shorter distances (Dunning et al., 1992; Ethier and Fahrig, 2011) while forest loss would increase bat movements (Kerth et al., 2002). Furthermore, we expected that Human Footprint Index (HFI; see methods for more description) and road density would also reduce bat movements by acting as barriers to movement (Claireau et al., 2019; Kerth and Melber, 2009; Laforge et al., 2019) and/or by enhancing shorter distance movements to access to resources for the most generalist species (Tucker et al., 2018).

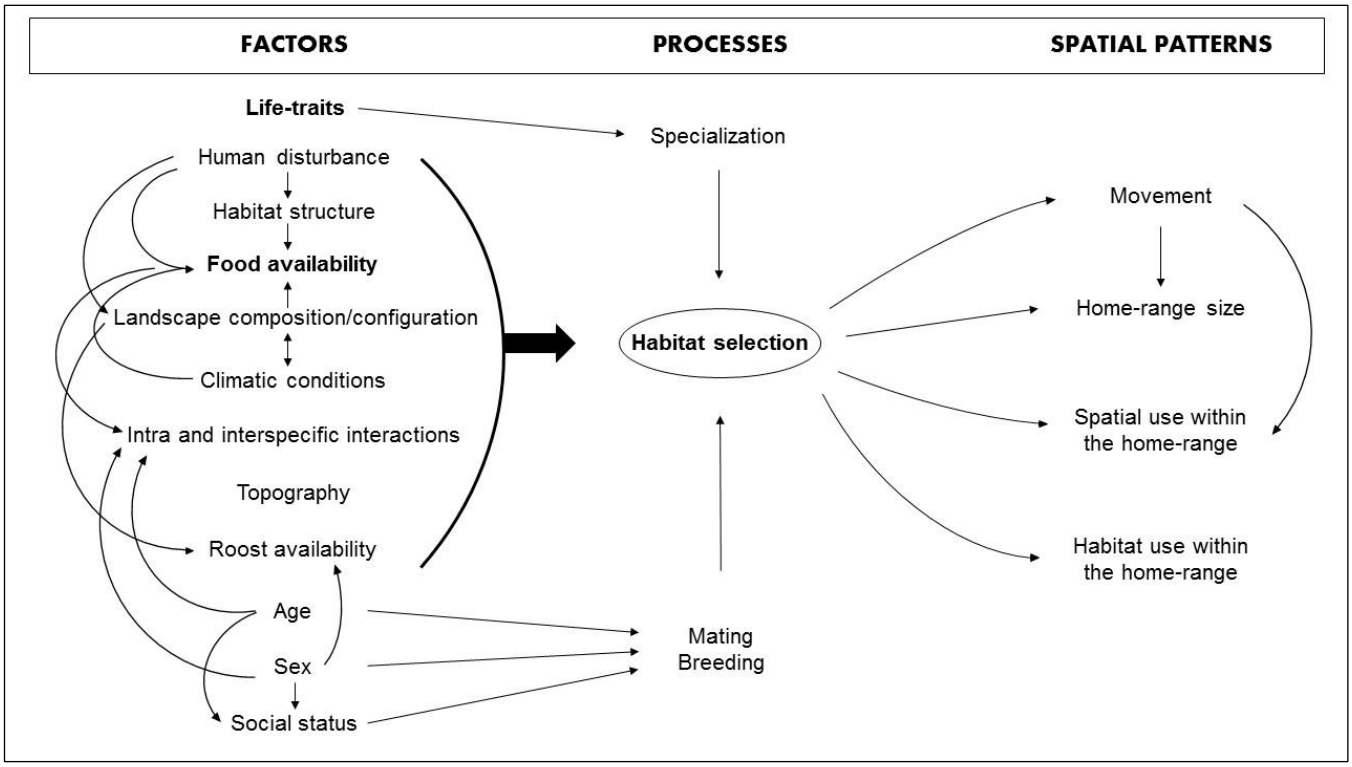

Figure 1 - Theoretical complex relationships among factors, processes and spatial patterns describing the ecology of home range in bats [adapted from Rolando, 2002]. Factors may directly or indirectly affect processes. In the former case the arrow starts from the factor considered and hits a certain process, whereas in the latter case the arrow starts from the factor considered and hits another factor. Food availability and life-traits (among factors) and habitat selection (among processes) are evidenced in bold types because of their importance. Age, sex and social status affect factors and processes in the sense that individuals of different age, sex and social status may behave differently with regard the factor or the process concerned. Spatial use within the home range refers to the presence of disjointed ranges, distinct core areas and various degree of overlap between adjacent home ranges.

However, life traits characteristics and landscape contexts are interactively driving species responses (Figure 1; Baguette et al., 2012). Two main types of life traits drive species responses to landscape modification, namely morphology which affects movements capacity and specialization to prey and/or foraging habitat (Bader et al., 2015; Keinath et al., 2017). We expected that bat movements would depend on body mass, aspect ratio, wing loading and a species habitat specialization index, all interacting with landscape variables. Aspect ratio (the square of the wingspan divided by wing area) and wing loading (body mass divided by wing area), two metrics derived from wing morphology, are widely used for estimating bat mobility (Bader et al., 2015; Norberg and Rayner, 1987; Roemer et al., 2019). There are different energetic costs and flight speeds associated with wing morphology among bats: a higher wing aspect ratio reduces the wing inertia and the flight cost while a higher wing loading induces a faster flight (Norberg and Rayner, 1987). We therefore predicted that species with either a high

aspect ratio or a high wing loading must have the optimal evolutionary strategy to travel the longest distances (i.e., largest home-range size). Allometric scaling relationships have shown that larger birds usually fly farther owing to energy efficiency, increased flight speeds and increased resource requirements (Alerstam et al., 2007). This relationship also seems to be true for bats since body mass is positively correlated with aspect ratio and wing loading (Norberg and Rayner, 1987). However, those three morphological traits provide complementary information and advocate for their simultaneous use in bat response models (Norberg and Rayner, 1987). We also predicted that the most habitat specialists would travel in average shorter distances between roost and foraging areas than generalists, meaning that the same landscape will be perceived as more fragmented by forest specialists than generalists. Consequently, high dispersal increases the risk of moving in a different, less favorable habitat and thus decreases the benefits of specialization according to both empirical and theoretical studies (Baguette and Van Dyck, 2007; Kisdi, 2002; Poisot et al., 2011). However, the opposite prediction is also possible because it depends on the scarcity of the habitat the species is specialized to and how it is distributed in the landscapes (Davidson-Watts and Jones, 2006; Samways and Lu, 2007).

2. MATERIALS AND METHODS

2.1. Literature search

To achieve our goals, we compiled data from studies that documented home-range size and/or daily distance between roosts and foraging areas through telemetry studies in temperate zones (only Europe and North America because most of the radiotracking studies on temperate bats were conducted in these two continents). In order to find studies, we first searched the Web of Science™, Google Scholar™ and ScienceDirect™ using the following character chain: (bat* OR Chiroptera) AND (telemetry OR radio-telemetry OR radiotracking OR radio-tracking OR tracking OR 'minimum convex polygon' OR MCP OR kernel OR radiotransmitter* OR radiotagging OR VHF) AND (Albania OR Austria OR Belgium OR Bosnia OR Bulgaria OR Croatia OR Czech Republic OR Denmark OR Estonia OR Finland OR France OR Germany OR Greece OR Hungary OR Ireland OR Italy OR Kosovo OR Latvia OR Lithuania OR Macedonia OR Moldova OR Montenegro OR Netherlands OR Norway OR Poland OR Portugal OR Romania OR Serbia OR Slovakia OR Slovenia OR Spain OR Sweden OR Switzerland OR United Kingdom OR England OR Scotland OR Canada OR USA OR United-States). In addition to this search, we checked the reference lists of all the papers previously found to build

the most exhaustive data set possible. We further search the references within any new studies until no new reference was found (Hall et al., 2016). We also gathered some studies from the World Bat Library (Geneva, Switzerland). This extensive literature research has been conducted between the 20th March 2017 and the 27th September 2019. We only selected telemetry studies that document movement behavior between roost and foraging areas and disregarded studies focusing only on roost selection and fission-fusion dynamic (Kerth et al., 2011). This procedure led to a total of 166 studies (119 in Europe and 47 in North America) published between 1988 and 2019 (Appendix 1) and spread over 22 countries (Figure 2). The dataset includes 82% of Peer-reviewed journals (n=39 journals), 14% of grey literature and 4% of PhD theses. The dataset concerns 51 species divided into five families (n=43 *Vespertilionidae*, n=4 *Rhinolophidae*, n=2 *Molossidae*, n=1 *Miniopteridae*, n=1 *Phyllostomidae*) and 17 different genera (Table 1).

2.2. Data extraction

Eight different readers participated in the data extraction following the same reading grid and data table to fill (Appendix 2). To verify that our extraction methodology does not induce reader bias, we then randomly redistributed 10 papers for each reader for a double blind-check of the extracted data. Then, the first author re-checked all the data to ensure that quantitative metrics have been reported with the proper unit (i.e., ha versus km², m versus km, SD versus SE). Two different response variables were extracted from the papers: the Minimum Convex Polygon (MCP) as most frequently used calculation method for home-range size (Harris et al., 1990; Mohr, 1947; Worton, 1987) and mean daily distances travelled between roosts and foraging areas. These two metrics related to space use present the advantage to be easily comparable between studies (Harris et al., 1990). Even if many of the telemetry studies on bats reported foraging habitat selection (habitat availability vs. habitat used at the home range scale), we did not extract this type of result because of substantial heterogeneity in habitat classification across studies. Furthermore, habitat use may be much more impacted by the imprecise locations than estimates of home-range size (Kauhala and Tiilikainen, 2002). Nevertheless, estimates of home-range size are very sensitive to methodological choices (Laver and Kelly, 2008), and to control these potential sources of bias in our analysis, we extracted the following methodological information from the papers: season, number of fixes, number of nights (as the duration survey; Mitchell et al., 2019), and transmitter weight. Regarding the latter, O'Mara et al. (2014) revealed that many of the studies used radio-transmitters exceeding 5% of the bat body mass (a value that has become the most recommended practice) that can

impact movements (Aldridge and Brigham, 1988). In our dataset, transmitters represented in average 5% (min = 2%; max = 13%; n individuals = 764) of the individual bat body mass.

In addition, we extracted the localization method to obtain fixes ('Homing-In', triangulation, bi-angulation, estimation of signal strength or a combination of them), the type of fixes used to calculate home-range size (roosting/foraging, roosting/commuting, foraging/commuting or all types of behaviors although it was rarely mentionned by the authors) and the smoothing percentage for MCP (from 90 to 100%) and Kernel calculation (from 30 to 100%). For each value of home-range size and distance travelled, we reported the type of data: mean, median, minimum, maximum when calculated for several individuals or individual. We indicated the number of individuals used for calculation of the median, minimum and maximum while the standard deviation was also reported for the mean. Finally, as some studies reported differential space use according to the sex, age or reproductive status of the radio-tracked bats (Flaquer et al., 2008; Henry and Thomas, 2002; Istvanko et al., 2016), we also reported these information for each home-range and distance data when available. All home ranges, irrespective of whether or not authors had demonstrated that home range estimates had plateaued (the great majority of them did), were included because authors were not always clear on this point.

2.3. Calculation of landscape-level variables

We reported the most accurate location of the roost of the studied colony(-ies) from each study. When accurate location was not available directly from the text (most of them certainly because of a conservation concern), we used information from the maps to relocate the roost(s). Compiled with the text description in the papers, we were able to find the study area on google maps and to extract the approximate coordinates for a total of 165 colony roosts (Figure 2). We localized different roosts from a given study when authors mentioned that distinct colonies used it but in the case of forest-dwelling species, colonies were often spread over a network of trees (i.e., 'fission-fusion') within a forest patch, we extracted coordinates from the barycenter of the different tree-roosts identified by the authors. All those coordinates were then reported on a geographic information system software (ArcGis 10; ESRI, Redlands, CA).

Table 1 – Weighted means and standard deviations of home-range size (MCP) and mean daily distances between roosts and foraging areas for 51 bat species across North-America and Europe. Each mean value is accompanied with the number of studies, number of roosts and number of radio-tracked individuals from which we calculated it ('n'). The total numbers of studies, roosts and individuals ('N') differed from those for the calculation of the presented means because some studies only documented home-range size through Kernel method and/or the maximum distance travelled between roosts and foraging areas (this is the same reason why some species have no documented means).

Family	Species	N studies	N relocated roosts	N individuals	Minimum Convex Polygon (MCP)				Mean daily distance between roosts and foraging areas			
					Mean (ha)	n studies	n roosts	n individuals	Mean (m)	n studies	n roosts	n individuals
Miniopteridae	*Miniopterus schreibersii*	2	2	33	11721.2 ± 9438.2	1	1	20	6850.0 ± 4070.0	1	1	13
Molossidae	*Nyctinomops macrotis*	1	1	4	-	-	-	0	-	-	-	0
	Tadarida teniotis	1	1	17	-	-	-	0	-	-	-	0
Phyllostomidae	*Leptonycteris curasoae*	1	2	72	-	-	-	0	19200.0 ± 6050.0	1	1	22
Rhinolophidae	*Rhinolophus euryale*	7	6	120	635.4 ± 852.1	7	7	120	2727.7 ± 1690.0	4	4	88
	Rhinolophus ferrumequinum	9	9	175	815.5 ± 842.1	6	7	97	2947.3 ± 1557.9	5	6	130
	Rhinolophus hipposideros	7	9	125	214.3 ± 195.2	6	8	119	1323.8 ± 641.0	2	2	27
	Rhinolophus mehelyi	3	3	44	214.9 ± 307.3	2	2	33	8277.8 ± 3564.9	2	2	36
Vespertilionidae	*Antrozous pallidus*	1	0	12	292.8 ± 241.5	1	1	12	1349.4 ± 1124.4	1	1	12
	Barbastella barbastellus	10	7	101	823.1 ± 200.8	7	6	80	6800.0 ± 4800.0	1	2	28
	Corynorhinus rafinesquii	4	3	89	160.6 ± 66.5	1	1	5	700 ± 436.3	1	1	5
	Eptesicus fuscus	4	4	72*	871.5 ± 529.8	2	2	21	1363.6 ± 468.4	1	1	33
	Eptesicus nilssonii	3	4	130	322.9 ± 547.8	3	3	130	-	-	-	14
	Eptesicus serotinus	2	4	136	7318.2 ± 8738.6	1	1	33	8200.0 ± 7100.0	1	1	88
	Euderma maculatum	1	1	4	29720.0 ± 4999.5	1	1	4	-	-	-	0
	Hypsugo savii	1	0	12	200.0 ± 140.0	1	1	12	-	-	-	0
	Lasiurus borealis	4	1	106	70.7 ± 37.7	1	1	13	960.0	1	1	13
	Lasiurus cinereus	2	1	37	-	-	-	0	-	-	-	0
	Myotis bechsteinii	13	10	215	31.3 ± 45.2	7	7	98	456.7 ± 286.2	8	8	115
	Myotis blythii	2	2	10	38.1 ± 11.0	1	1	10	3862.0 ± 1548.0	1	1	10
	Myotis brandtii	1	0	12	40.6 ± 70.0	1	1	12	791.0 ± 850.0	1	1	12
	Myotis capaccinii	3	2	83	3.9 ± 3.2	1	1	17	5457.3 ± 2376.3	2	2	62
	Myotis ciliolabrum	1	1	9	-	-	-	0	6000.0	1	1	9

Vespertilionidae	*Myotis dasycneme*	1	3	38	-	-	-	0	-	-	-	0
	Myotis daubentonii	6	5	173	3591.3 ± 1466.7	2	2	59	4002.0 ± 2102.0	3	3	49
	Myotis emarginatus	6	8	73	309.3 ± 235.9	4	6	48	3711.5 ± 1356.9	3	4	44
	Myotis evotis	1	0	12	-	-	-	0	-	-	-	0
	Myotis frater	1	0	10	85.0 ± 118.0	1	1	10	-	-	-	0
	Myotis gracilis	1	0	10	360.0 ± 460.0	1	1	10	-	-	-	0
	Myotis grisescens	1	5	42	7286.1 ± 4926.1	1	5	42	-	-	-	0
	Myotis lucifugus	4	4	76	1341.8 ± 788.2	2	3	25	254.0 ± 254.1	1	1	13
	Myotis myotis	5	7	50	36.2 ± 17.0	1	1	10	5323.2 ± 3178.5	4	6	50
	Myotis mystacinus	2	1	25	134.3 ± 118.8	2	2	25	2995.0 ± 1012.4	2	2	25
	Myotis nattereri	5	9	108	137.7 ± 129.7	4	7	71	10875.0 ± 7000.0	2	2	24
	Myotis petax	1	0	9	552.0 ± 909.0	1	1	9	-	-	-	0
	Myotis septentrionalis	4	4	73	22.1 ± 19.7	2	3	50	443.2 ± 346.2	1	1	33
	Myotis sodalis	8	6	150	352.7 ± 243.3	4	5	88	-	-	-	0
	Myotis volans	1	1	28	-	-	-	0	-	-	-	0
	Nyctalus leisleri	3	4	50	1194.3 ± 1314.2	2	3	20	1968.7 ± 1754.6	1	1	12
	Nyctalus noctula	3	3	75	216460.9 ± 169752.2	1	1	23	1347.0 ± 606.0	1	1	32
	Nycticeius humeralis	3	2	49	199.0 ± 140.4	3	3	49	-	-	-	0
	Pipistrellus hanaki	1	0	23	246.9 ± 153.5	1	1	23	-	-	-	0
	Pipistrellus kuhlii	2	2	31	164.0 ± 249.7	1	1	21	-	-	-	0
	Pipistrellus nathusii	1	1	14	-	-	-	0	1999.1 ± 705.2	1	1	14
	Pipistrellus pipistrellus	3	2	45	214.2 ± 132.2	2	4	37	977.7 ± 393.2	2	2	22
	Pipistrellus pygmaeus	5	9	154	645.7 ± 540.1	4	6	74	690.0 ± 180.0	1	1	12
	Plecotus auritus	3	0	49	15.0 ± 9.1	2	2	45	-	-	-	0
	Plecotus austriacus	2	3	45	397.7 ± 210.7	2	3	25	9191.9 ± 3918.9	1	2	37
	Plecotus macrobullaris	2	1	22	239.5 ± 284.4	1	1	8	1068.0 ± 1563.0	1	1	14
	Plecotus townsendii	4	3	58	92.3 ± 82.7	2	2	35	1742.9 ± 878.6	3	3	52
	Vespertilio murinus	1	0	19	5509.5 ± 2613.2	1	1	19	-	-	-	0

* One study for this species provided movement data but without the number of individuals tracked to obtain them

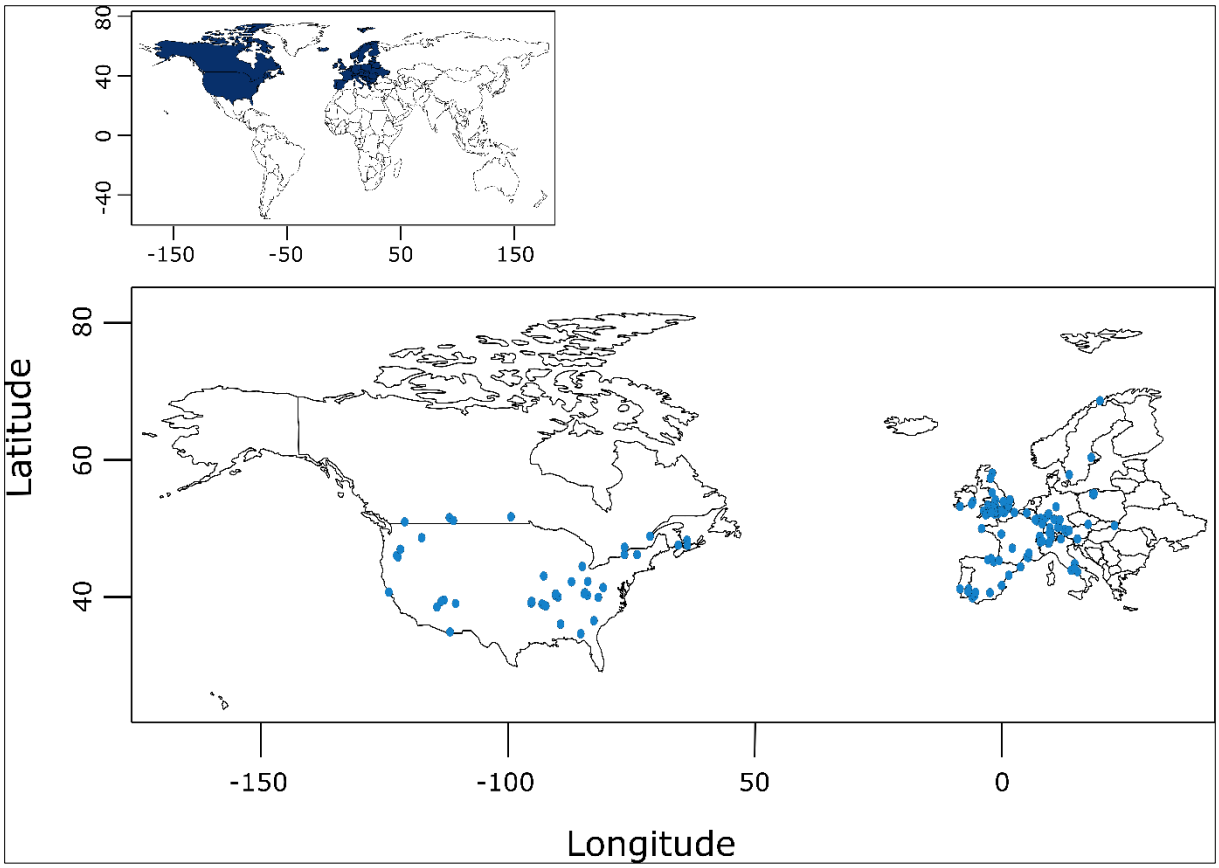

Figure 2 – Location of the 165 relocated roosts (light blue points) from telemetry studies in North-America and Europe.

We created four buffers (1, 5, 10 and 20 km radii) around each relocated roost to identify the strongest biologically relevant 'scale of effect' (Jackson and Fahrig, 2012). At each spatial scale, we quantified the following landscape variables: (i) the Shannon diversity index, calculated from all types of land cover in the landscape matrix; (ii) the proportion of forest as a proxy of forest loss; (iii) the number of forest patches as a proxy of forest fragmentation; (iv) the road density; and (v) the mean Human Footprint Index (HFI), an index with a global extent that combines multiple proxies of human influence. HFI take into account the extent of impervious surface, crop land, pasture land, human population density, night time lights, railways, roads, and navigable waterways (Venter et al., 2016). HFI ranges from 0 (natural environments) to 50 (high-density of impervious surface). We derived the HFI values among our landscapes at the two available years (i.e. 1993 and 2009; Venter et al., 2016). Although data for these two distinct years are highly correlated ($r > 0.9$), we have allocated to each relocated roost one of the two values of HFI according to the nearest year to the telemetric survey period. Land cover data were extracted from two different datasets: the 2012 Corine Land Cover with a resolution of 100 x 100 m for Europe (https://land.copernicus.eu/pan-

european/corine-land-cover), and the 2010 North American Land Cover with a resolution of 250 x 250 m (http://www.cec.org/tools-and-resources/north-american-environmental-atlas/north-american-land-change-monitoring-system). Although we compiled two land cover datasets with different resolutions, the calculation of our landscape metrics at larger spatial extent should provide highly correlated results for a given site regardless of the resolution level (Gastón et al., 2017). Furthermore, to compute the Shannon index of matrix diversity, we homogenized the accuracy level of habitat description in eight different covers: cropland, grassland, shrubland, woodland, bareland, urban, wetland and water bodies. Finally, road density were retrieved from the integrated gROADS database, a global roads open access dataset (http://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1) (Laurance et al., 2014). All landscape variables were computed with ArcGis 10 (ESRI, Redlands, CA) and their numeric details are presented in the Appendix 3.

2.4. Life-traits

The mean body mass was obtained from Dietz et al. (2009) for European species and from Harvey et al. (2011) for North-American species. The latter authors provided the minimum and maximum values per species, from which we calculated a mean value (Roemer et al., 2019). Aspect ratio and wing loading were obtained from Norberg and Rayner (1987). We used the 'Species habitat specialization Index' (SSI) for European species computed in (Barbaro et al., 2019) and Dubos et al. (In prep) and originally described in Julliard et al. (2006). This index has been calculated from a large-scale acoustic survey of bat communities (5595 nights of survey over 1158 sites) performed during nine years across France (http://vigie-nature.mnhn.fr/page/vigie-chiro). The SSI represent the coefficient of variation of the number of bat passes across 20 habitat classes (Corine Land Cover 2012). Although the analysis of the effect of this habitat specialization index on bat movements was only possible for a subset of our data (i.e., only European species), we argue that this is the most relevant and accurate method to test our prediction in comparison with other methods based on expert-opinion or on coarse information (for instance: IUCN Red List or Pantheria database). Finally, when one of those life-traits was not available for a given species (e.g. rare or recently described species), we allocated the value from the nearest congeneric species (Appendix 4).

2.5. Statistical analyses

a) Data preparation

We log-transformed home-range size and daily distance values as response variables to deal with data over-dispersion and to meet assumptions of normality and equal variance (Hall

et al., 2016; Jerina, 2012). Response variables were only built from mean and individual values. Means of home-range size and daily distance for each roost were obtained from different methods. When the information was not directly provided by the authors, we calculated these values from different sub-groups (male/female for instance) weighted by the number of individuals of each groups or from individual data provided by the authors. We also compiled the latitude of each roost as covariate to take into account the potential sampling bias as the survey duration is depending on the night length and the potential influence of climatic conditions on food availability which both may affect home-range size (Frafjord, 2013). All continuous variables used as fixed effects were scaled to correct for skewness and to make associated regression coefficients comparable in magnitude and their effects biologically interpretable (Schielzeth, 2010). We then tested for collinearity between explanatory variables: no landscape variables were correlated either with each other or with sampling effort (number of individuals, number of fixes and number of nights), life-traits and latitude (Pearson's correlation coefficient < 0.66; greatest correlation between HFI and road density). The only Pearson's correlation coefficient > 0.7 was between species body mass and wing loading (0.71) which is consistent with knowledge on bat morphology (Norberg and Rayner, 1987).

b) Effects of landscape and traits on bat movement at the colony level

We evaluated the influence of landscape structure and species traits on bat movements using linear mixed-effect models. All analyses were conducted in R version 3.1.1 (R Development Core Team, http://www.r-project.org) using the lmer function in the lme4 package to fit models (Bates et al., 2015). There were many variables with literature support to consider in our models, and no justifiable rationale for specifying particular combinations of interactions in the candidate set of models. Furthermore, given the large number of variables, it was not possible to compare all combinations and their interactions, and to avoid over-inflation in the response models. Even more importantly, there was a considerable variation in the amount of information reported among studies, meaning that we could not test all the covariates simultaneously in a same model because the resulting quantity of data and gradients of interest would have been too limited. We therefore used a multistep process to construct a 'best-supported model', an approach that has been used successfully in other studies with many possible explanatory variables (Keinath et al., 2017; Yamashita et al., 2007). All candidate models at each step contained a different subset of data and a base model that included study as a random factor to control for inter-study variation.

Step 1: we identified relationships between morphological traits and movement variations among bats by comparing models that differed only in their combinations of trait as fixed effects using the most extensive part of the data ('subset-trait'; see Tables 2 & 3). This step was not used for selection of the most important morphological trait but rather to later evaluate the robustness of those relationships with a more restrictive data subset. Then, we identified the most important landscape attributes by comparing models that differed only in their combinations of landscape metrics as fixed effects, including species ID as a random effect in all candidate models (Keinath et al., 2017) and only movement values associated with landscape data ('subset-landscape'). We also visually checked for potential non-linear effects of each landscape variable on biplots from generalized additive mixed models (GAMM, R package 'mgcv') and found only linear relations. With important landscape variables thus identified, we then removed species ID as a random effect and compared models with every interactions possible between each pair landscape*trait ('subset-landscape').

Step 2: we combined the landscape predictors and their interactions with traits previously identified as most important, as well as latitude and number of individuals as covariates in a 'full model' as follows:

$$LogMCP/LogDist \sim Lat + Body\ mass + Aspect\ ratio + Wing\ load + land.var + land.var:trait + n\ indiv + 1|Study$$

From this 'full model' backwards elimination was used to select the best set of fixed effects terms for inclusion in the best-supported model, having the subset of predictors with the highest performance (lowest AICc value; Tables 2 & 3). This procedure was repeated for the four different spatial scales. The best spatial scale was identified according to the highest marginal R^2 among the four best models obtained (one per scale).

Step 3: to evaluate the robustness of effects identified within the best-supported models, we used an approach in three sub-steps. First, we applied Bonferroni test (Simes, 1986) using the *outlier.test* function (R package *Car*, Fox et al. 2012) and did not identify outliers having significant impact on model fitting (i.e., no studentized residuals with Bonferroni p-value < 0.05). Second, we used Cook's distance as a measure of sensitivity (Cook, 1977; Martín and Pardo, 2009; Sarkar et al., 2011) by identifying the most potential influential observations (i.e., a large value of Cook's distance) on the covariate patterns (i.e., high leverage values). We identified those influential observations using the *influenceIndexPlot* function (R package *Car*, Fox et al. 2012), removed them from the data, re-fitted the best-supported model and check if it caused substantial change in the estimates of coefficients (Zhang, 2016; Tables 2 & 3). Third, we tested the robustness of the effects from the best-supported model by adding consecutively

as covariates the number of fixes, the number of nights and the transmitter weight used to obtain home-range size and daily distance values and compared estimates and significance of the coefficients (Appendix 5). As these information were scarce, this step represents a validation of the results within the most restrictive subset of the data ('subset-sampling'). Finally, each best-supported models were also validated by visual examination of residual plots to verify that the assumptions of normality are respected (Zuur et al., 2009). All variables showed a VIF value of < 2, indicating no multicollinearity between explanatory variables (Zuur et al., 2009).

Step 4: To test our prediction that stipulates that movement of a given bat species is likely to be reduced if this species is strongly associated to a specific habitat, we have reproduced the step 3 by adding SSI as covariate in the full model with a subset of the European data ('subset-europe'). Besides testing our prediction, this step allowed us to assess whether the model better fit the data with or without the inclusion of SSI, and to re-evaluate the consistency of other predictors (Tables 2 & 3).

c) Effects of landscape and traits on bat movement at the individual level

Finally, all the steps described above were also conducted at the individual level for home range and distance data of 2072 individuals of 33 species from 98 studies (Hall et al., 2016; Tables 2 & 3). Furthermore, the analysis at the individual takes into account the variance (i.e., accuracy) around the means through the individual variations among studies. Linear mixed-effect models also permitted analysis of the effects of biological status (age, sex and reproductive status) on home range size and mean daily distance. To do this, we compared models with every interaction possible between each pair landscape*biological status (selection within the step 1). Roost was added as a random effect to account for the likely correlation between observations on individual bats from the same roost (pseudo-replicas). The 'full' model was as follows:

$$indLogMCP/indLogDist \sim Lat + Body\,mass + Aspect\,ratio + Wing\,load + land.var + land.var:trait + Sex + Age + Repro + land.var:status + 1|Study + 1|Roost$$

Table 2 - Model coefficients, *p*-values, R^2 and sample sizes of linear mixed-effects models predicting the log-transformed mean home-range size (MCP) and mean daily distances between roosts and foraging areas at colony level. Predictor variables included fixed effects for the Shannon diversity of the landscape matrix measured at 20 km, forest proportion and Human Footprint Index (HFI) both measured at 5 km. All models also included 'study' as a random effect. Studies: number of studies, Species: number of species, Data: number of data (several MCP/Dist values could be available for the same study).

Step 1: Best model obtained with the 'subset-trait'							
LogMCP				**LogDist**			
Variables	Estimates	SE	*p*	Variables	Estimates	SE	*p*
Body mass	**0.530**	**0.187**	**< .01**	Body mass	0.185	0.098	.069
Aspect ratio	**0.602**	**0.219**	**< .01**	-	-	-	-
R^2 marginal	*.155*				*.032*		
R^2 conditional	*.787*				*.904*		
Studies	79				55		
Species	39				33		
Data	111				68		
Step 2: Best model obtained with the 'subset-landscape'							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**0.427**	**0.166**	**< .05**	**Body mass**	**0.195**	**0.091**	**< .05**
Aspect ratio	**0.689**	**0.263**	**< .05**	**Forest proportion5**	**-0.580**	**0.127**	**< .001**
Matrix diversity20	**-0.422**	**0.179**	**< .05**	**HFI5**	**-0.265**	**0.116**	**< .05**
R^2 marginal	*.180*				*.332*		
R^2 conditional	*.856*				*.922*		
Studies	64				44		
Species	31				30		
Data	91				56		
Step 3: Sensitivity test applied on the best model from the 'step 2' by omitting the most influential values identified by Bonferroni test and the Cook's distance (i.e., outliers and hat values)							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**0.341**	**0.164**	**< .05**	**Body mass**	**0.269**	**0.088**	**< .01**
Aspect ratio	**0.546**	**0.253**	**< .05**	**Forest proportion5**	**-0.600**	**0.109**	**< .001**
Matrix diversity20	**-0.459**	**0.172**	**< .01**	HFI5	-0.125	0.110	.262
R^2 marginal	*.152*				*.444*		
R^2 conditional	*.838*				*.912*		
Studies	63				42		
Species	30				29		
Data	90				53		
Step 4: Best model obtained with the 'subset-Europe' to add the Species Specialization Index (SSI) as covariate in the model selection							
	Estimates	SE	*p*		Estimates	SE	*p*
SSI	**-0.437**	**0.176**	**< .05**	**SSI**	**-0.328**	**0.101**	**< .01**
Wing loading	**0.502**	**0.148**	**< .01**	**Forest proportion5**	**-0.587**	**0.138**	**< .001**
Matrix diversity20	-0.366	0.216	.097				
R^2 marginal	*.136*				*.431*		
R^2 conditional	*.917*				*.820*		
Studies	48				36		
Species	21				22		
Data	68				46		

Table 3 - Model coefficients, *p*-values, R^2 and sample sizes of linear mixed-effects models predicting the log-transformed mean home-range size (MCP) and mean daily distances between roosts and foraging areas at individual level. Predictor variables included fixed effects for the Shannon diversity of the landscape matrix measured at 20 km, forest proportion and Human Footprint Index (HFI) both measured at 5 km. The model also included 'study' and 'site' as random effects. Bat movement of adult individuals were used as the reference (i.e., intercept).

Step 1: Best model obtained with the 'subset-trait'							
LogMCP				**LogDist**			
Variables	Estimates	SE	*p*	Variables	Estimates	SE	*p*
Body mass	**0.868**	**0.392**	**< .05**	**Body mass**	**0.362**	**0.163**	**< .05**
Aspect ratio	**0.843**	**0.404**	**< .05**	-	-	-	-
Wing loading	-0.795	0.504	.120	-	-	-	-
R^2 marginal	*.214*				*.029*		
R^2 conditional	*.755*				*.636*		
Studies	47				26		
Species	23				14		
Data	693				349		
Step 2: Best model obtained with the 'subset-landscape'							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**1.925**	**0.648**	**< .01**	Age	0.691	0.426	.107
Aspect ratio	0.974	0.493	.057	**Forest proportion5**	**-0.554**	**0.188**	**< .01**
Age	**0.839**	**0.266**	**< .01**	HFI5	-0.445	0.219	.059
Matrix diversity20	**-0.486**	**0.235**	**< .05**	**Age:Forest proportion5**	**-1.583**	**0.489**	**< .01**
	-	**-**	**-**	**Age:HFI5**	**-3.423**	**0.868**	**< .001**
R^2 marginal	*.180*				*.319*		
R^2 conditional	*.710*				*.695*		
Studies	36				20		
Species	24				9		
Data	448				235		
Step 3: Sensitivity test applied on the best model from the 'step 2' by omitting the most influential values identified by Bonferroni test and the Cook's distance (i.e., outliers and hat values)							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**1.864**	**0.657**	**< .01**	Age	-0.674	1.689	.690
Aspect ratio	0.914	0.506	.081	**Forest proportion5**	**-0.601**	**0.183**	**< .01**
Age	**0.857**	**0.272**	**< .01**	HFI5	-0.425	0.211	.062
Matrix diversity20	-0.461	0.240	.062	Age:Forest proportion5	-1.590	1.038	.127
	-	**-**	**-**	Age:HFI5	-0.892	2.533	.725
R^2 marginal	*.166*				*.288*		
R^2 conditional	*.727*				*.652*		
Studies	34				19		
Species	22				9		
Data	443				230		
Step 4: Best model obtained with the 'subset-Europe' to add the Species Specialization Index (SSI) as covariate in the model selection							
	Estimates	SE	*p*		Estimates	SE	*p*
SSI	**-0.996**	**0.243**	**< .001**	**SSI**	**-0.532**	**0.14**	**< .01**
Wing loading	**0.326**	**0.145**	**< .05**	Aspect ratio	0.101	0.204	.626
Age	0.449	0.233	.055	**Age**	**-0.716**	**0.233**	**< .01**
Matrix diversity20	**-0.649**	**0.265**	**< .05**	**Forest proportion5**	**-0.602**	**0.127**	**< .001**
Age:Matrix diversity20	-0.436	0.262	.097	**HFI5**	**-0.549**	**0.143**	**< .01**

R^2 marginal	*.293*	*.469*
R^2 conditional	*.721*	*.618*
Studies	38	19
Species	17	8
Data	527	230

3. RESULTS

We found significant negative relationships between bat home-range size and landscape matrix diversity and between forest proportion and daily distance from roosts to foraging areas (Table 2, Figures 3 & 4). The results were similar at both colony and individual levels (Tables 2 & 3, Figures 3 & 4). Landscape matrix diversity had the most significant effect on home range size at 20 km radius scale while forest proportion had the most significant effect on mean daily distance at 5 km radius scale. On average, home range sizes were reduced by up to 42% within the most habitat-diversified landscapes (Figure 3) and daily distances by up to 30% within the most forested landscapes (Figure 4).

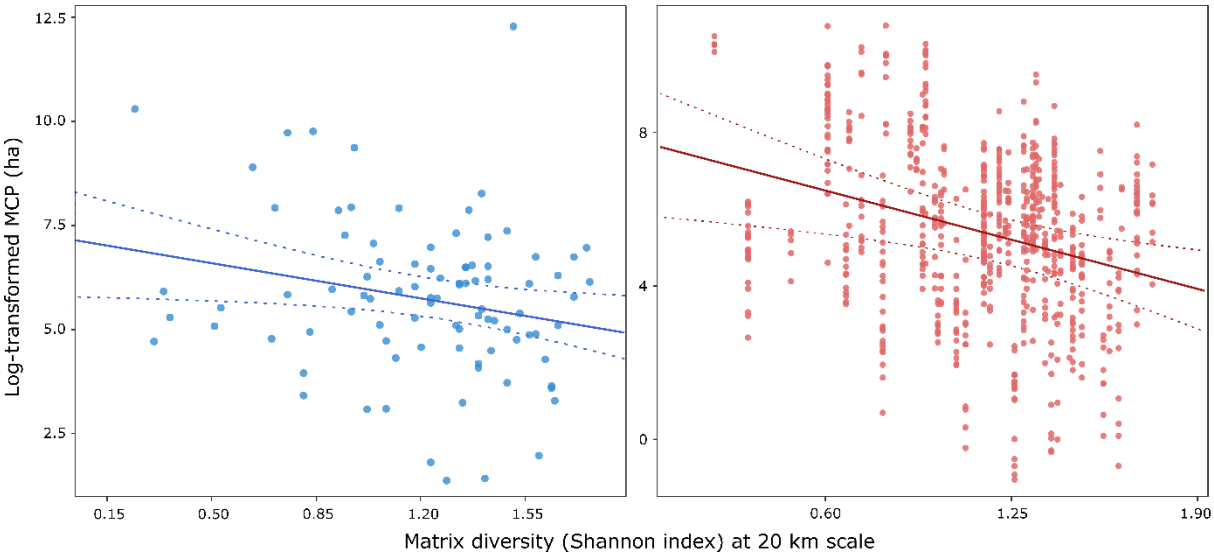

Figure 3 – Bat home-range size at the colony level (i.e., mean; blue) and individual level (red) with increasing Shannon diversity of landscape matrix and compiled at 20 km radius scale. Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (dashed lines).

We found a positive relationship between body mass and both home range size and daily distance (Tables 2 & 3, Figure 5). However, this trend was not fully confirmed for the effect on daily distance at individual level (Table 3). Body mass was the most selected morphological trait across different models and data subset in comparison with wing loading and aspect ratio; yet home range size significantly increased with aspect ratio (Tables 2 & 3). The positive effect of wing loading on home range size was only significant for the data subset reduced to European

species (Tables 2 & 3). Finally, habitat specialization (SSI) had a significant negative influence on home range size and daily distance, both at colony and individual levels (Tables 2 & 3, Figure 6).

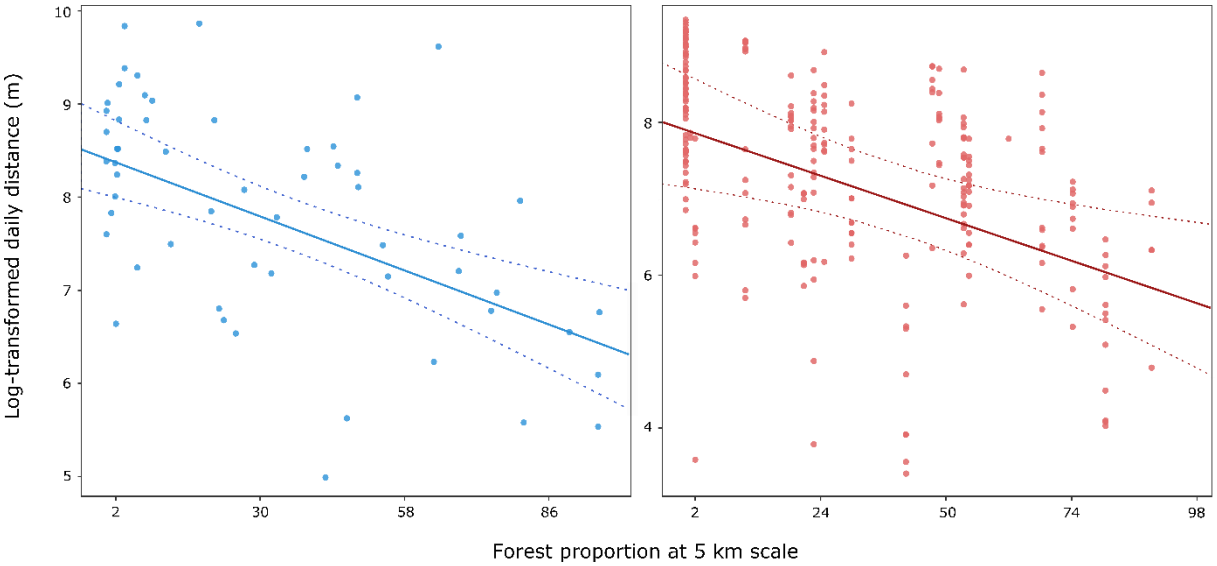

Figure 4 – Bat daily distances between roosts and foraging areas at the colony level (i.e., mean; blue) and individual level (red) with increasing forest proportion within a 5 km radius from the colony. Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (dashed lines).

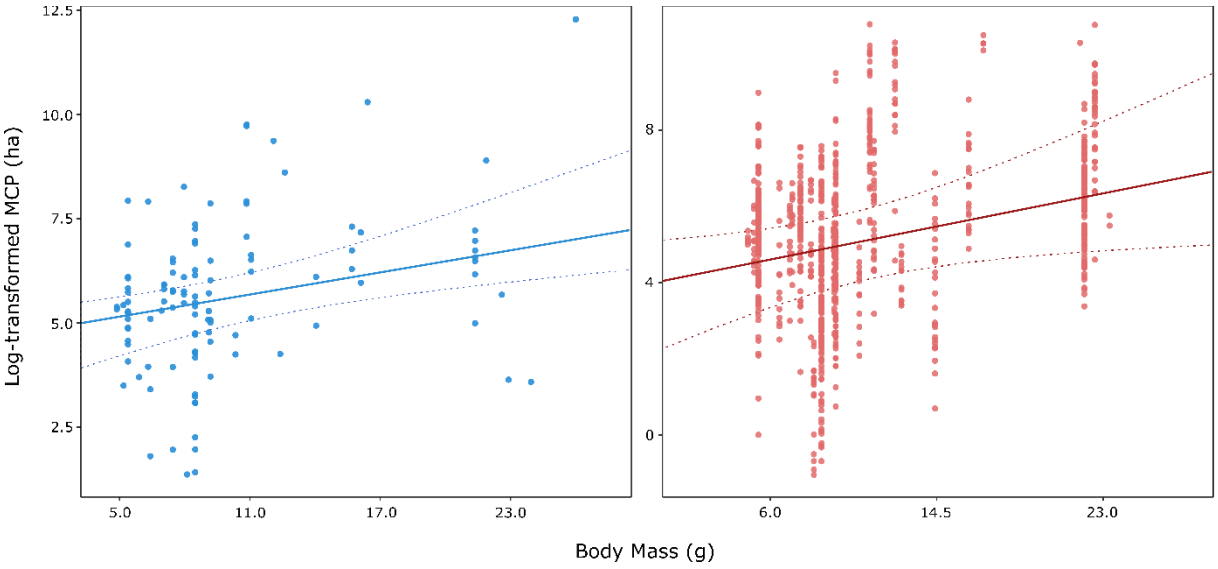

Figure 5 – Bat home-range size at the colony (i.e., mean; blue) and individual levels (red) with increasing body mass. Plots include regression lines from the linear mixed-effects models and 95% confidence intervals.

Our best-supported models (i.e., with landscape and trait variables simultaneously included) explained 62–92% of the variation in bat movements at colony and individual levels when accounting for both random and fixed effects, and 14–47% of the variation when accounting for fixed effects alone (Tables 2 & 3). Although Human Footprint index (HFI) was selected in all but one best-supported models to explain daily distance variations (but not as systematically as for matrix diversity and forest proportion) and the magnitude relatively constant whatever the data subset analysed, it was only significant when SSI variable was also taken into account and species data reduced to European species (Tables 2 & 3).We did not find any significant effects of latitude, road density, number of forest patches and number of individuals on home-range size and daily distance (Tables 2 & 3).

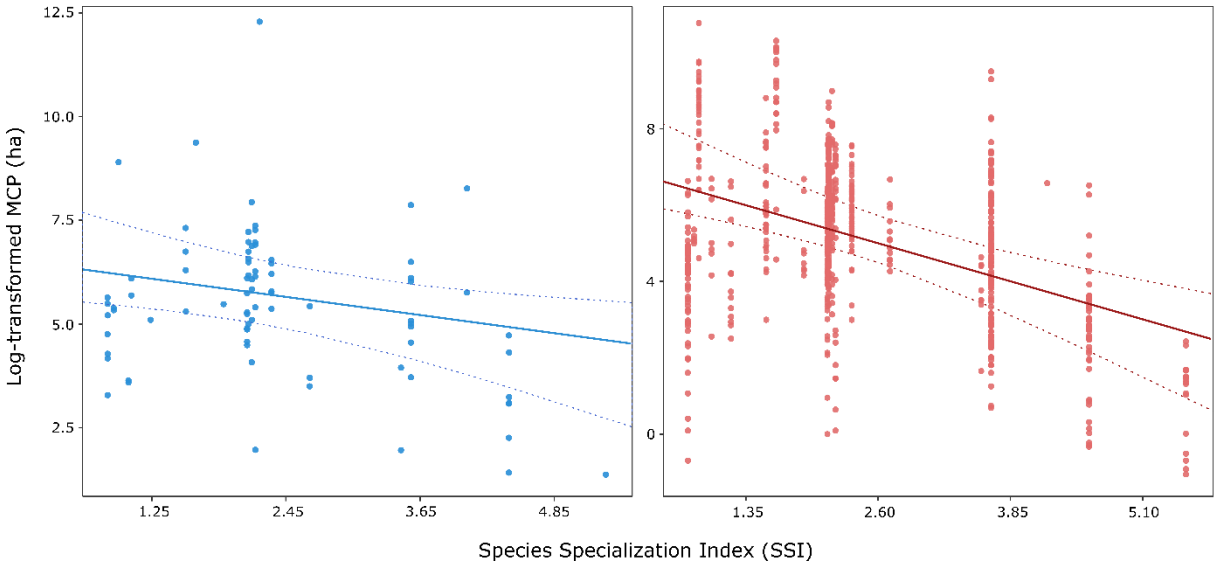

Figure 6 – Bat home-range size at the colony level (i.e., mean; blue) and individual level (red) with increasing habitat specialization index (most habitat specialized species are on the right). Plots include regression lines from the linear mixed-effects models (solid lines) and associated 95% confidence intervals (dashed lines).

4. DISCUSSION

We have shown that the magnitude and spatial extent of bat movements depend on landscape composition. Home range sizes were on average 42% smaller in areas of highest matrix habitat diversity (Shannon diversity index equals to 1.8) compared to most homogeneous landscapes (Shannon diversity index 0.2) and mean daily distances were on average 30% shorter within the most forested landscapes (forest amount of 95%) compared to the least forested landscapes (1%). The decrease in bat movement magnitude with increasing matrix diversity is likely to be explained by higher proximity of the different habitats required to

complete daily life-cycle in more heterogeneous landscapes (e.g., food resources or movement cost; Dietz et al., 2013; Presley et al., 2019). Many of the studies used in our analyses also studied foraging habitat selection and evidenced that temperate insectivorous bats (i) tend to forage in a wide range of habitats and (ii) most often roost outside their preferential foraging habitat, as they depend on the availability of potential roosting structures (trees or human-made structure) in the landscape (Ancillotto et al., 2014; Downs et al., 2016; Fonderflick et al., 2015; Parsons and Jones, 2003; Shiel et al., 1999; Voigt et al., 2016). We thus argue that bat species have smaller home-range sizes in the more diversified environments, where the spatial arrangement of different foraging and commuting habitats is more optimal (higher interspersion) such as bats can access multiple and diverse foraging habitats while reducing distance costs (Bontadina et al., 2002). Therefore, a single landscape including habitat patches with different but complementary resources within close proximity is likely to favor landscape complementation, a key process for shaping bat movements at the matrix scale (Charbonnier et al., 2016; Dunning et al., 1992; Ethier and Fahrig, 2011). Like for birds, the link between bat movement and matrix diversity might also suggest that it is important to maintain landscape complementarity of habitat patches in human-modified areas that have most often shifted from heterogeneous (i.e., diversified) to homogeneous landscapes (i.e., dominated by impervious surfaces and croplands), at least in temperate countries. The maintenance of a fine-grained landscape heterogeneity might reduce the distances covered by individual bats and, in turn, the potential negative effects of these increased travel distances (Tucker et al., 2019). Since forest loss does not necessarily induce an increase of matrix diversity at the landscape scale, the negative impact of forest proportion on daily movements is not contradictory. First, forests are well-known as key habitats for most temperate bats (Boughey et al., 2011; Plank et al., 2012). Forest edge, interior and canopy can act either as a navigational reference (i.e., commuting), a source of insect prey (i.e., foraging), a shelter from wind, a preferential roost (i.e., roosting), or as protection from predators, depending on the bat guild (Dietz et al., 2009; Morris et al., 2010). Second, large patches of continuous forest may be of better quality than small patches (Arroyo-Rodríguez and Mandujano, 2006). Large patches may provide both more diverse habitats in forest context (e.g., higher spatial heterogeneity in stand structure and forest management, clearings, logging-tracks) and potentially more tree micro-habitats and deadwoods (i.e., food availability and diversity). Habitat and microhabitat diversity, as well as deadwood are known to have a positive effect on bats even on edge- and open-space foraging species (Bouvet et al., 2016; Langridge et al., 2019; Paillet et al., 2018). Therefore, landscape complementation processes may also explain the negative relationship between forest amount and mean daily

movement, bats having to travel less to access all required resources in forested landscapes. Consequently, it is consistent that the loss of forest, a key habitat, increases bat movements to achieve their different daily requirements through the landscape complementation/supplementation process but perhaps also because animals typically have faster movements in non-forested habitats from the matrix (Crone et al., 2019) or because landscape quality influences movement tortuosity (Tucker et al., 2018). With the already long list of evidence for the critical impact of forest loss on biodiversity (Betts et al., 2017), this environmental process may lead to an increase of displacement cost for bats and thus question directly their survival. Actually, this opposed influence of matrix diversification at 20 km radius scale with the forest loss calculated at 5 km radius scale on movement may depend on the different estimation method and nature of the data. First, mean daily distance is more influenced by 'routine' behaviour while MCP method is more influenced by 'unusual' behaviour (i.e., peripheral fixes) as this method is generally calculated from all fixes obtained without taking into account the spatial density of the fixes (Harris et al., 1990). Second, this result may reveal that forest habitats close to roosts is important to facilitate commuting and foraging behaviour of shorter mean daily distances (Charbonnier et al., 2016), while matrix diversity at larger spatial scale may reduce the longest distances to reach less used foraging areas when food availability is scarce. Finally, we know that the quality of foraging habitats surrounding roosts play a decisive role in roost choice for temperate bats (Boughey et al., 2011; Fonderflick et al., 2015; Perry et al., 2007) but also in the temporal dynamics of the colony size (Froidevaux et al., 2017). Thus, because bats are highly dependent on the availability of appropriate and sustainable structures to roost in the landscape, finding such roosts in an optimal landscape structure may be often difficult (Popa-Lisseanu et al., 2009). Promoting bat movements through the landscape surrounding roosts at large spatial scales is therefore crucial for bat conservation (Almenar et al., 2009).

When morphological traits were selected in our best-supported models, they had always a positive and often significant influence on bat movements. Those results support our predictions that heavier bat species may fly farther owing to higher energy efficiency (higher aspect ratio), increased flight speeds (higher wing loading) and increased resource requirements (Alerstam et al., 2007; Norberg and Rayner, 1987). This is important to notice that morphological traits seem better at explaining home-range size (MCP) than mean daily distance variations. Spatio-temporal food availability is a key factor influencing bat movements and the longest distances travelled by daily foragers may come from the need to compensate for a local and temporary food depletion at proximity of the roost. The ability of bats to modulate their

travel distances is driven by morphological traits while the mean daily distance is probably more driven by habitat specialization than by morphological constraints. With the subset of European species, the selection and the significance of the morphological traits changed (body mass and aspect ratio were not selected or replaced by wing loading). The unbalanced proportions of the different bat guilds across our data (the reason why we could not include this factorial factor in our models) confirms this explanation. Indeed, 73% of our studied species are aerial hawkers in background-cluttered space or gleaners in highly cluttered space while 27% are aerial hawkers in uncluttered space or trawlers (see Segura-Trujillo et al., 2016 for the detail informations on each guild). As predicted, the most habitat-specialized species travelled on average shorter distances between roosts and foraging areas and had smaller home-range size. Specialist species may perceive the average landscape as more fragmented and hostile and their long distance movement may be more costly than for generalist bats (Baguette and Van Dyck, 2007; Kisdi, 2002; Poisot et al., 2011). This pattern may also be explained by competition processes (e.g., competitive exclusion principle) where generalist bat species may be less competitive than generally more agile specialists having a more accurate sonar, and be forced to exploit more distant foraging areas (Roeleke et al., 2018). Our results confirm the complex relationships between morphological traits, habitat specialization and movements (Keinath et al., 2017) and points out how important is the co-evolution between morphological traits and habitat specialization (Baguette et al., 2012). Finally, this study alerts once again on the biotic homogenization of bat communities with the expanding of human-modified landscape by favoring larger and generalist species at the expense of smaller and specialist species (Gili et al., 2019; Kalda et al., 2015; Monck-Whipp et al., 2018).

Interestingly, we did not find a significant effect of the number of radio-tracked individuals to explain mean home-range size variations at the colony level. We argue this result means that most of the telemetry studies gave only MCP values when the asymptote has been reached (i.e., plateaued). This is probably due to the fact that it has become a methodological requirement following recommendations made by Harris et al. (1990). We also found no or unstable effect of road density and HFI, respectively. Tracking bats in the most urbanized areas may be more challenging, leading to a lack of data for this type of landscapes (LaPoint et al., 2015; Voigt et al., 2019). Furthermore, HFI index may be too coarse, combining multiple proxies of human influence with a large resolution. Thus, because bats prove very sensitive to urbanization (Russo and Ancillotto, 2015) and roads (Claireau et al., 2019; Medinas et al., 2019), we cannot support our initial prediction that HFI and road density would reduce bat movements.

Contrary to our expectations, we did not find significant effect of sex and reproductive status on bat movements. Within bat telemetry studies, some found significant differences of space use between males and females (Broders et al., 2006; Encarnação, 2012; Istvanko et al., 2016) but some others did not (Adam et al., 1994; Almenar et al., 2011; Anthony and Sanchez, 2019; Elmore et al., 2005). Some authors also documented significant differences of space use depending on the reproductive status of the females (i.e., gestating, lactating and post-lactating) (Baker et al., 2008; Ciechanowski et al., 2017; Clark et al., 1993; Henry et al., 2002) but some others did not (Almenar et al., 2011; Johnson et al., 2019, 2007). However, when authors documented significant differences among sex and reproductive status, they also found differences in habitat selection. Thus, we argue that our result strongly confirms that food availability, rather than bats' biological individual status, better explain the observed inter and intraspecific variability in home-range size and daily distances (Almenar et al., 2011, 2009; Amelon et al., 2014; Arlettaz, 1996; Henry et al., 2002; Hillen et al., 2011; Kirkpatrick et al., 2018; Popa-Lisseanu et al., 2009). Although our global analysis at the individual level did not identify significant differences of space use according to sex and reproductive status, age seems to contribute to bat movement variations. While juveniles had significantly greater home-range sizes, their daily distances between roosts and foraging areas were reduced in comparison with adults. These results are not necessarily contradictory: depending on the time-lag between the first roost emergence and the survey period, juveniles may first prefer to forage close to the roost to improve flight maneuverability and foraging success in the most productive and safe habitats (Flaquer et al., 2008) but may then have a bolder behavior in exploring their new territories (Goiti et al., 2006). However, sensitivity analysis showed that multiple exclusion of studies can have substantial effect on the significance of age effect. Consequently, those results should be interpreted cautiously.

The random effect (i.e., study) explained a large portion of the variance in bat movements (c. 40–80%). Previous work has underlined the great methodological variation among radio-tracking studies (Laver and Kelly, 2008). Nevertheless, finding significant landscape effects on bat movements despite the heterogeneous methodology among bat tracking studies reminds that bats are highly sensitive to landscape structure and food distribution (Presley et al., 2019). This high variability among radio-tracking studies did not allow us to test simultaneously all our predictors from a single dataset, militating for more methodological prerequisites in the future (Harris et al., 1990; Worton, 1987). However, we believe that our step-by-step analytical approach with different subsets is also an opportunity to demonstrate the robustness of our results and should be perceived as multiple sensitivity

tests. We also note that we did not account for the seasonal variation, which may impact bat movements in relation with food availability (Law, 1993) because information provided by the authors were often too coarse on this point. We also underline that we did not account for the colony size of the studied roosts although intra- and interspecific interactions is often seen as a main driver in shaping bat movements (benefit from social information transfer versus food competition cost) (Cvikel et al., 2015; Hillen and Veith, 2013; Kerth et al., 2001; Roeleke et al., 2018; Salinas-Ramos et al., 2019; Voigt et al., 2017). Finally, our bat movement dataset was obtained from studies carried out between 1988 and 2016 and the sampling years did not necessarily coincide with that of the habitat maps used to calculate landscape predictors, minoring the potential bias of unaccounted temporal evolution of the landscapes. However, we argue that the large resolution and extent for our calculation metrics coupling with the relatively small land cover changes documented at the continental scale for North America and Europe (Colditz et al., 2014; European Environement Agency, 2017) make our land cover data representative for the time scale studied. We also hear the argument that our pattern related to the forest proportion could be due to a potential detectability bias either because there are more obstacles between transmitters and receivers in closed environments or because remaining forests are mainly found in landscapes with high topography (because too difficult to exploit). We found no relations between the number of fixes per night and the forest proportion, rejecting this argument because in this case field trackers should spend more time searching for individuals than locating them, decreasing the number of fixes per night.

5. CONCLUSION

With more than 30 years of bat telemetry data accumulating over 22 countries across North-America and Europe, this unique dataset strongly supports the very close relationship between bat movements and landscape composition. Despite the well-known high methodological variation in telemetry studies literature (Laver and Kelly, 2008), we revealed for the first time that compiling telemetry studies can be valuable to enhance our global understanding of bat movements (Hall et al., 2016). We have demonstrated the importance of resource availability and spatial distribution on shaping bat movements, highlighting the possible effects of landscape homogenization and forest loss, where individuals may need to fly farther to meet their ecological requirements through the landscape complementation key processes. It is possible that continuing habitat homogenization (i.e., agriculture intensification or urban expansion) in landscapes with a high diversity of habitats will have negative impacts

on the abundance and diversity of bats (Gili et al., 2019; Kalda et al., 2015). This might, in turn, result in altered bat communities dominated by larger and more generalist species at the expense of smaller specialists (i.e., biotic homogenization). Our study provides important insights on bat movement mechanisms and knowledges for bat conservation. In the near future, the use of remote sensing data (e.g., LIDAR) may push forward the frontiers in the field of animal movement ecology, especially in structurally complex habitats as forests (Milanesi et al., 2016; Neumann et al., 2015). Furthermore, telemetry studies are likely to be progressively improved/replaced by technological advances in automatic radio-tracking system (Gottwald et al., 2019) and in miniaturized GPS (Weller et al., 2016), representing great opportunities to re-examine and validate our patterns.

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Since this study was last treated in the context of this PhD thesis, I am considering complementary analyses to this work:

- ***Testing other potential response variables available: Mean maximum distance and home-range size calculated from Kernel density method.***
- ***Testing another covariates: a diet trait highly expected to respond to the spatial distribution of food availability and a topography variability index to test for a potential detectability bias in our results.***
- ***Using linear regressions to estimate missing values of number of fixes depending on home-range size and test it as a new covariate.***

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Appendix 2

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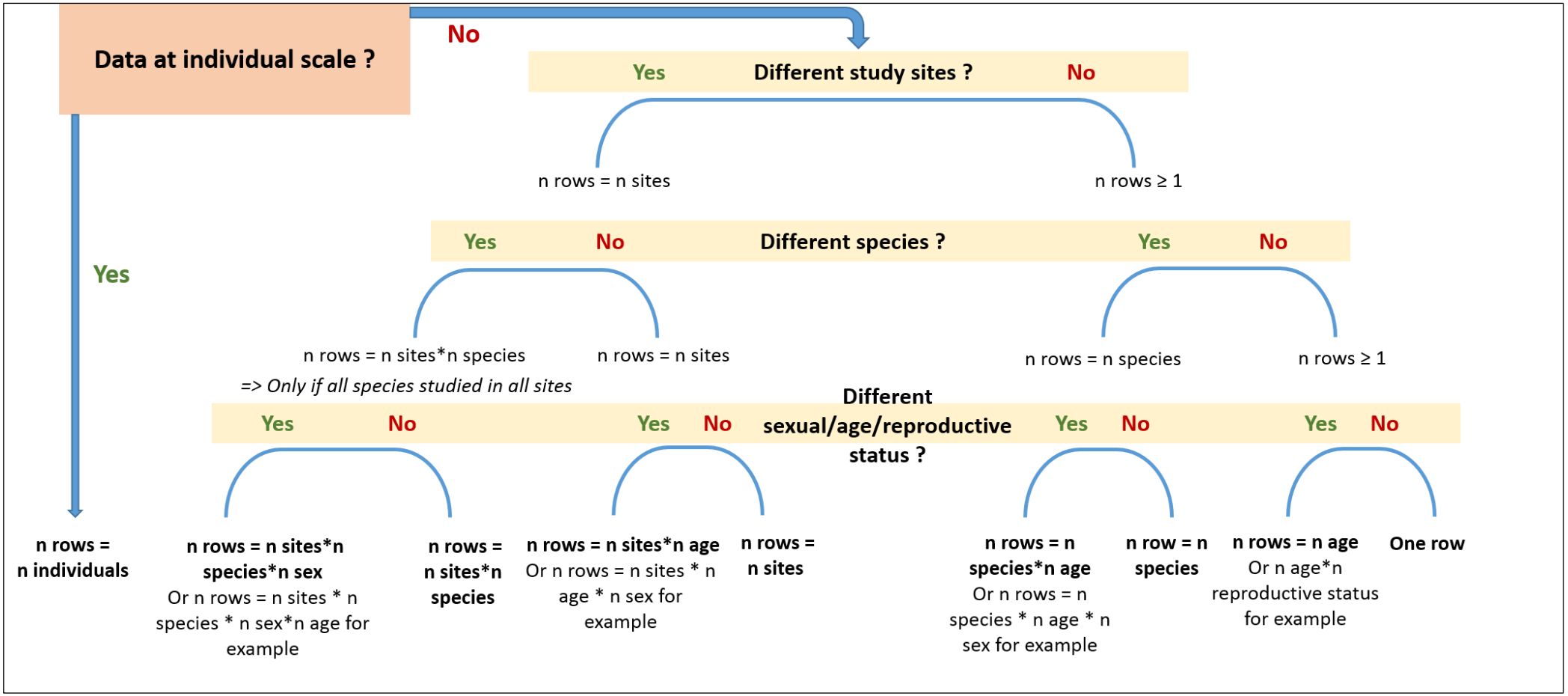
Appendix 2 - Workflow diagram representing the reading and data extraction process followed by all the different readers for each used study.



Appendix 3 - Mean, standard deviation, minimum and maximum of the raw (not scaled) landscape predictors used in the analysis, according to the buffer size considered.

Predictors	Buffer (1 km)	Buffer (5 km)	Buffer (10 km)	Buffer (20 km)
Human Footprint Index (HFI)	19.0 ± 11.1 (0.1 - 45.2)	19.2 ± 10.6 (0.2 - 48.5)	18.7 ± 9.6 (0.7 - 41.4)	18.4 ± 8.9 (1.7 - 38.1)
Road Density (km/km²)	0.5 ± 0.8 (0.0 - 3.5)	0.5 ± 0.6 (0.0 - 2.2)	0.5 ± 0.6 (0.0 - 2.2)	0.5 ± 0.5 (0.0 - 1.6)
Forest proportion (%)	34.2 ± 32.7 (0.0 - 100.0)	30.4 ± 29.0 (0.0 - 100.0)	27.3 ± 25.6 (0.0 - 97.0)	25.2 ± 22.9 (0.0 - 97.3)
Number of forest patches	1.6 ± 1.5 (0.0 - 6.0)	16.7 ± 14.3 (0.0 - 59.0)	56.6 ± 41.2 (0.0 - 184.0)	199.0 ± 134.1 (0.0 - 696.0)
Matrix Shannon Diversity	0.6 ± 0.4 (0.0 - 1.5)	0.9 ± 0.4 (0.0 - 1.7)	1.0 ± 0.4 (0.1 - 1.7)	1.1 ± 0.3 (0.1 - 1.7)

Appendix 4 - Description of the life traits used in the analysis (except 'Guild'). Letters are guilds according to Segura-Trujillo et al., (2016): A (us) = Aerial in uncluttered space; A (bcs) = Aerial in background-cluttered space; A (hcs) = Aerial in highly cluttered space. G (hcs) = Gleaning in highly cluttered space; T (bcs) = Trawling in background-cluttered space.

Species	Guild	Body mass	Aspect ratio	Wing loading	SSI
Antrozous pallidus	G(hcs)	22.20	6.10	8.10	NA
Barbastella barbastellus	A(bcs)	8.50	6.00	9.10	2.18
Corynorhinus rafinesquii	G(hcs)	9.08	5.90	5.90	NA
Eptesicus fuscus	A(bcs)	15.90	6.40	9.40	NA
Eptesicus nilssonii	A(bcs)	11.00	6.60	8.10	NA
Eptesicus serotinus	A(bcs)	21.50	6.50	12.20	0.94
Euderma maculatum	G(hcs)	16.20	6.60	8.04	NA
Hypugo savii	A(bcs)	7.00	7.50	8.00	1.55
Lasiurus borealis	A(us)	12.30	6.70	14.00	NA
Lasiurus cinereus	A(us)	26.80	8.10	16.50	NA
Leptonycteris curasoae	F	25.00	5.90	10.60	NA
Miniopterus schreibersii	A(bcs)	12.00	7.00	10.20	1.64
Myotis bechsteinii	G(hcs)	8.50	6.00	9.00	4.48
Myotis blythii	G(hcs)	22.50	6.70	10.10	1.03
Myotis brandtii	A(bcs)	6.00	6.00	7.10	2.67
Myotis capaccinii	T(bcs)	8.14	6.60	10.50	5.36
Myotis ciliolabrum	A(bcs)	4.50	6.10	6.70	NA
Myotis dasycneme	A(bcs)	15.10	6.80	10.40	4.10
Myotis daubentonii	T(bcs)	8.00	6.30	7.00	4.10
Myotis emarginatus	G(hcs)	7.50	5.90	7.10	2.33
Myotis evotis	A(bcs)	6.80	6.00	6.10	NA
Myotis frater	NA	NA	NA	NA	NA
Myotis gracilis	NA	NA	NA	NA	NA
Myotis grisescens	A(bcs)	10.80	6.40	8.20	NA
Myotis lucifugus	A(bcs)	6.40	6.00	7.50	NA
Myotis myotis	G(hcs)	23.50	6.30	11.20	1.03
Myotis myotis/Myotis blythii	G(hcs)	23.00	6.50	10.65	1.03
Myotis mystacinus	A(bcs)	5.30	6.00	7.10	2.67
Myotis nattereri	G(hcs)	8.50	6.40	6.10	0.84
Myotis petax	NA	NA	NA	NA	NA
Myotis septentrionalis	A(bcs)	6.50	5.80	6.80	NA
Myotis sodalis	G(hcs)	7.11	5.40	6.50	NA
Myotis volans	A(bcs)	7.00	5.80	8.30	NA
Nyctalus lasiopterus	A(us)	44.00	7.20	19.70	2.24
Nyctalus leisleri	A(us)	15.50	7.90	19.30	1.55
Nyctalus noctula	A(us)	25.50	7.40	16.10	2.22
Nycticeius humeralis	A(bcs)	9.11	6.80	10.70	NA
Nyctinomops macrotis	A(us)	20.80	9.70	NA	NA
Pipistrellus hanaki	A(bcs)	5.50	7.50	8.10	NA
Pipistrellus kuhlii	A(bcs)	6.50	6.30	8.50	1.23
Pipistrellus nathusii	A(bcs)	8.00	7.20	9.80	2.56
Pipistrellus pipistrellus	A(bcs)	5.00	7.50	8.10	0.90
Pipistrellus pygmaeus	A(bcs)	5.50	7.50	8.10	2.15
Plecotus auritus	G(hcs)	7.50	5.70	7.10	3.50
Plecotus austriacus	G(hcs)	8.00	6.10	7.90	1.06
Plecotus macrobullaris	G(hcs)	8.00	5.70	7.10	1.89
Plecotus townsendii	G(hcs)	10.30	5.90	7.20	NA
Rhinolophus euryale	G(hcs)	9.18	6.20	8.10	3.59
Rhinolophus ferrumequinum	G(hcs)	21.00	6.10	12.20	2.12
Rhinolophus hipposideros	G(hcs)	5.50	5.70	7.10	2.11
Rhinolophus mehelyi	G(hcs)	13.90	6.20	11.28	3.59
Tadarida teniotis	A(us)	25.00	9.80	19.00	1.31
Vespertilio murinus	A(us)	12.50	7.00	10.20	NA

Appendix 5 – Complementary analysis by adding consecutively as covariates in the best supported-models, the number of fixes, the number of nights and the transmitter weight used to compare estimates and significance of the coefficients, as another sensitivity test of our results.

The addition of covariates such as the number of individuals, the number of fixes, the number of nights or the transmitter weight never changed the significant effects of landscape factors on bat movements and only the number of fixes had a significant positive effect on mean home-range size (individual unit; Table S5.1 & S5.2). However, by adding one of these covariates, we lose sometimes significance of morphological trait effects (Table S5.1 & S5.2). We explain this because our dataset is unbalanced between relatively small and large species making morphological effects very sensitive to the pool of species considered. Yet, as previously mentioned the quantity of movement data rely to sampling effort is relatively very low and could not be tested simultaneously. Thus, we argue that we should not conclude from this complementary analysis and that using studies as a random effect should take into this consideration in our models.

Table S5.1 - Model coefficients, *p*-values, R^2 and sample sizes of linear mixed-effects models predicting the log-transformed mean home-range size (MCP) and mean daily distances between roosts and foraging areas at colony level. Predictor variables included fixed effects for the Shannon diversity of the landscape matrix measured at 20 km, forest proportion and Human Footprint Index (HFI) both measured at 5 km. The model also included 'study' as a random effect.

Adding the number of individuals as covariate							
LogMCP				**LogDist**			
Variables	Estimates	SE	*p*	Variables	Estimates	SE	*p*
Body mass	**0.425**	**0.163**	**< .05**	**Body mass**	**0.207**	**0.097**	**< .05**
Aspect ratio	**0.689**	**0.265**	**< .05**	**Forest proportion5**	**-0.574**	**0.128**	**< .001**
Matrix diversity20	**-0.438**	**0.179**	**< .05**	HFI5	-0.236	0.116	.090
n individuals	-0.119	0.129	.360	n individuals	-0.002	0.120	.987
R^2 marginal	*.180*				*.336*		
R^2 conditional	*.869*				*.912*		
Studies	64				44		
Species	31				30		
Data	91				55		
Adding the number of fixes as covariate							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**0.315**	**0.131**	**< .05**	Body mass	-0.011	0.098	.911
Aspect ratio	**0.648**	**0.27**	**< .05**	**Forest proportion5**	**-0.692**	**0.136**	**< .001**
Matrix diversity20	**-0.407**	**0.177**	**< .05**	HFI5	-0.103	0.177	.564
n fixes	-0.105	0.146	.478	n fixes	0.064	0.130	.630
R^2 marginal	*.201*				*.559*		
R^2 conditional	*.852*				*.954*		
Studies	44				23		
Species	22				16		
Data	65				30		
Adding the number of nights as covariate							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**0.341**	**0.16**	**< .05**	Body mass	0.143	0.088	.117
Aspect ratio	0.333	0.284	.247	**Forest proportion5**	**-0.537**	**0.129**	**< .001**
Matrix diversity20	**-0.597**	**0.194**	**< .01**	HFI5	-0.224	0.131	.096
n nights	-0.294	0.234	.214	n nights	-0.196	0.146	.190
R^2 marginal	*.171*				*.538*		
R^2 conditional	*.859*				*.903*		
Studies	48				29		
Species	28				24		
Data	71				37		

Table S5.2 - Model coefficients, *p*-values, R^2 and sample sizes of linear mixed-effects models predicting the log-transformed mean home-range size (MCP) and mean daily distances between roosts and foraging areas at individual level. Predictor variables included fixed effects for the Shannon diversity of the landscape matrix measured at 20 km, forest proportion and Human Footprint Index (HFI) both measured at 5 km. The model also included 'study' and 'site' as random effects. Bat movement of adult individuals were used as the reference (i.e., intercept).

Adding the number of fixes as covariate							
LogMCP				**LogDist**			
Variables	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	0.197	0.144	.172	Age	**0.838**	**0.451**	**< .001**
Aspect ratio	**0.596**	**0.290**	**< .05**	**Forest proportion5**	**-0.420**	**0.177**	**< .05**
Age	0.346	0.211	.101	HFI5	-0.238	0.283	.417
Matrix diversity20	**-0.555**	**0.237**	**< .05**	**Age:Forest proportion5**	**-1.711**	**0.467**	**< .001**
	-	-	-	**Age:HFI5**	**-3.526**	**0.817**	**< .001**
n fixes	**0.283**	**0.071**	**< .001**	n fixes	-0.169	0.140	.227
R^2 marginal	*.169*				*.274*		
R^2 conditional	*.740*				*.666*		
Studies	32				15		
Species	17				8		
Data	516				196		
Adding the number of nights as covariate							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	**0.268**	**0.128**	**< .05**	**Age**	**-1.948**	**0.475**	**< .001**
Aspect ratio	0.355	0.272	.199	**Forest proportion5**	**-0.506**	**0.173**	**< .05**
Age	**0.406**	**0.201**	**< .05**	**HFI5**	**-0.486**	**0.188**	**< .05**
Matrix diversity20	**-0.801**	**0.236**	**< .01**	Age:Forest proportion5	-5.452	2.903	.062
	-	-	-	**Age:HFI5**	**-2.223**	**0.803**	**< .001**
n nights	-0.460	0.276	.104	n nights	-3.895	2.325	.096
R^2 marginal	*.179*				*0.409*		
R^2 conditional	*.729*				*0.662*		
Studies	36				14		
Species	21				8		
Data	563				194		
Adding the transmitter weight as covariate							
	Estimates	SE	*p*		Estimates	SE	*p*
Body mass	0.174	0.150	.246	Age	0.677	0.429	.116
Aspect ratio	**0.524**	**0.245**	**< .05**	**Forest proportion5**	**-0.353**	**0.15**	**< .05**
Age	**0.610**	**0.193**	**< .01**	**HFI5**	**-0.453**	**0.187**	**< .05**
Matrix diversity20	**-0.598**	**0.229**	**< .05**	**Age:Forest proportion5**	**-1.556**	**0.503**	**< .01**
	-	-	-	**Age:HFI5**	**-3.327**	**0.900**	**< .001**
Transmitter weight	0.268	0.367	.465	Transmitter weight	0.205	0.466	.664
R^2 marginal	*.129*				*.266*		
R^2 conditional	*.738*				*.654*		
Studies	45				18		
Species	22				9		
Data	613				213		

CHAPTER 3

Reducing light pollution improves connectivity for bats in urban landscapes

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RESEARCH ARTICLE

Reducing light pollution improves connectivity for bats in urban landscapes

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ABSTRACT

Context: Light pollution can alter animal movements and landscape connectivity. This is particularly true in urban landscapes where a need to incorporate conservation issues in urban planning is urgent.

Aim: We investigated how potential light-reduction scenarios at conurbation scale change landscape connectivity for bats.

Methods: Through random stratified sampling and species distribution modelling, we assessed the relative importance of light pollution on bat presence probability and activity. We recorded bats during one entire night on each 305 sampling points in 2015. In 2016, we surveyed 94 supplementary points to evaluate models performance. We used our spatial predictions to characterize landscape resistance to bat movements. Then we applied a least-cost modelling approach to identify nocturnal corridors and estimated the impact of five light-reduction scenarios on landscape connectivity for two light non-tolerant bat species.

Results: We found that light pollution detected from satellite images was a good predictor of bat presence and activity up to 700 m radius. Our results exhibited contrasting responses to average radiance: *M. daubentonii* responded negatively, *P. nathusii* had a positive response for low values then a negative response after a threshold radiance value of 20 $W.m^{-2}.sr^{-1}$ and *E. serotinus* responded positively. Five and four light-reduction scenarios significantly improved landscape connectivity for *M. daubentonii* and *P. nathusii* respectively.

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

KEYWORDS

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

1. INTRODUCTION

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

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

environments that are protected at the European level (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora).

To investigate the effect of ALAN on landscape connectivity, insectivorous bats are a good study case, as they are both nocturnal and very sensitive to habitat loss and fragmentation (Mickleburgh et al. 2002; Frey-Ehrenbold et al. 2013). Studies have found that bat occurrence and activity can be negatively or positively affected by ALAN depending on their foraging strategy, their flight ability, and on the landscape scale considered (Azam et al., 2016; Hale, Fairbrass, Matthews & Sadler, 2012). For example, at a local scale, the illumination of hedges or riverbanks near colonies of slow-flying gleaner species such as *Rhinolophus spp.* and *Myotis spp.* was observed to have a negative impact on bat activity, altering individuals' movement behaviour as they sought to avoid the newly illuminated areas (Kuijper et al., 2008; Stone, Jones & Harris, 2009). In contrast, fast-flying species that hunt insects at dusk in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.*, can benefit at a local spatial scale from new foraging areas provided by ALAN (Azam et al., 2015; Lacoeuilhe, Machon, Bocq & Kerbiriou, 2014). However, ALAN has been shown to decrease landscape connectivity by altering movement and gap-crossing behaviour of *Pipistrellus pipistrellus* (Schreber 1774) individuals in an urban matrix (Hale et al. 2015). These findings suggest that ALAN can act as a barrier for bats and thus further increase landscape fragmentation. This highlights the importance of integrating light pollution measures in sustainable urban-planning strategies in order to maintain biodiversity in urban landscapes through darker environments (Gaston et al. 2015). Yet knowledge concerning how bat communities respond to urbanization and ALAN is currently insufficient to ensure the conservation or development of effective nocturnal corridors (McDonnell and Hahs 2008; Hale et al. 2012; Mathews et al. 2015). This is notably due to the fact that highly urbanized areas are often under-sampled, as sampling bats in cities is challenging, leading to a lack of data for this type of landscape (LaPoint et al., 2015).

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

assess the effects of different light-reduction scenarios on landscape connectivity. A summary of the methodological procedure is shown in Figure 1.

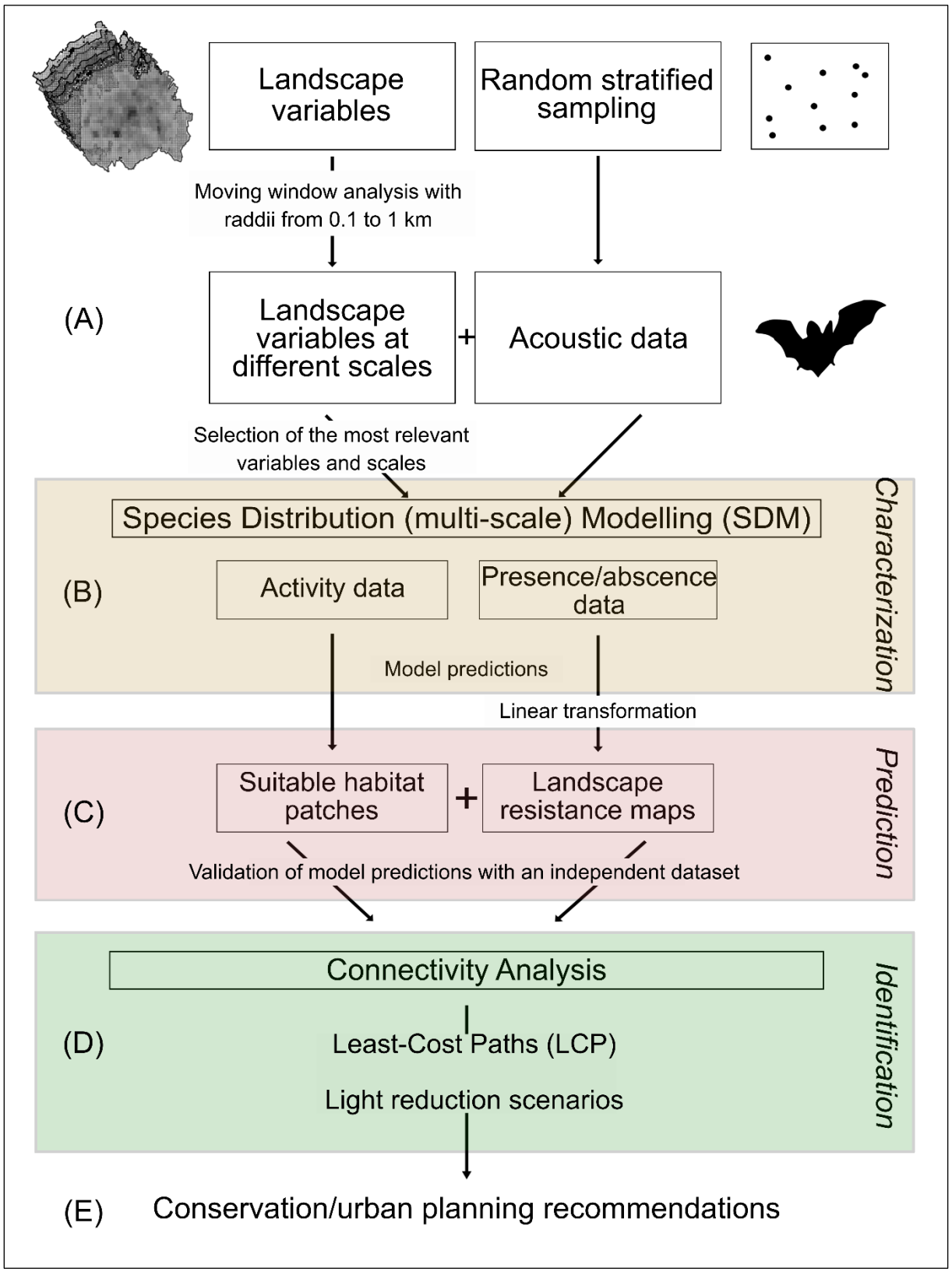

Figure 1 - Summary of methodological procedure followed to assess the effects of light-reduction scenarios on landscape connectivity for bats

2. MATERIALS AND METHODS

2.1. *Study area*

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

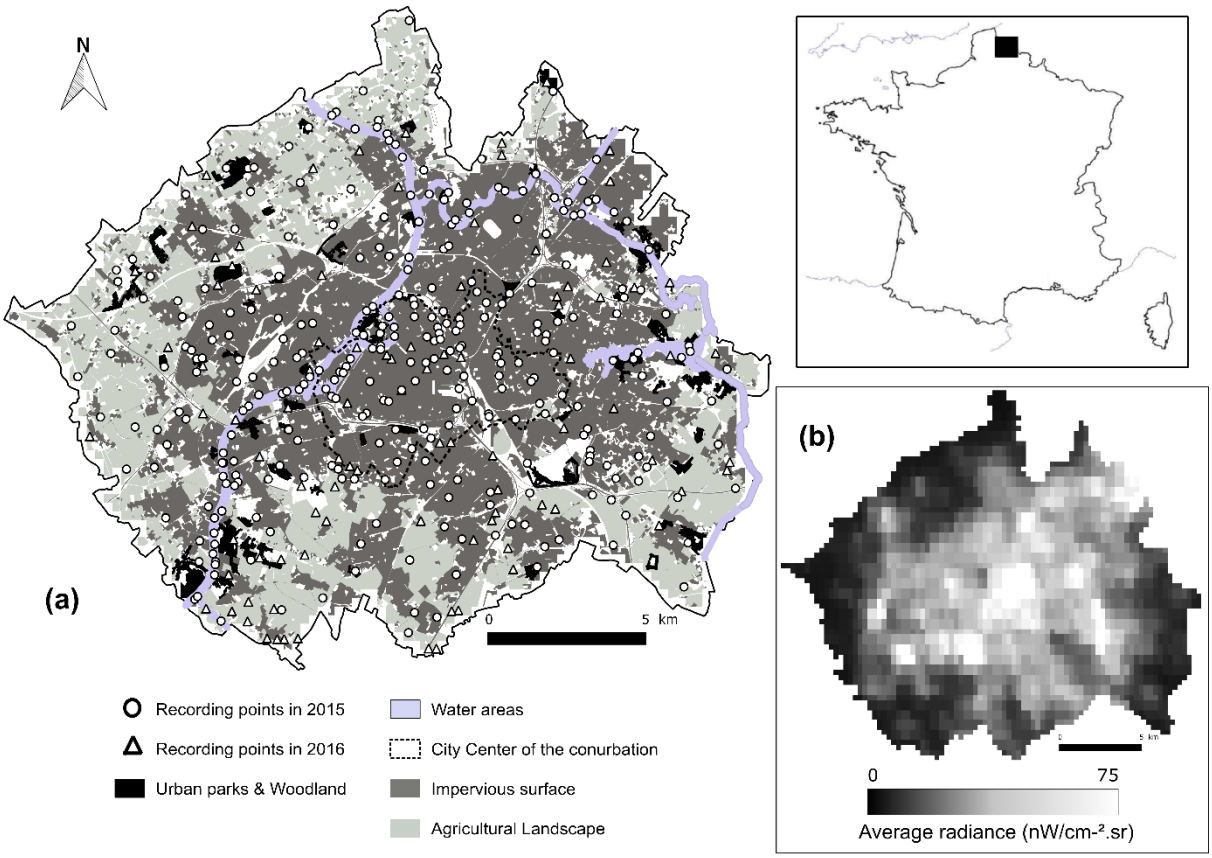

Figure 2 - (a) Map of the study area (the conurbation of Lille, France) showing the locations where acoustic sampling was carried out (recording points) in the summers of 2015 and 2016, as well as the main landscape elements. (b) Spatial gradient of average radiance in the study area obtained from the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

2.2. Sampling design

When using species distribution models (SDMs), a crucial assumption in defining landscape-resistance values is that all the habitats in the studied landscape have been randomly sampled with the same effort (Beier et al., 2008). Thus we defined a random stratified sampling method to record bat passes in every landscape context in the study area in terms of three covariates: proportion of impervious surfaces (including buildings and paved areas such as roads, sidewalks, driveways and parking lots), proportion of tree cover, and ALAN (Fig. 2). These variables were selected because they are known to influence bat presence and activity (Azam et al., 2016; Fonderflick, Azam, Brochier, Cosson & Quékenborn, 2015; Hale et al., 2015) and because their variations in the study area are large enough to yield significant gradients. The data concerning ALAN in the study area was obtained from VIIRS Nighttime Imagery (2012), consisting of a 2-month composite raster of radiance data (in $nW/cm^{-2}.sr$) collected by the Suomi NPP-VIIRS Day/Night Band during two time periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh et al. 2013). This data was produced by the Earth Observation Group, NOAA National Geophysical Data Centre (http://www.ngdc.noaa.gov/eog/viirs/download_monthly.html). The VIIRS Nighttime Imagery that we downloaded in 2014 had a resolution of 300 x 463 m. The pixel was oblong and in WGS84 coordinates system. We needed to convert this raster in another coordinates system (lambert 93) to use it with land uses data from the French National Institute for Geographic and Forestry Information (http://www.ign.fr/). The value of average radiance of each new pixel in LB93 was set to the value of the nearest initial pixel. By doing the interpolation, the pixels became square with a resolution of 250 x 250 m (Fig. 2). We carefully checked that the change in pixel shape did not alter pattern of the data. Then, all the other landscape variables were built using a grid at a resolution of 250 m x 250 m with the software QGIS 2.14 (QGIS development team, 2016). For each cell, we calculated the values of the three variables and grouped them into five categories of equal size (0–20%, 20–40%, 40–60%, 60–80%, 80–100% for the proportion of impervious surfaces and tree cover and 2.6–17, 17–31.4, 31.4–45.8, 45.8–60.2, 60.2–74.6 $nW/cm^{-2}.sr$ for ALAN).

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

occurrence and activity (Straka et al. 2016). This procedure allowed us to randomly select 305 cells in 2015 and 94 cells in 2016 (Fig. 2).

2.3. Bat surveys

We used acoustic surveys to gather bat presence–absence and activity data to define an activity index (AI), which is the number of minutes in which at least one bat call was recorded (Miller 2001; Haquart 2013). We recorded all bat passes during one full night (30 minutes before dusk to 30 minutes after dawn) for each cell using stationary automated ultrasound detectors (Song Meter SM2BAT, Wildlife Acoustics, USA) fitted with multidirectional microphones (SMX-US weatherproof ultrasonic microphone, Wildlife Acoustics, USA). The position of the detectors in the cells was not identical because of the constraints of hiding these in an urban landscape. The sampling was carried out between 1 June and 31 August in 2015, corresponding to the seasonal peak of activity of bat species in this region, as recommended by the French national bat-monitoring program 'Vigie-Chiro' (http://www.vigienature.mnhn.fr/). Since bats echolocate continuously (several calls per seconds) while commuting or foraging, we assumed detection probability was perfect. Recordings were only made when there was no rain, the wind was below 30 km/h and the ambient temperature above 12 °C. We used the software SonoChiro© (Bas et al. 2013) to automatically classify the echolocation passes to the most accurate taxonomic level possible. We then checked this classification by screening all ambiguous passes with Syrinx software version 2.6 (Burt 2006) and using existing identification keys (Barataud et al. 2015). Identification was possible to species level for most of our acoustic data, as there is low bat-species diversity in the study area. This avoided problematic acoustic overlaps between certain species pairs such as *Pipistrellus nathusii*/*Pipistrellus kuhlii*, *Myotis daubentonii/Myotis mystacinus/Myotis bechsteinii* and *Eptesicus serotinus/Nyctalus leisleri*. In fact, *P. kuhlii*, *M. mystacinus*, *M. bechsteinii* and *N. leisleri* are very rare in the study area according to regional atlas data (Dutilleul 2009). Nevertheless, to reduce false absences, the recording points where we were only able to identify a group of species that includes the studied species (but in which the studied species itself was not identified with 100% certainty) were excluded from the analysis of that species (Boughey et al. 2011).

2.4. Species distribution modelling (SDM)

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

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

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

2.5. Connectivity analysis

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

2.5.1. *Selection and localization of suitable habitat patches*

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

2.5.2. Landscape resistance maps

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

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

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

2.5.3. Least-cost paths

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

2.5.4. Light-reduction scenarios

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

3. RESULTS

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

3.1. Most relevant variables

While the percentage of impervious surfaces was not identified as a variable having a significant effect on the presence probability or activity of bats (except on the activity of *M. daubentonii*), average radiance had significant effects on both the presence probability and the activity of the three species (except on the activity of *P. nathusii*). In all models, the average radiance was the second or third most important variable. Our results showed contrasting trends: the effect of average radiance was positive for *E. serotinus*, whereas it was negative for *M. daubentonii* (Fig. 3 & 4). In the case of *P. nathusii*, average radiance had a positive effect at low values, then a negative effect after a threshold radiance of 20 $W.m^{-2}.sr^{-1}$ (Fig. 3C & 4C). 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 (it was always significant) explaining the distribution of the three species in terms of both presence probability and activity (Table 1). We never found the same groups of selected variables between activity models and presence probability models (Table 1). The number of patches with tree cover and the distance to vegetation had significant effects only on bat activity but not on presence probability. In contrast, the percentage of surface area covered by water only had a significant effect on presence probability but not on activity (Table 1).

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

Species	Landscape variables and spatial scales (m)						Deviance explained	AIC	AUC	COR	Sensitivity	Specificity	NRMSE
	100	200	300	500	700	800							
Presence probability													
Pipnat	$light_3^{*}$ $road_4^{*}$					$water_2^{**}$ $distwater_1^{**}$	*24.4%*	*319.5*	*0.73****	*0.87****	*77.78*	*48.98*	
Eptser					$light_3^{**}$ $distwater_1^{*}$	$water_2^{*}$	*13.9%*	*251.1*	*0.72**	*0.65*	*20.00*	*96.43*	
Myodau		$water_4$ $road_5$ $distwater_1^{**}$	$light_3^{*}$			$veget_2^{*}$	*27.3%*	*214.5*	*0.75****	*0.68**	*25.00*	*96.15*	
Activity													
Pipnat	$urban_3$					$light_4$ nTP_2^{***} $distwater_1^{***}$	*39.3%*	*1348.2*		*0.3***			*0.22*
Eptser				$light_2^{***}$	$distwater_1^{***}$	$distveget_3^{*}$	*35.2%*	*506.8*		*-0.03*			*0.17*
Myodau	$light_3^{**}$ $road_2^{***}$ $urban_5^{**}$ $distveget_4^{*}$					$distwater_1^{***}$ $veget_6$	*62%*	*554.7*		*0.5****			*0.15*

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

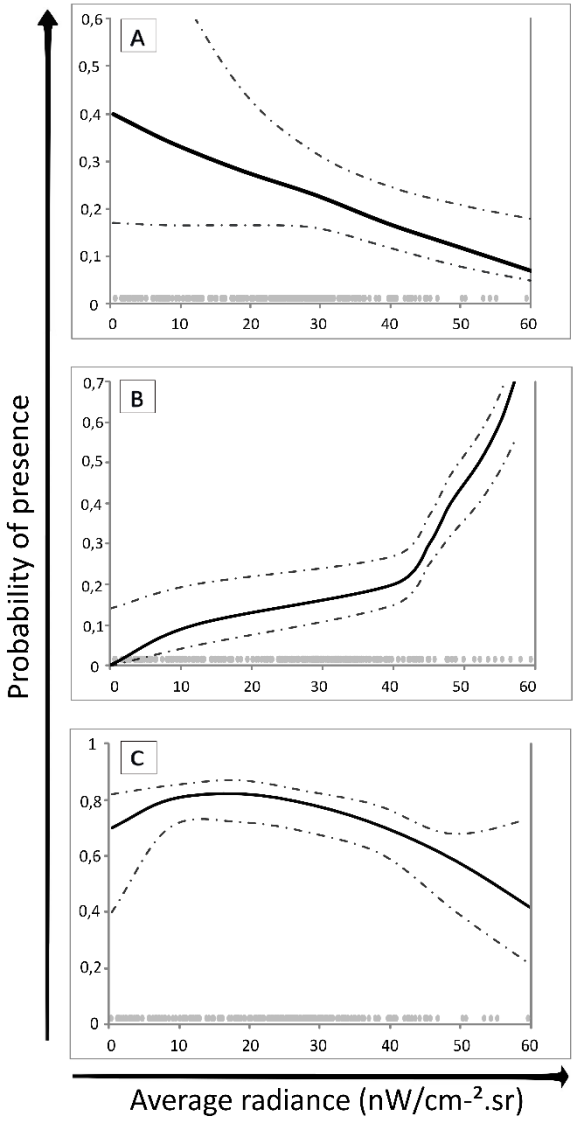

Figure 3 - Representative GAM response curves showing species presence probability at a location along the average radiance gradient. **A** is the response of *M. daubentonii* at a scale of 300 m, **B** is the response of *E. serotinus* at a scale of 700 m, and **C** is the response of *P. nathusii*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

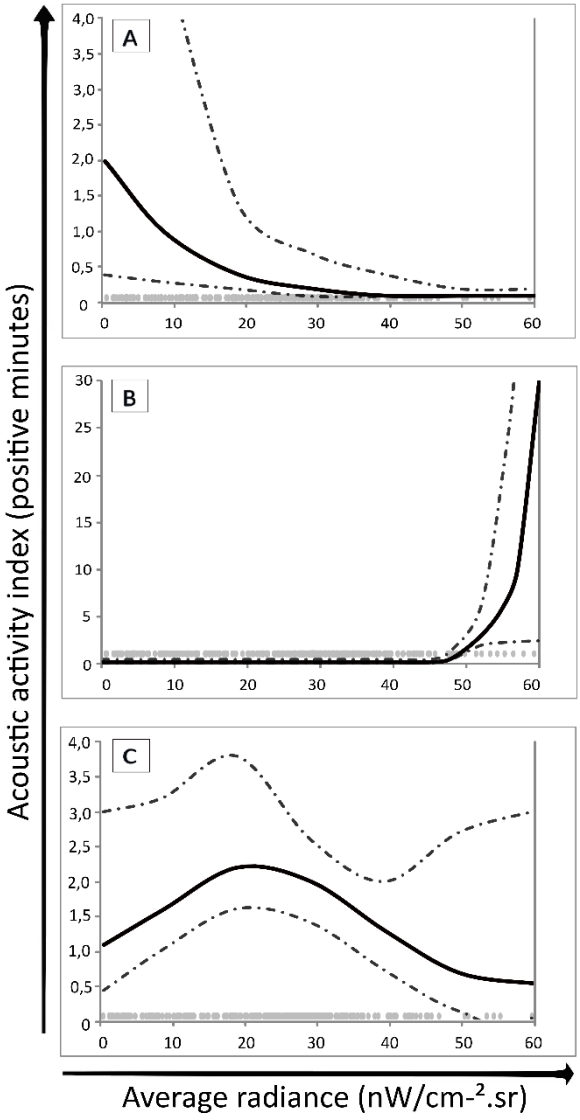

Figure 4 - Representative GAM response curves showing species activity at a location along the average radiance gradient. **A** is the response of *M. daubentonii* at a scale of 100 m, **B** is the response of *E. serotinus* at a scale of 500 m, and **C** is the response of *P. nathusii* at a scale of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

3.2. Model evaluation

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

3.3. Predicted distribution

The presence probability of *E. serotinus* and *M. daubentonii* was concentrated on areas with water. In contrast, *P. nathusii* had a more homogeneous spatial distribution (Fig. 5.1). The most urbanized and illuminated section of the conurbation's major canal was the least suitable section for *M. daubentonii* and *P. nathusii*, whereas it was the most conducive for *E. serotinus* (Fig. 5.1). Our results also showed that the city centre is on the whole a barrier to bat movement, although *E. serotinus* was predicted to have two suitable patches in urban parks of the centre (Fig. 5.1).

The activity-based models demonstrated the importance of parks for bat foraging in urban areas (Fig. 5.2). Indeed, the only habitat patches in the city centre predicted to be very suitable for all species were the largest urban parks of the city, which are located along the banks of the canal in the middle of the most illuminated section of the watercourse. The activity of *M. daubentonii* was much higher along the canals outside the city (in the northern and southern sections) than in the centre of Lille, except in urban parks. *E. serotinus* was very active in urban parks and forest patches of the study area. The activity of *P. nathusii*, which had a wider distribution in the study area but was not very abundant, was most concentrated in urban parks near canals and at suburban boundary zones between agricultural landscapes, suburban areas and forests (Fig. 5.2). Based on these predictive activity maps and a French bat activity framework (Haquart 2013), we identified 14 suitable habitat patches for *E. serotinus*, 47 for *M. daubentonii* and 22 for *P. nathusii* (Fig. 5.3).

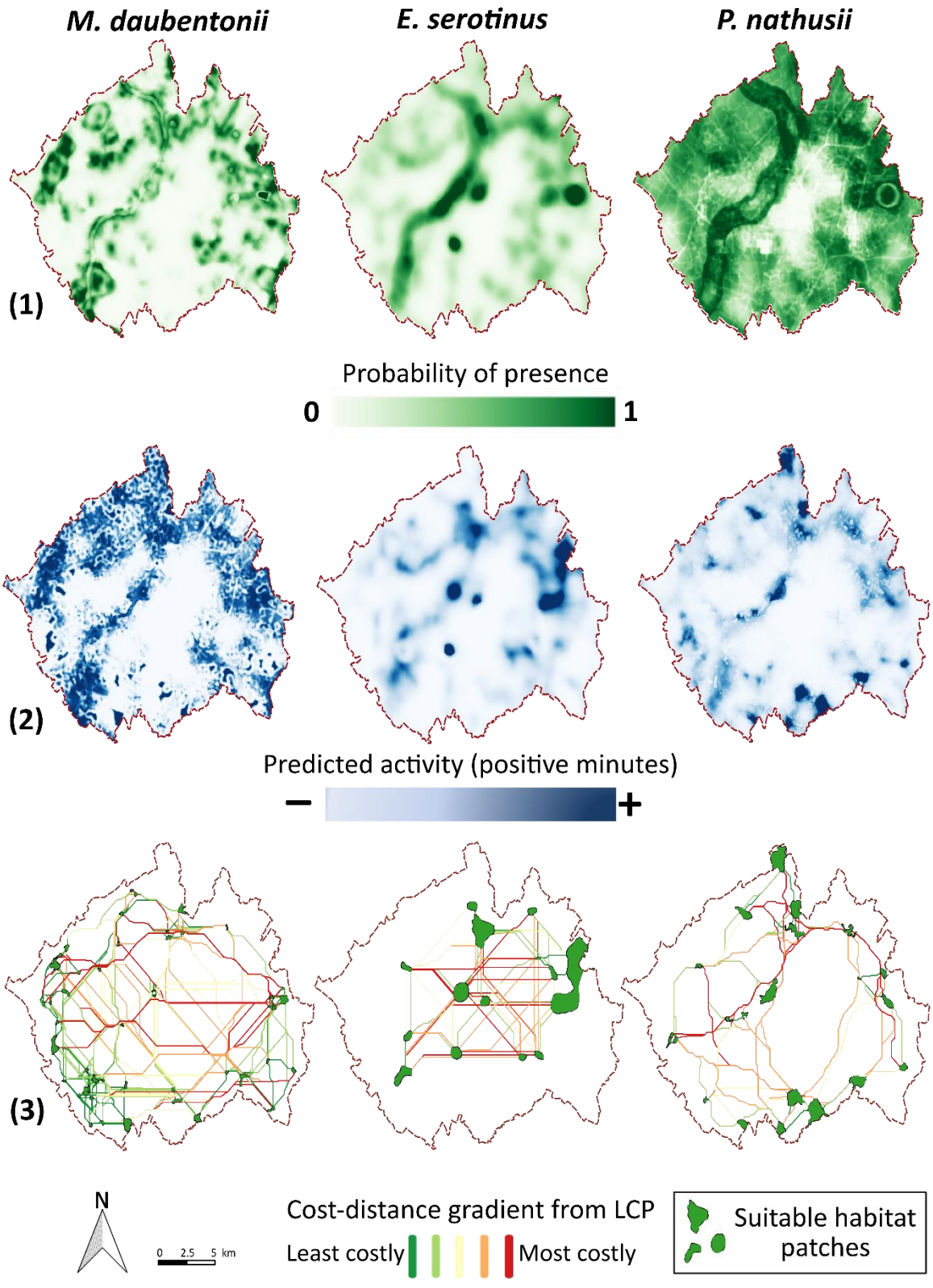

Figure 5 - Modelled distribution of presence probability **(1)** and activity **(2)** of the three studied species. **(3)** represents the least-cost paths identified in the study area. The activity gradient (defined by minutes in which at least one bat call of the species was recorded) has values bounded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

3.4. Least-cost paths and light-reduction scenarios

We assessed all the least-cost paths (LCPs) connecting each pair of suitable habitat patches (91 for *E. serotinus*, 1081 for *M. daubentonii* and 231 for *P. nathusii*) (Fig. 5.3) and then tested them for the five light-reduction scenarios (We did not apply these scenarios to the LCPs of *E. serotinus* because of its positive response to light). For *M. daubentonii*, all scenarios improved connectivity by significantly reducing the LCP cost-distance values (Fig. 6). For *P. nathusii* as well, all scenarios improved connectivity in the study area, except for scenario 2, which significantly increased the LCP cost-distance values. The scenarios ranged from more to less effective in the following order: (4)>(5)>(3)>(1)>(2) for *M. daubentonii*, and (1)>(3)>(4)>(5) for *P. nathusii* (Fig. 6).

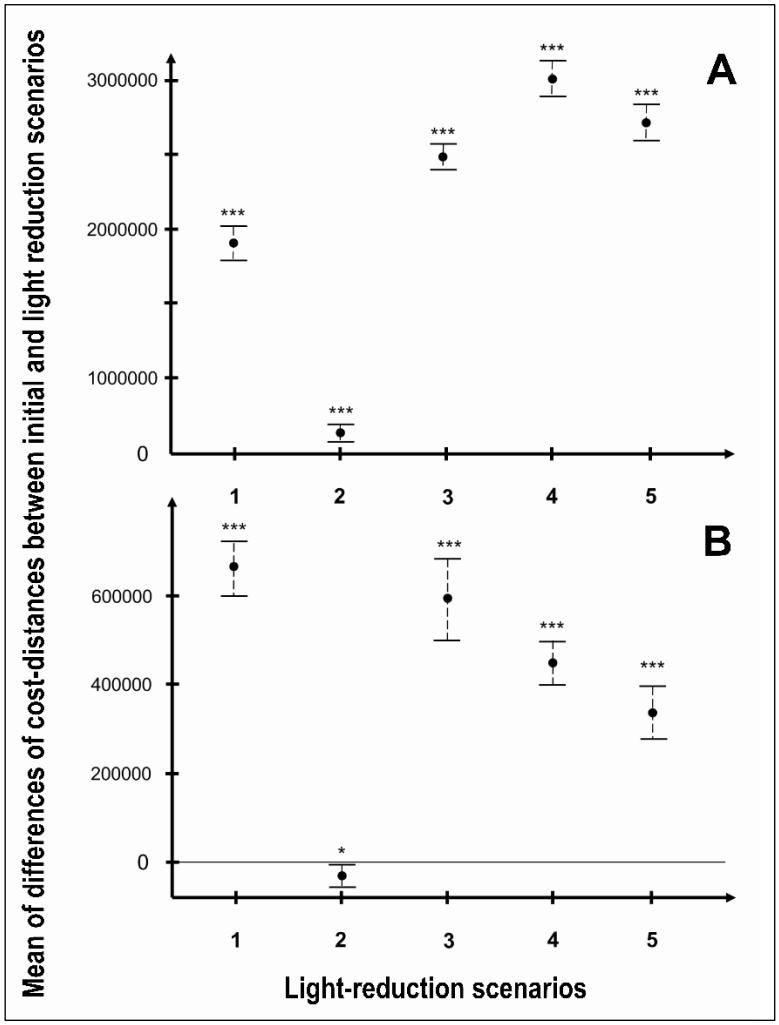

Figure 6 - Means of differences (with 95% confidence intervals) of paired cost-distances between the LCP with initial radiance intensity and the LCP after each light-reduction scenario using Student's *t*-test on the two studied species sensitive to light. **A**: *M. daubentonii*; **B**: *P. nathusii*.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

4. DISCUSSION

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

4.1. Model evaluation

While the presence probability models resulted in relatively accurate predictions, this was less the case with the activity models (Table 1). We expect this lack of accuracy is due to the fact that we measured activity very locally, while it is very sensitive to spatial and temporal variations in prey resources. Furthermore, predicting activity levels using only landscape variables is very difficult since spatial variation in species abundance can be driven by other factors, such as the complex interaction between stochastic temporal variations in abundance and dispersal of species in space (Ives and Klopper 1997). For example, we observed a non-negligible difference in precipitation levels between 2015 (mean rainfall/day = 1.6 mm ± 3.1) and 2016 (mean rainfall/day = 7.4 mm ± 11.2) during the same period (June–July, when sampling was carried out). As Erickson & West (2002) found that average summer precipitation can explain the largest proportion of variance in bat activity levels, this difference in rainfall could be a factor that limited the model's prediction performance. In any case, the weak prediction performance was not a problem because we used activity levels only to identify the most suitable habitat patches. We kept the same patches to test the different light-reduction scenarios, so their comparison is relevant irrespective of the quality of the predictions.

By the evaluation of spatial autocorrelation, we found virtually no autocorrelation for presence probability but some significant but low values of Moran's I for activity (see Appendix 2). This spatial autocorrelation is potentially linked to very high local abundances unexplained by the models because of the very high variance somewhat inherent to this kind of species, the activity variable, and unavailable missing variables (proximity of roosts, spatial and temporal peak of food resources abundances). The presence of this autocorrelation suggests that caution must be taken in interpreting the statistical tests associated to these models on activity. Moreover autocorrelation is supposed to inflate type I error but not to bias the estimates of the

models (the response curves). The patterns we obtained could thus be discussed. This conclusion is reinforced by the fact that the results of activity modeling, related to light average radiance, are highly consistent with those of the probabilities of presence (Fig. 3 & 4). Furthermore we only used presence probability to assess landscape connectivity and efficiency of light-reduction scenarios. The modelling of bat activity was only used to locate the nodes that we linked with the least-cost paths, a selection that would not be impacted by spatial autocorrelation.

4.2. ALAN: a major impact of urbanization on bats

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

Our study is the first to precisely describe the effect of ALAN on the presence probability and activity of *P. nathusii* and *M. daubentonii* (Fig. 3 & 4). The negative response of *M. daubentonii* to average radiance is consistent with previous studies of *Myotis spp*. as a group (Stone, Jones, & Harris, 2012). Indeed, *Myotis* species are light-sensitive: these slow fliers systematically seek to avoid the potentially increased predation risk in illuminated zones (Rydell 1991). *P. nathusii* had an intermediate response to ALAN, with a light-tolerance threshold of ≈ 20 W.m².sr-1 (Fig. 3C & 4C). We believe that this response pattern is driven by a trade-off between the benefits of the concentration of insects at low-intensity light and the cost of increased predation risk from high-intensity light. *E. serotinus* had a positive response to average radiance due to its ecological plasticity and fast flight capacity, allowing these bats to exploit illuminated foraging areas rich in insects (Fig. 3B & 4B). This positive response at scales of 500 m (for activity) and 700 m (for presence probability) (Table 1) is not consistent with the results of Azam et al. (2016), who found that average radiance had a negative effect on the presence probability of this species at all considered landscape scales (200, 500, 700 or 1000 m). We hypothesize that in highly urbanized landscapes, *E. serotinus* is more light-tolerant than in more natural landscapes, with streetlights becoming sub-optimal foraging areas as there

are few optimal foraging areas for the species in the study area (Stone, Harris & Jones, 2015). Such contradictory results highlight that the relationship between bat activity/presence and ALAN is complex and may be dependent on species, context and scale (Azam et al., 2016; Hale et al., 2012; Mathews et al., 2015).

4.3. Key landscape variables for bats in urban contexts

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

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

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

species in Europe (Arthur and Lemaire 2009), which is consistent with the fact that it was the only species in our study with two suitable habitat patches in the city centre (apart from the banks of watercourses) (Fig. 5).

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

4.4. Light reduction improves urban landscape connectivity

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

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

For *M. daubentonii*, every light-reduction scenario significantly improved landscape connectivity because of this species' general negative response to radiance (Fig. 6). *M. daubentonii* is a specialist gleaner bat species that is mostly present in wetlands, flies at low altitudes and depends on vegetation to commute. So the light-reduction scenarios for urban areas (1 & 2) were the least effective in improving connectivity for *M. daubentonii* simply because those areas are not used by this species. The next most effective scenarios to improve

connectivity for this species were reducing ALAN in urban parks (third most effective) and wetlands (second most effective). Surprisingly, the most effective scenario to increase landscape connectivity for *M. daubentonii* was light reduction on main roads. We believe this is mostly due to the spatial distribution of the main roads in our study area (see appendix S3.1), where these cross or are close to wetlands (ponds and canals) and urban parks. Reducing ALAN on main roads potentially improved the quality of wetlands and urban park habitats to a greater extent than light reduction solely on wetlands or solely on urban parks. But this result seems very context dependent and should be tested in other cities.

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

4.5. Methodological approaches

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

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

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

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

5. CONCLUSION

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

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Appendix 3

Appendix.1

Model performance evaluations

The models were trained with the data collected in 2015; the performance evaluations were based on data from independent field sampling. In 2016, we built another random stratified sampling in the exact same way as in 2015. Along the gradients of the same three landscape variables, we sampled 94 new recording points in the study area at the same period as in 2015. All the 2016 recording locations were at least 200 m from the 2015 recording locations. 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) the sensitivity (Thuiller, Lafourcade & Araujo, 2010). We assessed the predictive performance of the activity models using the Root Mean Square Error (RMSE). In order to compare the performance of different models, the RMSE was normalized by dividing it by the difference between the maximum predicted value and the minimum value (NRMSE) (Loague and Green, 1991). The greater the percentage of NRMSE, the less effective the 2015 model in predicting bat activity in 2016. We also used the Pearson correlation coefficient (COR) to compare the 2015 predictions and the 2016 observations (Elith et al., 2006) as another index to evaluate the performance of the presence and activity models. To evaluate the presence probability model, 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.2

Multiscale landscape variables and statistical analysis

For the statistical analysis, we created gridded landscapes at a 50-m resolution (Bellamy, Scott & Altringham, 2013) for eight variables: (1) the proportion of impervious surfaces and (2) the total length of roads (considered as a potential confounding factor of average radiance, Azam et al., 2016), (3) the average radiance, (4) the proportion of tree cover, (5) the proportion of surface covered by water, (6) the mean number of tree patches, (7) the mean distance of the cell centroid to water, and (8) the mean distance of the cell centroid to tree patches. These were chosen as they are known to influence bat activity and movement 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 bat presence probability or activity may vary according to the spatial scale, and that the most influential scale differs between species. Furthermore, multiscale habitat models often yield better predictions than single-scale models (Grand, Buonaccorsi, Cushman, Griffin & Neel, 2004). Each variable was thus calculated for 10 different scales (100, 200, 300, 400, 500, 600, 700, 800, 900 and 1000 m) by measuring cell statistics within different sizes of moving windows centred on each raster cell. For each variable/species pair we selected the most relevant scale by first fitting 10 univariate models to the 10 different scales (Bellamy et al., 2013) using AIC criteria (*Akaike Information Criterion) (Akaike, 1974).* Then we regrouped all the scaled-landscape variables in a full model for each species and used a backward leave-one-out stepwise procedure to delete variables in order to identify the subsets of scaled-landscape variables with the highest performance and select the best model for each species (Parolo, Rossi & Ferrarini, 2008). To avoid multicollinearity in the models, we evaluated the correlations between 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 model (Fox and Monette, 1992); all variables had a VIF of <5, indicating no obvious problem of multicollinearity between the variables. We also tested for spatial autocorrelation on model residuals using Moran's I with 10 lags of 500 m. Concerning residuals from presence probability modeling there was virtually no spatial autocorrelation: for *Myotis daubentonii* no value of Moran's I were significant; for both *Pipistrellus nathusii* and *Eptsesicus serotinus* we found just three very low significant values

(Moran's I below 0.12). On the contrary there was more spatial autocorrelation with residuals from activity modeling: for each of the three studied species we found four significant values (Moran's I below 0.17).

Table S2.1 The correlograms presenting results of spatial autocorrelations assessments from presence probability modeling (***p < 0.001; **p < 0.01; *p < 0.05)

Myotis daubentonii					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.08	-0.01	0.01	0.12	ns
1000	0.03	0.00	0.00	0.24	ns
1500	0.01	0.00	0.00	0.33	ns
2000	0.02	0.00	0.00	0.17	ns
2500	0.01	0.00	0.00	0.31	ns
3000	0.00	0.00	0.00	0.46	ns
3500	0.02	0.00	0.00	0.15	ns
4000	0.00	0.00	0.00	0.45	ns
4500	0.00	0.00	0.00	0.48	ns
5000	-0.05	0.00	0.00	0.98	ns
Pipistrellus nathusii					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.06	-0.01	0.01	0.19	ns
1000	0.08	0.00	0.00	0.02	*
1500	0.03	0.00	0.00	0.21	ns
2000	0.08	0.00	0.00	0.00	**
2500	0.10	0.00	0.00	0.00	***
3000	0.05	0.00	0.00	0.02	*
3500	0.05	0.00	0.00	0.01	**
4000	0.00	0.00	0.00	0.48	ns
4500	0.02	0.00	0.00	0.15	ns
5000	-0.01	0.00	0.00	0.69	ns
Eptesicus serotinus					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.11	-0.01	0.01	0.04	*
1000	0.05	0.00	0.00	0.10	ns
1500	0.05	0.00	0.00	0.06	ns
2000	0.04	0.00	0.00	0.05	*
2500	0.09	0.00	0.00	0.00	***
3000	0.04	0.00	0.00	0.04	*
3500	-0.01	0.00	0.00	0.69	ns
4000	0.02	0.00	0.00	0.18	ns
4500	0.00	0.00	0.00	0.50	ns
5000	0.00	0.00	0.00	0.45	ns

Table S2.2 The correlograms presenting results of spatial autocorrelations assessments from activity modeling (***p < 0.001; **p < 0.01; *p < 0.05)

Myotis daubentonii					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.17	-0.01	0.01	0.00	**
1000	0.13	0.00	0.00	0.00	***
1500	0.08	0.00	0.00	0.01	*
2000	0.05	0.00	0.00	0.03	*
2500	0.04	0.00	0.00	0.04	*
3000	0.01	0.00	0.00	0.34	ns
3500	0.00	0.00	0.00	0.39	ns
4000	0.00	0.00	0.00	0.38	ns
4500	-0.01	0.00	0.00	0.57	ns
5000	-0.02	0.00	0.00	0.81	ns
Pipistrellus nathusii					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.15	-0.01	0.01	0.02	*
1000	0.10	0.00	0.00	0.01	**
1500	-0.03	0.00	0.00	0.79	ns
2000	0.06	0.00	0.00	0.02	*
2500	0.10	0.00	0.00	0.00	***
3000	0.02	0.00	0.00	0.21	ns
3500	0.00	0.00	0.00	0.45	ns
4000	0.03	0.00	0.00	0.07	ns
4500	0.04	0.00	0.00	0.02	*
5000	0.00	0.00	0.00	0.46	ns
Eptesicus serotinus					
Scales (m)	I Moran	Expected	Variance	p-value	Significativity
500	0.17	-0.01	0.00	0.00	**
1000	0.13	0.00	0.00	0.00	***
1500	0.14	0.00	0.00	0.00	***
2000	0.10	0.00	0.00	0.00	***
2500	0.12	0.00	0.00	0.00	***
3000	0.08	0.00	0.00	0.00	***
3500	0.02	0.00	0.00	0.12	ns
4000	0.00	0.00	0.00	0.37	ns
4500	-0.01	0.00	0.00	0.69	ns
5000	-0.03	0.00	0.00	0.85	ns

Appendix.3

Privately lit areas not included in the light-reduction scenarios included airports, aerodromes and 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 infrastructure, allotment gardens, stadiums, and sports facilities.

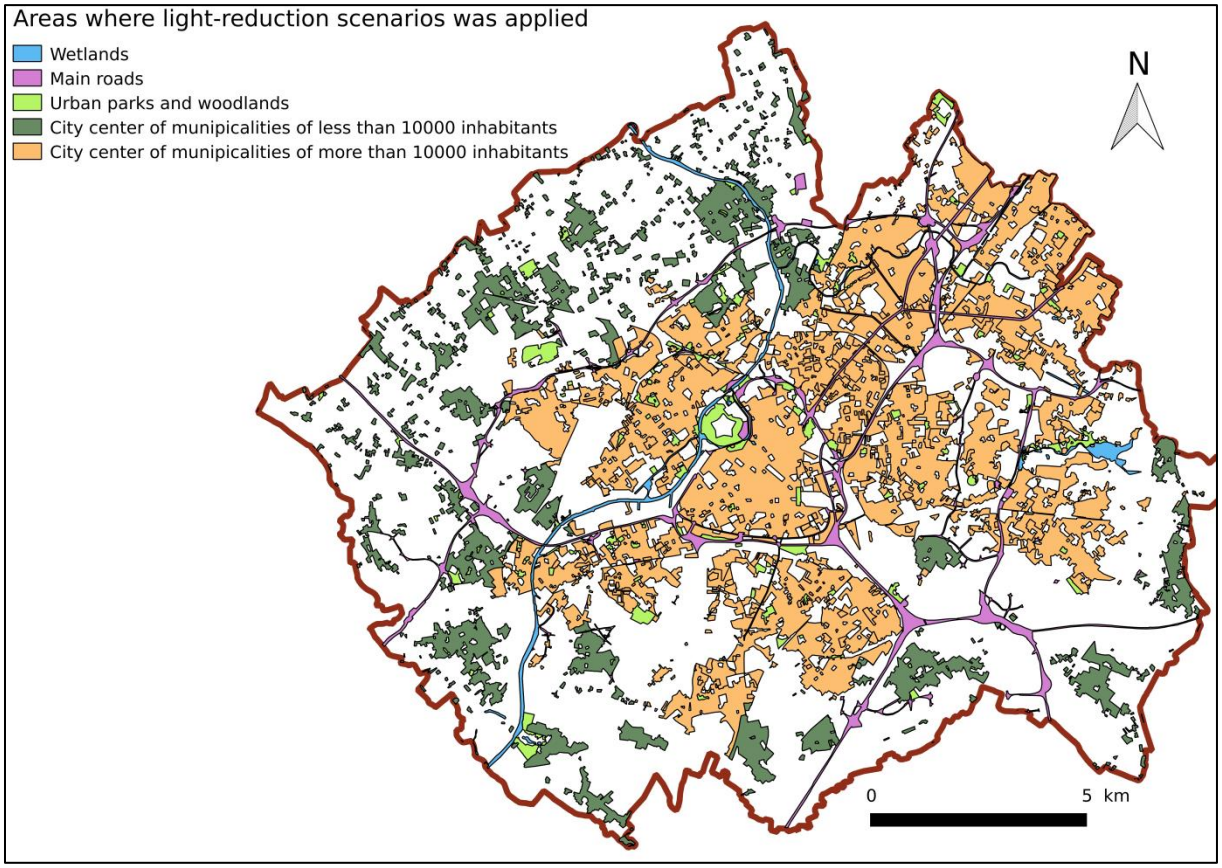

Fig.S3.1 Spatial distribution of the five light-reduction scenarios on the study area

Table.S3.2 The initial intensity of radiance before light-reduction scenario, the standard deviation and the surface area of zones where light reduction was applied

	(1)	**(2)**	**(3)**	**(4)**	**(5)**
Radiance mean ***(nW/cm-2.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

(1) urban municipalities of more than 10,000 inhabitants; (2) urban municipalities of less than 10,000 inhabitants; (3) urban parks; (4) main roads; (5) wetlands.

CHAPTER 4

Landscape context matters for attractiveness and effective use of road underpasses by bats

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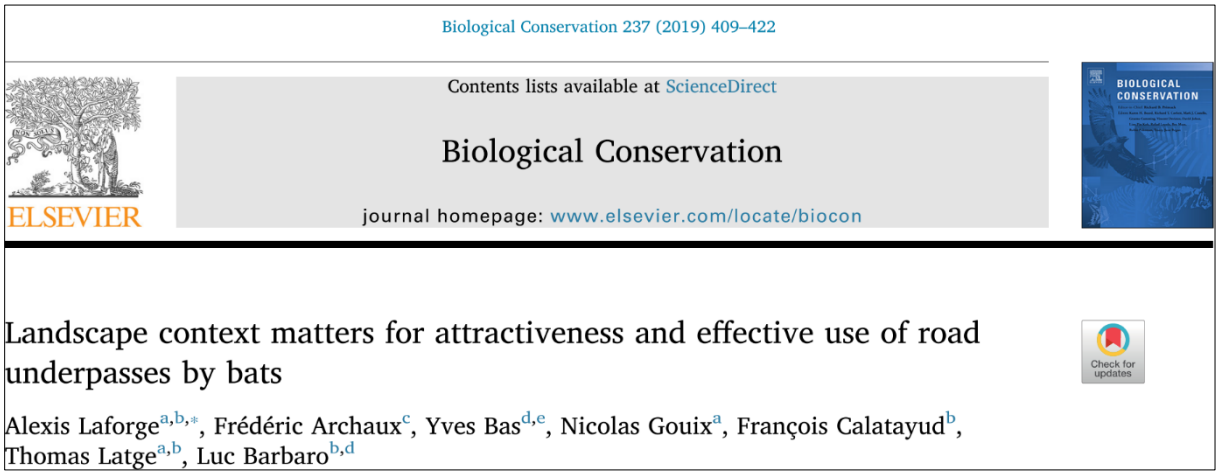

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Landscape context matters for attractiveness and effective use of road underpasses by bats

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ABSTRACT

Context: The worldwide expansion of road networks is a major concern in biological conservation because of its predominantly negative effects on terrestrial fauna. Roads also affect bats, acting as barriers to movements and causing direct mortality by collisions with vehicles. Among wildlife crossing structures existing to maintain landscape connectivity, road underpasses are considered as one of the most effective conservation measure for bats. While a few studies assessed the effects of underpass attributes on bat use, none to date has assessed the impact of landscape context on underpass use and attractiveness.

Aim: To address this knowledge gap, we monitored bat activity during three consecutive nights around 24 underpasses selected along a gradient of forest cover. We compared bat activity below and above underpasses (i.e., underpass use), at road sections with and without underpasses and at habitats adjacent to roads (i.e., underpass attractiveness).

Results: We found a significant positive effect of forest cover on both underpass use and attractiveness for *Myotis* spp and *Barbastella barbastellus*, and significant negative effects of distance to the nearest forest patch for *Rhinolophus* spp and hedgerow length for *Myotis* spp.

Conclusions: Our study highlights the key influence of landscape context on road underpass efficiency to maintain landscape connectivity for bats. We advocate incorporating a landscape-scale approach in the decision-making process of underpass location during road project planning to enhance efficiency of such costly crossing structures.

KEYWORDS

Chiroptera, Wildlife crossing structures, Landscape connectivity, Landscape permeability, Conservation measure improvement

1. INTRODUCTION

Road network have expanded worldwide by 12 million km since 2000, and 25 million km of additional roads are expected by 2050 (Laurance et al., 2014). In line with the recent rise of road ecology issues in the field of biological conservation, there is now widespread evidence for overall negative effects of roads on biodiversity. These effects include direct mortality caused by vehicle collisions (Clevenger et al., 2003; Santos et al., 2011), habitat loss and fragmentation reducing landscape permeability and increasing barriers or filters to animal movement (Tucker et al., 2018). Consequently, individual animals may not be able to access critical food resources, breeding grounds or hibernacula. This may reduce population size and movements between populations, leading to a stronger inbreeding (Brehme et al., 2013; de Oliveira et al., 2011; Seidler et al., 2015; Tucker et al., 2018). Studies have evidenced that animal abundance and diversity are generally lower on both sides of roads where environmental conditions are strongly affected by the road (Clarke et al., 2013; Forman and Deblinger, 2000; Martin et al., 2018; Nafus et al., 2013; Northrup et al., 2012). Survival, foraging and breeding success of various animal taxa are also influenced by the proximity to roads (Halfwerk et al., 2011; Lukanov et al., 2014; Luo et al., 2015; Meillère et al., 2015; Tennessen et al., 2014). Increasing the density of road networks can therefore isolate populations, disconnect vital resources, cause severe habitat loss and ultimately impede population persistence for a wide range of taxa, including mammals, amphibians, reptiles, birds and invertebrates (Bennett, 2017; Ward et al., 2015).

In their seminal review, Fahrig and Rytwinski (2009) found that species with a particular combination of life traits, i.e., low reproductive rate, long life-span, high daily mobility and a sensitivity to noise/light pollution are the most vulnerable to landscape fragmentation and mortal vehicle casualties associated with roads. Bats typically share all these traits and attributes, so that they are likely to be particularly impacted by road network. Several factors explain why bat activity and species richness are lower on, or close to, roads (Berthinussen and Altringham, 2012a; Kitzes and Merenlender, 2014; Medinas et al., 2019) : (i) collisions with motor vehicles may significantly contribute to overall bat mortality (Fensome and Mathews, 2016; O'Shea et al., 2016); (ii) food resources of bats may be depleted along roads (Martin et al., 2018); and (iii) road traffic noise masks echolocation calls of species such as *Myotis myotis* and *Myotis daubentonii*, which reduces their foraging efficiency and forces them to avoid roadside habitats when foraging (Luo et al., 2015; Schaub et al., 2008). Finally, artificial light is another road-related pollution which can negatively impact bat occurrence and activity (Azam et al., 2016; Hale et al., 2012), alter movement behavior - bats avoiding the illuminated

areas - and hence decrease overall landscape connectivity (Hale et al., 2015; Kuijper et al., 2008; Laforge et al., 2019; Stone et al., 2009). Taken together, these impacts make roads an important driver of landscape fragmentation for bats, which can impact population viability and thus deserve routine consideration during road construction (Fahrig and Rytwinski, 2009).

To reduce impacts of roads and maintain functional landscape connectivity, several conservation measures aiming at crossing roads in safe conditions are already implemented worldwide. These can be divided in two categories: (i) underpasses such as bridges and culverts and; (ii) overpasses such as bat gantries and hop-overs (Claireau et al., 2018; Glista et al., 2009; Møller et al., 2016). Overpasses are specifically built to facilitate bat movements, while underpasses are generally set for drainage or human activities (minor roads, agricultural tracks or hiking paths for instance) but are favorable to a many taxa including bats. Underpasses have been shown to be effective at maintaining bat commuting routes and road permeability (Dekker et al., 2016; Møller et al., 2016) and seem more effective than overpasses (Abbott et al., 2012a, 2012b; Bach et al., 2004; Claireau et al., 2018).

Most previous works on underpasses compared bat activity above and below the roads to quantify bat underpass use. Underpasses are more used by bat species flying at low heights with high maneuverability, such as clutter-adapted and foliage-gleaning species by opposition to hawkers, open aerial foragers and edge-adapted species (Abbott et al., 2012a; Bhardwaj et al., 2017). However, this is not always true and underpasses close to hedgerows and natural corridors can be used by virtually all bat guilds (Abbott et al., 2012a; Berthinussen and Altringham, 2012b). So far, experiments carried out on underpass use by bats mainly focused on how attributes of road underpasses could influence their efficiency. Hence, among underpasses, bridges seem to be more efficient than culverts (Abbott et al., 2012a; Bhardwaj et al., 2017), and underpass width and height, but not length, are important for determining their use by bats (Abbott et al., 2012a; Bhardwaj et al., 2017; Boonman, 2011).

It is not enough to evaluate the effectiveness of underpasses solely through their use but also through their attractiveness, which is a key element often missing in previous assessments. For example, an underpass can be effective in reducing road collision risk but only for a negligible part of a given bat population crossing roads daily. In addition, an underpass could be attractive but not actually used, and could thus act as a potential ecological trap by attracting more bats in the vicinity of the roads and increasing the collision risk. Only Abbott et al., (2012a) compared bat activity at roads with and without underpasses, showing that underpasses can have a certain attractiveness, i.e., bat activity was higher at roads with underpasses than at roads without underpasses.

Most studies that investigated the use of underpasses by bats only considered local factors such as dimensions, type of structure or presence of corridors without considering variation in landscape context (Bennett, 2017). This is a major concern for bat conservation, since the efficiency of an underpass to facilitate individual movements and overall landscape permeability is expected to depend not only on its local characteristics, but also on its location in a given landscape (Abbott et al., 2012a; Bennett, 2017). Landscape context is known as a key factor influencing the spatial variations of bat casualties by vehicles (Gaisler et al., 2009; Lesiński, 2008, 2007, Lesiński et al., 2011a, 2011b; Medinas et al., 2013), and of bat activity at road verges (Medinas et al., 2019). Furthermore, bat activity and consequently road collision risk is higher when multiple roads cross high quality habitats such as forests, wetlands, streams or hedgerows (Roemer, 2018). Bat community composition, activity and species diversity are expected to change with the proportion of key wooded habitats for bat roosting, foraging and commuting, such as forests and hedgerows, occurring at the landscape scale (Arroyo-Rodríguez et al., 2016; Charbonnier et al., 2016; Fuentes-Montemayor et al., 2017; Heim et al., 2015).

Finally, the relationships between bats and landscape contexts are species/guilds dependent (Ducci et al., 2015; Mendes et al., 2016) which is also the case between bats and their response to roads and underpasses (Abbott et al., 2012a, 2012b; Bhardwaj et al., 2017; Kerth and Melber, 2009; Medinas et al., 2019, 2013). Thus, it is expected that landscape context will influence differently the use and attractiveness of underpasses depending on the species or guilds.

The main objective of our study was thus to evaluate how the landscape context, and especially the amount of forests and hedgerows in the surrounding landscape, change underpass use and attractiveness for bats, irrespective of local underpass attributes. More precisely, we tested the predictions that (i) road underpass attractiveness for bats would decrease with increasing forest cover and total hedgerow length because a more wooded landscape would reduce the need for bats to cross roads when commuting between roosting and foraging sites; (ii) bat use of road underpasses would increase with surrounding forest cover and total hedgerow length because of higher abundance of clutter-adapted and gleaning bat species, which are more reluctant to cross roads in open air; and (iii) underpass attractiveness and use would be more influenced by landscape attributes for species that are highly dependent on tree elements to commute because of their low and slow flights (i.e., gleaners and clutter-adapted species) while local features would be more influential for aerial hawkers. We expect, by conducting analyses per species and group of species, to precisely evaluate which landscape features help the most species to use underpasses, therefore improving the success in future conservation and land-management plans.

2. MATERIALS AND METHODS

2.1. Study area

We conducted our study in the Occitanie region (N 43.70, E 1.56), south-western France. The study area has a predominantly temperate climate with diverse influences (Atlantic, Continental, Mediterranean and mountainous). We monitored bat activity along four main roads: N124 (average daily traffic in 2015: 12,128; heavy vehicles: 8.1%), N21 (7,923; 10.15%), N126 (10,957; 9.35%), A68 (24,470, 8%) and N88 (20,933; 8.5%; see Fig. 1 and Table 1). Information on the average daily traffic was obtained from the database of "Direction Interdépartementale des Routes du Sud-Ouest" (DIRSO), a government agency in charge of monitoring and maintenance road structures (http://www.dir.sud-ouest.developpement-durable.gouv.fr). The roads are surrounded by mosaic agricultural landscapes (crops, vineyards, pastures) including patches of grasslands and woodlands of various sizes, tree-lined hedgerows, rivers, minor roads, scattered rural housing and small-medium conurbations with an elevation of <400m a.s.l. (Fig. 1). In comparison with previous studies on underpass use by bats in Northern Europe (Abbott et al., 2012a, 2012b; Bach et al., 2004; Boonman, 2011), our study area has a less dense road network with more preserved landscapes and hosts a higher bat diversity with 27 bat species recorded at the regional scale (Bodin et al., 2011).

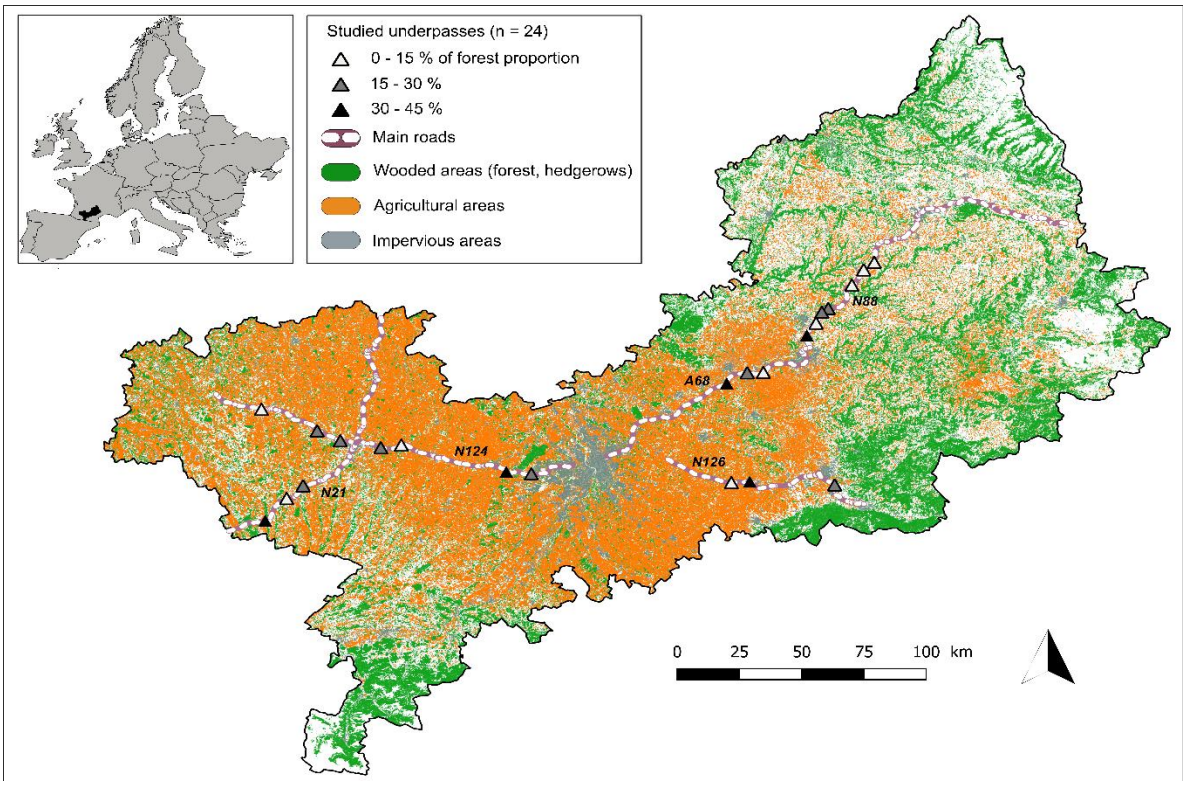

Figure 1 - Land use map of the study area, indicating the location of sampled roads and underpasses.

2.2. Underpass selection procedure

To select underpasses, we used the DIRSO database encompassing all geolocated underpasses in the study area (n=551). We then defined a 'landscape' as the area within a 1 km radius around each underpass. We used this spatial extent based on a trade-off between mean daily movements of bat species occurring in the study area (about 1–3 km) and the need to maximize the landscape gradient we targeted to sample (Bodin et al., 2011; Ethier and Fahrig, 2011; Pasher et al., 2013). Furthermore, it has been shown on other taxa that the cumulative ecological effect of the road system on biodiversity at landscape scale (i.e., the road effect-zone) can extend 800 m (Forman, 2000; Forman and Deblinger, 2000). To eliminate potential landscape-scale confounding factors, we reduced the candidate set of underpasses by selecting landscapes which had small areas of impervious surface (<20%; buildings and paved areas such as roads, sidewalks, driveways and parking lots) and of water surface (<10%) (Ethier and Fahrig, 2011). This step reduced the set of underpasses (N=213), for which we calculated forest cover for each landscape (as predictor of interest used to stratify our sample of underpasses) and categorized this predictor into three classes: 0-15%, 15-30%, 30-45% (Fig.1). In the study area, interior and edges of forests provide the most important foraging and commuting areas for both gleaner/clutter-adapted bat species (*Myotis* spp., *Plecotus* spp., *Rhinolophus* spp.) and for edge-adapted species (*Pipistrellus* spp., *Eptesicus serotinus*, *Barbastella barbastellus)*. They also represent tree roosting areas for many aerial hawking species (Cel'uch and Kropil, 2008; Müller et al., 2013; Plank et al., 2012). In addition, we further carried out field validation of the selected underpass dimensions and entrance cluttering (which reduced the set of underpasses to N=68). To ensure that all sampled underpasses could be used by the whole bat community, we selected underpasses with entrance dimensions of at least two meters in width and height, following previous studies (Abbott et al., 2012a, 2012b; Bach et al., 2004; Berthinussen and Altringham, 2012b; Bhardwaj et al., 2017; Boonman, 2011). For each underpass, we calculated 11 environmental predictors: 4 local predictors (habitat within underpasses, width and height of the underpasses and presence or absence of hedgerows at least at one entrance of the underpasses), one road-related predictor (number of lanes on the road above the underpasses) and 6 landscape predictors (forest proportion, forest contrast as the difference of forest cover between the two demi-buffers at both sides of the roads above the underpasses, hedgerow length, hedgerow contrast as the difference in hedgerow length between the two demi-buffers at both sides of the roads above the underpasses, distance between underpass and the nearest water body and distance between underpass and the nearest forest patch; see Table 1).

Table 1 - Summary of sampled underpasses, road attributes and landscape variables. Variable names in bold are predictors tested in the models. Hab_under: habitat within the underpass ; Wide and Height refer to the dimensions of underpass entrances; Hedge: presence or absence of an hedgerow at one or two entrance(s) of the underpasses ; Forest contrast: difference of forest cover between the two demi-buffers at both sides of the roads above the underpasses; Hedgerow contrast: difference in hedgerow length between the two demi-buffers at both sides of the roads above the underpasses; Distance to water: distance between underpass and the nearest water body; Distance to forest: distance between underpass and the nearest forest patch.

Underpasses (n = 24)								**Roads**				**Landscape variables (Buffer 1 km)**					
Site	Type	**Hab_under**	**Wide (m)**	**Height (m)**	Length (m)	**Hedge**	*Year of construction*	Road	Wide (m)	**Lanes**	Speed limit (km/h)	**Forest (%)**	**Forest contrast (%)**	**Hedgerow length (m)**	**Hedgerow contrast (m)**	**Distance to water (m)**	**Distance to forest (m)**
11	Culvert	**road**	**10**	**5**	35	**Yes**	*2001*	N124	20	**4**	110	**7.5**	**8.7**	**10792.1**	**2367.8**	**1046.0**	**118.0**
58	Culvert	**road**	**6**	**4.5**	15	**Yes**	*1992*	N126	14	**3**	80	**3.3**	**2.0**	**11913.5**	**704.8**	**134.0**	**265.0**
74	Culvert	**track**	**3.5**	**2.5**	40	**Yes**	*1995*	N126	12	**2**	80	**17.0**	**14.4**	**11815.9**	**2148.4**	**594.0**	**246.0**
110	Culvert	**river**	**4.5**	**3**	50	**Yes**	*2007*	N124	20	**4**	110	**11.7**	**9.2**	**21959.4**	**515.4**	**920.0**	**150.0**
120	Culvert	**river**	**7**	**4**	30	**Yes**	*1987*	A68	25	**4**	130	**12.5**	**4.6**	**10083.0**	**696.0**	**297.0**	**205.0**
123	Culvert	**river**	**4**	**2.5**	46	**Yes**	*1987*	A68	40	**5**	130	**27.1**	**5.9**	**7826.0**	**1814.6**	**690.0**	**583.0**
126	Culvert	**road**	**6.5**	**5**	40	**Yes**	*1991*	A68	35	**4**	130	**30.8**	**12.5**	**9865.8**	**300.4**	**315.0**	**327.0**
164	Culvert	**road**	**5**	**5.5**	20	**Yes**	*1999*	N124	12	**2**	80	**16.2**	**1.9**	**20329.6**	**4065.1**	**908.0**	**210.0**
176	Bridge	**river**	**6**	**3**	12	**Yes**	*1900*	N124	9	**2**	80	**12.0**	**2.1**	**19129.6**	**4483.3**	**954.0**	**365.0**
196	Bridge	**river**	**4**	**3**	18	**Yes**	*1846*	N21	8	**2**	80	**9.9**	**12.7**	**18207.7**	**1303.1**	**815.0**	**72.0**
201	Culvert	**road**	**8**	**4.5**	25	**No**	*1995*	N124	20	**4**	90	**30.7**	**25.6**	**6388.9**	**3673.2**	**1467.0**	**140.0**
218	Bridge	**river**	**3**	**3**	30	**Yes**	*1900*	N21	10	**2**	80	**11.9**	**4.8**	**12503.3**	**1342.8**	**1060.0**	**272.0**
225	Bridge	**river**	**4**	**5**	5	**Yes**	*1900*	N124	9	**2**	80	**18.7**	**14.8**	**14545.4**	**1393.5**	**1466.0**	**46.0**
311	Bridge	**river**	**15**	**6**	10	**Yes**	*1900*	N21	10	**2**	80	**33.5**	**16.1**	**10222.0**	**1665.5**	**1311.0**	**85.0**
464	Culvert	**track**	**8**	**5**	30	**No**	*2014*	N88	30	**4**	110	**9.9**	**4.7**	**15537.5**	**6416.8**	**1503.0**	**190.0**
471	Culvert	**track**	**6**	**4**	30	**No**	*2014*	N88	30	**4**	110	**4.3**	**7.7**	**16419.8**	**2244.9**	**310.0**	**224.0**
476	Culvert	**track**	**8**	**4**	38	**No**	*2014*	N88	30	**4**	110	**5.4**	**6.3**	**11903.2**	**4240.7**	**897.0**	**457.0**
485	Culvert	**track**	**5**	**4**	30	**Yes**	*2011*	N88	30	**4**	110	**16.2**	**19.3**	**12800.4**	**3608.0**	**1131.0**	**138.0**
487	Culvert	**river**	**5**	**3.5**	92	**Yes**	*2003*	N88	30	**4**	110	**17.2**	**10.9**	**10120.0**	**30.0**	**1013.0**	**112.0**
489	Culvert	**river**	**2.5**	**2.5**	100	**Yes**	*2003*	N88	30	**4**	110	**20.2**	**25.1**	**10950.6**	**420.3**	**1098.0**	**100.0**
494	Culvert	**river**	**3**	**3**	100	**Yes**	*2007*	N88	30	**4**	110	**14.1**	**10.8**	**12430.2**	**329.8**	**1532.0**	**140.0**
501	Culvert	**track**	**8**	**4**	32	**Yes**	*2003*	A68	25	**3**	110	**41.0**	**12.2**	**15813.8**	**5333.8**	**1539.0**	**150.0**
514	Culvert	**road**	**11**	**5**	30	**No**	*2009*	N124	20	**4**	110	**13.7**	**12.8**	**10807.1**	**2709.2**	**2787.0**	**83.0**
530	Culvert	**river**	**10**	**3**	34	**Yes**	*2007*	N126	15	**2**	80	**24.4**	**20.1**	**22044.6**	**2650.0**	**1869.0**	**208.0**
Mean	-	-	**6.4**	**3.9**	37.2	-	1979	-	21.4	**3.3**	100.4	**17.0**	**11.1**	**13517.0**	**2269.1**	**1069.0**	**203.6**
SD	-	-	**3.0**	**1.0**	25.7	-	48.5	-	9.6	**1.0**	18.1	**9.6**	**6.8**	**4301.7**	**1743.7**	**580.0**	**127.8**
Min	-	-	**2.5**	**2.5**	5.0	-	1846	-	8.0	**2.0**	80.0	**3.3**	**1.9**	**6388.9**	**30.0**	**134.0**	**46.0**
Max	-	-	**15.0**	**6.0**	100.0	-	2014	-	40.0	**5.0**	130.0	**41.0**	**25.6**	**22044.6**	**6416.8**	**2787.0**	**583.0**

This selection procedure finally reduced the set of candidate underpasses to 24 (mean distance between sites: 84.4 ± 55.3 km; Fig. 1). Mostly because we excluded urban landscapes during underpass selection procedure, none of our studied underpasses had street lights above, around or inside. We found bat roosting inside only one studied underpass (≈ 15 *Pipistrellus* spp), that was consequently deleted from the data set to avoid bias in estimating underpass use for the *Pipistrellus* spp. All the landscape predictors were calculated with ArcGis 10 (ESRI, Redlands, CA) based on land use data from the French National Institute for Geographic and Forestry Information (http://www.ign.fr/). The land use data were obtained by photo-interpretation to an accuracy ranging from 1 to 30 m spatial resolution depending on the type of habitat sampled.

2.3. Sampling design

To test our two predictions (i.e., forest cover and hedgerow length would decrease underpass attractiveness but increase underpass use), we first assessed if the presence of an underpass attracted bats in comparison with neighboring road sections without an underpass. As the attractiveness of an underpass could also depend on the habitat crossed by the underpass, we compared bat activity within underpasses with bat activity in the same habitat adjacent to the road. Moreover, a higher attractiveness for a given underpass does not necessarily mean a more frequent use by bats, so that we built a sampling design and calculated ad hoc metrics to take this into account (Fig. 2).

Bat activity was recorded with autonomous ultrasound recorders (Batlogger A, Elekon AG, Lucerne, Switzerland). Each recorder was calibrated to automatically trigger in reaction to any sound whose frequency was between 8 and 192 kHz and with a signal-to-noise-ratio level above 6 dB (Claireau et al., 2019a). Five recorders were deployed at four different locations in the landscape for each underpass (Fig. 2). To assess the attractiveness, two recording points were settled 200 m away from each other and from studied underpasses to avoid recordings of same bat calls at multiple recorders: one recording point on the road edge without underpass and one in the same habitat present within underpass (Fig. 2). Three recording points were dedicated to evaluating the underpass use: one within the road structure in the middle of the underpasses and two on both road edges above the underpasses (Fig. 2). As Batloggers are omnidirectional recorders and therefore cannot distinguish between bats effectively crossing roads and bats simply active in the vicinity of the roads, our sampling design provided the proportion of bats using the underpasses from those in proximity to the underpasses (real road-crossing above underpasses or not).

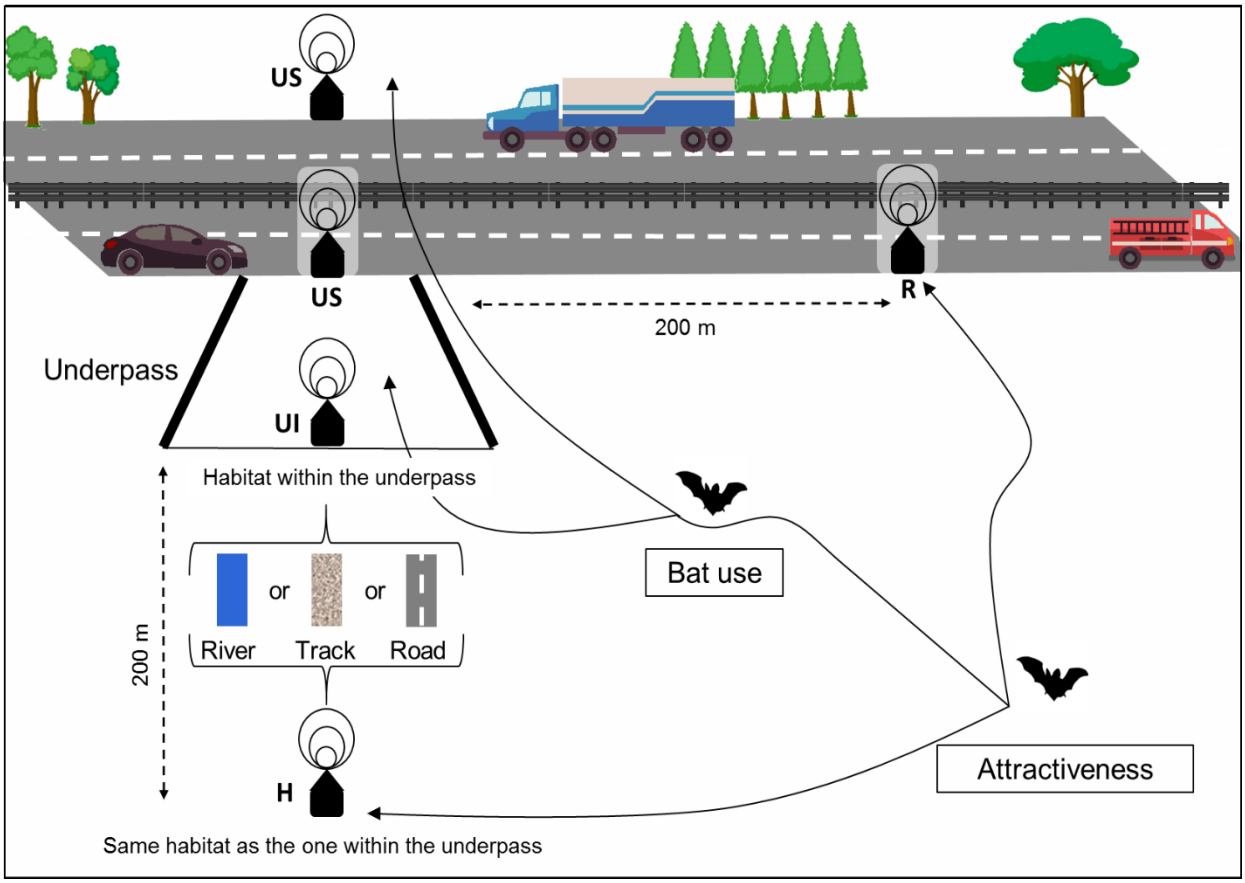

Figure 2 - Scheme of sampling design indicating the locations of the different recorders for each studied underpass. We installed one recorder under the underpasses (UI) and two recorders at each road edges above the underpasses (US) to assess bat use. We also installed two recorders at 200 m from the underpasses: one in the adjacent habitat (H) and one at a road section without underpass (R).

2.4. Bat recording and identification

We simultaneously surveyed three underpasses from at least two different forest classes (i.e., 15 deployed detectors) for three consecutive full nights. Each recorder was programmed to start recording ultrasound calls half an hour before sunset and to end half an hour after sunrise. The sampling was carried out between 1 July and 13 August 2018, corresponding to (i) the seasonal peak of bat species activity in the study region, as recommended by the French national bat-monitoring program 'Vigie-Chiro' (http://www.vigienature.mnhn.fr/), (ii) the parturition time which is an important period for conservation of bats and (iii) one of the seasonal peaks in bat mortality from vehicle collisions (Fensome and Mathews, 2016; Medinas et al., 2013). Recordings were only performed when there was no rain, the wind was below 30 km/h and the ambient temperature above 12 °C. If we had at least one night with more than two hours of rain, we started again the three days of recording.

We identified bat call sequences to species using an acoustic automatic classifier software *Tadarida* (Bas et al., 2017). Then, we used Syrinx software version 2.6 (Burt, 2006) to manually check the identification of the bat passes from the classifier at the genus level. To make identification as unambiguous as possible and to make error risk negligible, we considered groups of similar species, mostly based on their echolocation call types, which greatly limits potential misidentification issues (Millon et al., 2015). *Rhinolophus* spp, *Plecotus* spp and *Myotis* spp are considered as gleaners foraging in clutter environments (Arlettaz et al., 2001). Despite the different genus, we opted for creating a composite group of *Pipistrellus/Miniopterus* spp whose echolocation calls are very similar (Medinas et al., 2019). *Pipistrellus/Miniopterus* spp are considered as aerial hawkers foraging mostly on flying preys in open spaces (Dietz et al., 2009; Holderied and von Helversen, 2003). We conducted analyses at the species level only for *Barbastella barbastellus,* a typical edge-foraging species which produces very distinctive calls (Obrist et al., 2004).

For each group of species, we defined the response variable as the number of bat passes during three consecutive nights (named 'bat activity'), where one bat pass was defined by one or several echolocation calls during a 5 second interval (see e.g., Azam et al., 2016). This time interval is considered as a good compromise in regard to the mean duration of all bat species passes (Kerbiriou et al., 2018).

Using Syrinx software version 2.6 (Burt, 2006), we also checked and evidenced that very few echolocation calls were simultaneously detected above and within the underpasses (<0.02% of the total bat passes for a given group of species) and that this negligible overlap only concerned *Rhinolophus* spp and *Barbastella barbastellus*.

2.5. Data analysis

We modelled the activity for each bat group separately, using Generalized Linear Mixed Models (GLMMs). Models were fitted using a negative binomial error distribution with a log link function to take into account the over-dispersion of our data (Zuur et al., 2009). Underpass attributes, road characteristics and landscape predictors were included in these models as fixed factors while 'underpass' was included as a random effect to account for the non-independence of the five spatial replicates among each underpass. To assess differences in bat activity between locations of recording points, we used 'location' as an extra predictor: H (Habitat), UI (Underpass Inferior), US (Underpass Superior), R (Road), see Fig. 2. In the models, we assigned two different weights depending on the location of the recording points: 1 for H, UI, R (always one recording point of each location in the landscapes) and 0.5 for US (always two recording

points of this location in the landscape, see Fig. 2). Among our 11 predictors (Table 1), all the continuous variables were centered and rescaled (with a mean of 0 and a standard deviation of 1) to achieve a set of unit-free predictors that are directly comparable and to aid model fitting (Ashrafi et al., 2013). Then we used a forward stepwise procedure to identify the subsets of predictors with the highest performance, and further select the best final model according to its best fit to the data using the Akaike Information Criterion corrected for small samples (AICc) (Mac Nally et al., 2018). We assessed the quality of our best models by comparing it to the null model using AICc and the likelihood-ratio chi-squared test (Mac Nally et al., 2018).

To assess underpass use and attractiveness for each group of species, we compared bat activity levels between the different locations of recording points in the landscape. Hence, at each step of the model selection procedure, we ran the models twice: (1) once with the predictors in interaction with the factorial variable "location" and (2) then again with all the same predictors in addition to "location" as follows:

*(1) Bat activity ~ location * environmental predictors+ 1|site*

(2) Bat activity ~ location + environmental predictors + 1|site

This also allowed us to dissociate the predictors that influence bat activity differently between locations (interactive effect) from the predictors that affect bat activity similarly between locations (additive effect). To avoid multicollinearity of predictors in the models, we evaluated the correlations between variables using Pearson's coefficient to detect obvious correlations (Zuur et al., 2009). Only variables with correlation coefficients between -0.70 and 0.70 were included simultaneously in the models (Dormann et al., 2013). All the statistical analyses were carried out in R (v3.5.1; R Development Core Team, 2011) using packages "glmmTMB" and "DHARMa".

To assess the use and attractiveness of underpasses, we applied two different ratios (symmetric around 0) adapted to our sampling design:

$$Underpass\ use = \frac{pUI - pUS}{pUI + pUS}$$

$$Underpass\ attractiveness = \frac{\frac{pUI + pUS}{2} - pH\ (or\ pR)}{\frac{pUI + pUS}{2} + pH\ (or\ pR)}$$

where *p* is the predicted activity of bats from models for each locations (UI; US; H or R). The ± 95 % confidence intervals of the ratios have been calculated from 100,000 bootstrap

iterations (Manly, 1997), based on the values of the estimates and the variance-covariance matrix of the GLMMs.

Differences in bat activity among location of recording points and the response curves of the predicted activity for each location used to calculate the ratios are presented in Appendix A and B, respectively (see Table 2 for ratio interpretations). A threshold of 10% was used to define the range of values considered as ecologically irrelevant (i.e., indicating no significant difference in bat activity; see Abbott et al 2012a).

Table 2 - Interpretation of ratio values used to assess underpass use and attractiveness for bats

Ratio values	Use	Attractiveness compared to adjacent habitat	Attractiveness compared to unequipped road sections
1	100% of individuals were recorded within underpasses but none above it	100% of individuals were recorded in the vicinity of underpasses but none in the adjacent habitat	100% of individuals were recorded at road sections with an underpass but none at unequipped road sections
Between 0.1 and 1	Significant bat preference for using underpasses	Significant underpass attractiveness for bats	Significant underpass attractiveness for bats
Between -0.1 and 0.1	No significant preference	No significant attractiveness	No significant attractiveness
Between -0.1 and -1	Significant bat avoidance of underpass interiors	Significant bat preference for adjacent habitat	Significant bat preference for unequipped road sections
-1	100% of individuals were recorded above underpasses but none within it	100% of individuals were recorded in the adjacent habitat but none close to underpass	100% of individuals were recorded at unequipped road sections but none at road sections with underpass

3. RESULTS

3.1. Total bat activity and species recorded

We recorded 114,618 bat passes at 111 recording points (9 recording points failed) spread over 24 landscapes/underpasses. The group *Pipistrellus/Miniopterus* spp represented 90.6% of the total bat passes and was recorded at 100% of recording points, these values were respectively 6.1% and 89.0% for *Myotis* spp, 1.0% and 57.6% for *Barbastella barbastellus*, 0.4% and 54.9% for *Rhinolophus* spp and 0.3% and 60% for *Plecotus* spp.

3.2. Myotis spp

Forest cover and hedgerow length had significant negative effects on the attractiveness of underpasses in comparison with adjacent habitats for *Myotis* spp: along the gradients, the ratios decreased respectively from 0.6 to -0.2 for forest cover and from 0.9 to -0.7 for hedgerow length (Fig. 3). From 3% to 28% of forest cover in the surrounding landscape, *Myotis* spp activity was

significantly higher at roads with underpasses than at adjacent habitats. However, their activity reversely became higher at adjacent habitats than at underpasses from 38% of forest cover onwards (Fig. 3). By contrast, *Myotis* spp were more active at underpasses only when landscapes included between 6 and 15 km of hedgerows and became more active at adjacent habitats beyond 17 km of hedgerows (Fig. 3).

For *Myotis* spp, road sections with underpasses were always more attractive (i.e., roads with underpasses displayed more activity) than adjacent road sections without underpasses (i.e., R points) along the gradients of forest cover and hedgerow length (Fig. 3). While the attractiveness of road sections with an underpass increased with forest cover (from 55% to 85% of bat passes recorded at road sections with an underpass), it decreased with hedgerow length from 90% to 55% (Table 3 and Fig. 3).

Myotis spp were always significantly more active inside than in the vicinity of underpasses along the respective gradients of forest cover and hedgerow length (Fig. 3). Landscape-scale forest cover increased underpass use by *Myotis* spp (from 50% to 70%) but hedgerow length decreased it (from 80% to 20%; Fig. 3). For *Myotis* spp, underpass use and attractiveness were not affected by local predictors. However, the habitat within the underpasses impacted significantly the total activity (all recorded points combined) of *Myotis* spp, which ranged from the highest to lowest in the following order: river under bridge > river under culvert > track > road (Fig. 5).

3.3. Rhinolophus spp

For horseshoe bat, distance between underpass and the nearest forest patch decreased the attractiveness in comparison with adjacent habitats but did not affect attractiveness in comparison with road sections without underpass (Fig. 3). Underpasses height did not affect attractiveness in comparison with adjacent habitats but slightly increase attractiveness in comparison with adjacent road sections without underpasses (Fig. 4).

Distance to the nearest forest patch strongly decreased underpass use by *Rhinolophus* spp (from 0.9 to -1.0), which moreover used preferentially underpasses when located at a distance not exceeding 260 m from the nearest forest patch (Table 3 and Fig. 3). Between 260 m and 600 m from the nearest forest patch, horseshoe bat activity was higher around underpasses than within it (Fig. 3).

At local scale, underpass height had a significant negative effect on their use by horseshoe bats (the predicted ratio decreasing from 0.8 to -0.4; Fig. 4). It is predicted that most horseshoe bats would use underpasses preferentially when their height lies between 2.5 and 4.7 m (Fig.

4). As for *Myotis* spp, the habitat within the underpasses impacted significantly the total activity of *Rhinolophus* spp which is the highest when there was a river under a bridge (Fig. 5).

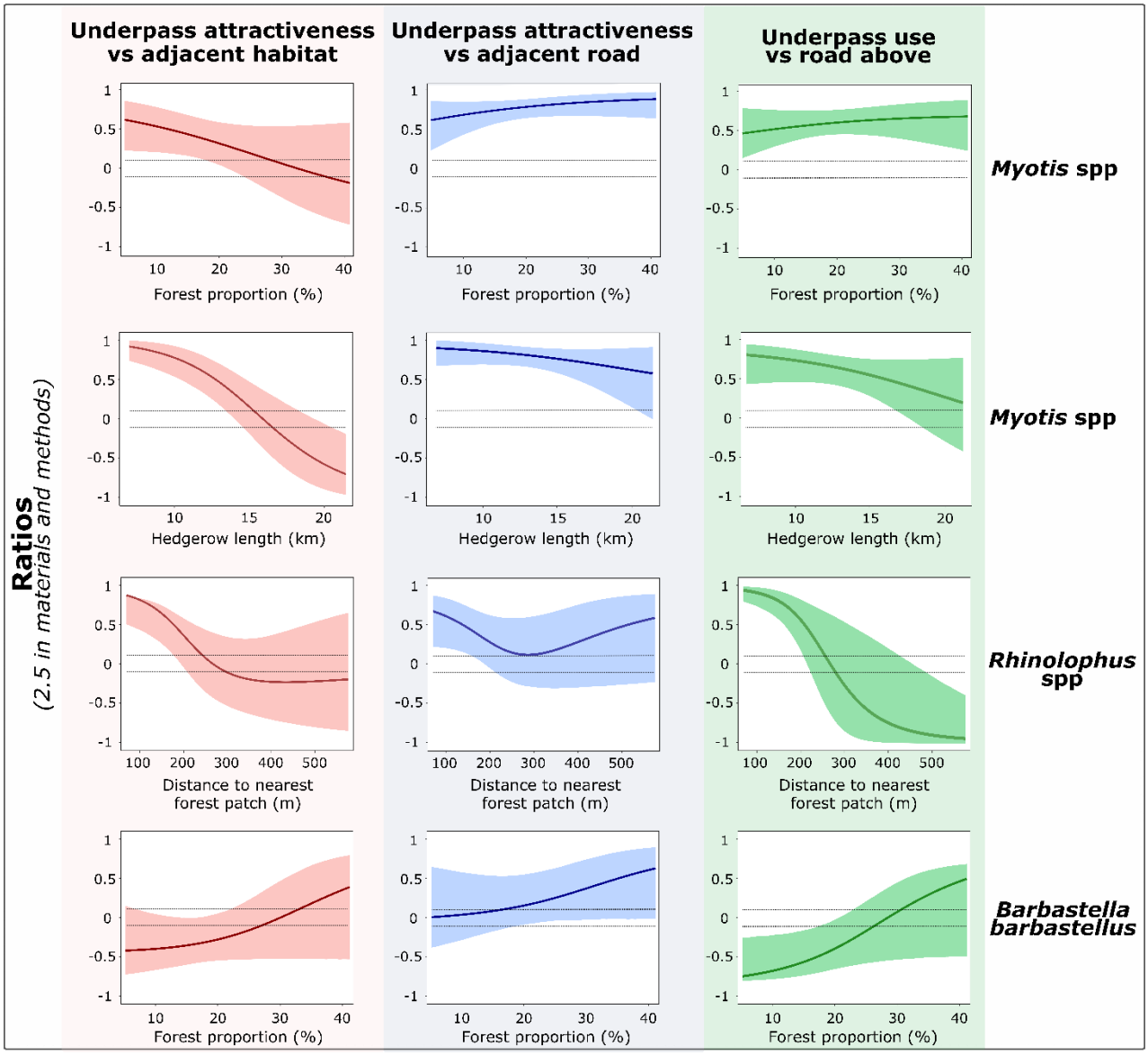

Figure 3 - Ratios of road underpass use and attractiveness for bats in response to landscape context calculated from the predictions of Generalized Linear Mixed Models. The ± 95 % confidence intervals of the ratios have been calculated from 100,000 bootstrap iterations based on the values of the estimates and the variance-covariance matrix of the GLMMs. The two parallel dotted lines represent the range of values considered as ecologically irrelevant.

3.4. Barbastella barbastellus

For barbastelle bat, forest cover significantly increased underpass attractiveness in comparison with adjacent habitats (from -0.4 to 0.4; Table 3 and Fig. 3). Barbastelle bat activity was higher at adjacent habitats when forest cover was between 3 and 28% while the reverse was found in landscapes with more than 32% of forest (Fig. 3).

Landscape-scale forest cover also increased underpass attractiveness in comparison with road sections without underpass (from 0.0 to 0.6; Table 3 and Fig. 3). We did not find a significant ecologically relevant difference in barbastelle bat activity between road sections with or without underpass, in landscapes with forest proportion ranging between 3 and 18%. Beyond 18% of forest in the surrounding landscape, barbastelle bats were more active around underpasses than at road sections without underpass.

Landscape-scale forest cover increased underpass use by *B. barbastellus* (from -0.85 to 0.5; Fig. 3), which only used preferentially underpasses in landscapes with more than 30% of forest (Fig. 3). For this species, underpass use and attractiveness were not affected by local predictors.

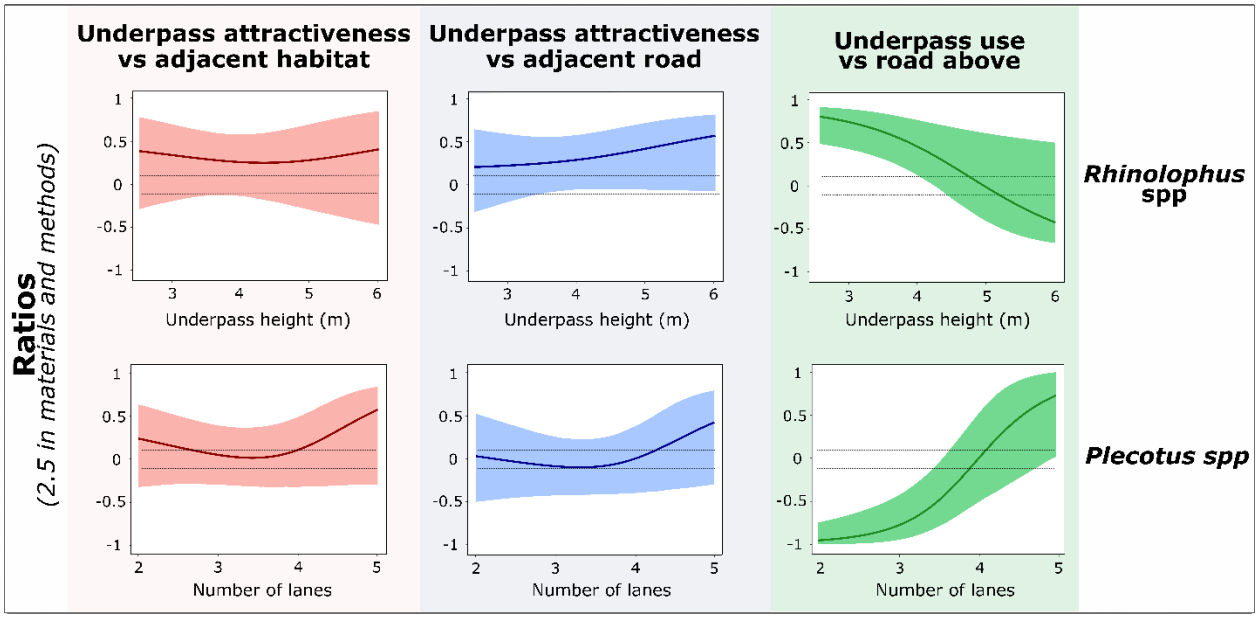

Figure 4 - Ratios of road underpass use and attractiveness for bats in response to local road underpass attributes calculated from the predictions of Generalized Linear Mixed Models. The ± 95 % confidence intervals of the ratios have been calculated from 100,000 bootstrap iterations based on the values of the estimates and the variance-covariance matrix of the GLMMs. The two parallel dotted lines represent the range of values considered as ecologically irrelevant.

3.5. Plecotus spp

Landscape context did not affect underpass use and attractiveness for *Plecotus* spp, whose total activity decreased significantly with distance to the nearest water body. Long-eared bat activity also increased significantly with the contrast in forest cover between the two sides of the underpasses/roads (Appendix C).

At local scale, the number of road lanes above the underpasses did not significantly influence underpass attractiveness for long-eared bats when compared with both adjacent

habitats and road sections without underpasses (Fig. 4). By contrast, long-eared bats used underpass more when the number of lanes was higher (ratio increasing from -0.9 to 0.7): they tended to avoid underpass interiors below four road lanes and used preferentially underpasses beyond four lanes (Fig. 4).

3.6. Pipistrellus/Miniopterus spp

Landscape context significantly influenced neither underpass use nor attractiveness for the *Pipistrellus/Miniopterus* group (Table 3). However, the habitat within the underpasses impacted significantly the total activity of this group of species: it was highest when there was a river under a bridge (no significant difference with tracks) and the lowest when there was a road (bridge and culvert combined) or a river under a culvert (Fig. 5).

For all the relationships detailed above, the AICc value of the best model was at least 14.8 points lower than the corresponding null model and likelihood-ratio chi-squared tests between the best and null models were systematically significant (Table 3).

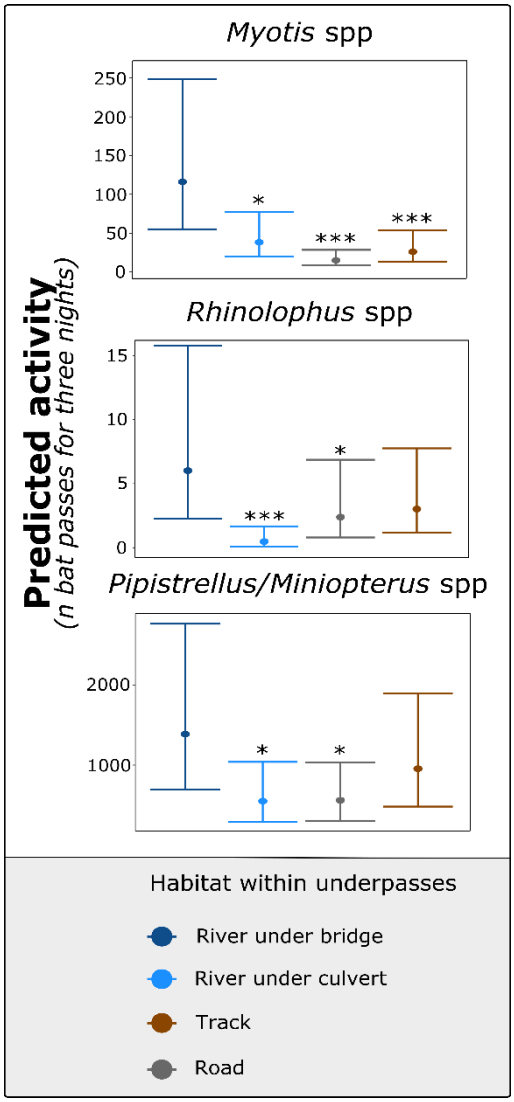

Figure 5 - Effect of local habitat within underpasses on total bat activity (all locations of recording points combined) for three groups of species: *Myotis* spp and *Rhinolophus* spp and *Pipistrellus/Miniopterus* spp, Predictions were obtained from Generalized Linear Mixed Models (GLMMs) fitted with a negative binomial error distribution and a log link function. Dots represent the means and the error bars show 95% confidence intervals. Bat activity at rivers under bridges were used as the reference (i.e., intercept) in each model (***P <0.001; **P <0.01; *P <0.05).

Table 3 - Estimates ± SE and χ^2 values from AIC-based selection of best models for each bat species groups and *Barbastella barbastellus* (* = P <0.05; ** = P <0.01; *** = P <0.001). Estimates and standard errors were obtained from a multiple comparison test (ANOVA) and χ^2 values from a Wald test.

Scale	Predictors	*Myotis* spp		*Plecotus* spp		*Pipistrellus/ Miniopterus* spp		*Rhinolophus* spp		*Barbastella barbastellus*	
		Estim. ± SE	Chisq	Estim. ± SE	Chisq	Estim. ± SE	Chisq	Estim. ± SE	Chisq	Estim. ± SE	Chisq
Local	**Location of recording point**	UI 5.66 ±0.55***	49.14***	US 1.18 ±0.54**	0.32	UI 7.65 ±0.46***	27.90***	UI 2.52 ±0.68***	18.69***	H 1.78 ±0.49***	7.9*
	Habitat within underp.	RB 4.40 ±0.41***	24.69***	-	-	RB 7.43 ±0.36***	7.44*	RB 1.53 ±0.44***	19.52***	-	-
	Height	-	-	-	-	-	-	-	10.02**	-	-
	Lanes	-	-	-	1.09	-	-	-	-	-	-
Landscapes	**Hedgerow length**	-	4.80*	-	-	-	-	-	-	-	-
	Hedgerow contrast	-	-	0.42 ±0.19*	4.5*	-	-	-	-	-	-
	Forest cover	-	0.87	-	-	-	-	-	-	-	3.30*
	Dist. to forest	-	-	-	-	-	-	-	0.09	-	-
	Dist. to water	-	-	-0.73 ±0.22***	11.04***	-	-	-	-	-	-
Interaction	**location:Lanes**	-	-	UI 1.60 ±0.79*	9.18*	-	-	-	-	-	-
	location:Height	-	-	-	-	-	-	H -0.81 ±0.44* UI -1.20 ±0.68* R -1.16 ±0.71*	6.76*	-	-
	location:Forest cover	H 0.68 ±0.26**	7.9*	-	-	-	-	-	-	UI 1.54 ±0.73*	5.07
	location:Dist. to forest	-	-	-	-	-	-	UI -1.97 ±0.86**	12.60**	-	-
	location:Hedgerow length	H 0.42 ±0.27* UI -1.06 ±0.47**	16.14**	-	-	-	-	-	-	-	-
	Δ AICc	40.8		14.8		23.9		21.5		28.7	
	Chisq	95.5***		26.1**		34.1***		47.6***		36.8***	
	R^2m (R^2c)	0.68 (0.75)		0.63 (0.70)		0.23 (0.37)		0.70 (0.76)		0.26 (0.89)	

Bat activity recorded at adjacent habitat (H), at road sections without underpass, within (UI) and above underpasses (US). RB means the modality "River under Bridge". Δ AICc = difference of AICc values between the best and the null models; Chisq = likelihood-ratio chi-squared test between the best and the null models; R^2m = marginal coefficient of determination; R^2c = conditional coefficient of determination.

4. DISCUSSION

4.1. Landscape context matters to determine underpass use and attractiveness for bats

Our study validates our predictions that taking into account the landscape context greatly enhances the road underpass use and attractiveness for bats, as previously shown for other road-sensitive taxa (Carr et al., 2002; Clevenger and Waltho, 1999). More precisely, the present study showed that landscape contexts conditioned the locations of bat commuting routes along and across a given road. This main result is consistent because landscape configuration is a key driver of bat movements through the 'landscape complementation' process allowing bats to access different non-substitutable critical resources across different habitats within the landscape mosaic (Dunning et al., 1992; Ethier & Fahrig, 2011). As expected, we found that the effects of landscape context on underpass use and attractiveness for bats are species and guild specifics. More specifically, we found significant effects for gleaners and clutter-adapted species such as *Rhinolophus* spp and *Myotis* spp, as well as for *Barbastella barbastellus*, but not for *Plecotus* spp and *Pipistrellus/Miniopterus* spp. Forest cover, hedgerow length and distance to the nearest forest patch were the major landscape attributes significantly influencing bat attractiveness and use of underpasses, likely because wooded elements are often used by bats for commuting between roosting and foraging sites (Boughey et al., 2011; Downs and Racey, 2006; Entwistle et al., 1996; Nicholls and Racey, 2006; Russ and Montgomery, 2002; Verboom and Huitema, 1997). Wooded landscape elements are also known to provide acoustic navigational landmarks for species with limited perceptual range using echolocation (Holderied et al., 2006; Jensen et al., 2005; Verboom and Spoelstra, 1999) but also important food resources (i.e., insects), shelter from wind, roosting sites and protection against avian predators (Ekman and de Jong, 1996). Forests are therefore key roosting and foraging habitats for most European bat species and greatly influence presence, abundance and diversity of bat communities at the landscape scale (Arroyo-Rodríguez et al., 2016; Charbonnier et al., 2016; Fuentes-Montemayor et al., 2017; Heim et al., 2015).

4.1.1. Underpass attractiveness

Contrary to our prediction that road underpass attractiveness for bats would decrease with increasing forest cover and total hedgerow length, we found that forest cover increased underpass attractiveness in comparison with road sections without underpasses for *Myotis* spp and *B. barbastellus*. On the contrary, hedgerow length reduced this attractiveness for *Myotis* spp which is in line with our initial predictions. We thus suggest that increasing hedgerow density at the landscape scale provides more potential commuting routes for bats to cross a

given road, limiting the attractiveness of underpasses. In addition, it is likely that changing commuting routes for safer crossing roads using new underpasses is less costly for bats in a forest-dominated matrix than in an agricultural matrix (Abbott et al., 2012b; Kerth and Melber, 2009; Krull et al., 1991).

Our finding that forest cover decreased road underpass attractiveness in comparison with adjacent habitats for *Myotis* spp but increased it for *B. barbastellus* is supported by a radio-tracking study by Kerth and Melber (2009). In a forest context, they found that a smaller proportion of *Myotis bechsteinii* effectively crossed the motorway in comparison with barbastelle bats. They thus suggested that in a forest habitat context, roads acted more as a barrier to foraging movements for *Myotis bechsteinii* than for *B. barbastellus*. Furthermore, previous findings also indicated that, in less forested landscapes including small forest patches, most *Myotis* individuals forage regularly outside forests, thus increasing their home range size and the probability of crossing roads during their nightly movements (Kerth et al., 2002). Other studies have shown that gleaning bat activity and species richness decreased when approaching roads (Berthinussen and Altringham, 2012a; Claireau et al., 2019; Kitzes and Merenlender, 2014; Zurcher et al., 2010). This seems particularly true in woodland habitats because, as interior forest foragers, gleaning bats tend to avoid the vicinity of roads with lower tree cover and lower prey abundance than in the adjacent habitats (Fensome and Mathews, 2016; Medinas et al., 2019). Thus, we assume that these specific *Myotis* activity patterns resulted from a combination of different ecological mechanisms, i.e., smaller home-ranges in forest contexts, road-related barrier effects, increased activity with distance to roads and higher prey abundance in adjacent habitats, all leading to fewer road crossing events for *Myotis* spp in a forest context. The decrease in underpass attractiveness in comparison with adjacent habitats with the increase in total hedgerow length for *Myotis* spp could also result from the same ecological mechanisms, since hedgerows are known to be very important landscape features for foraging and commuting individual movements for these species (Dietz et al., 2009, 2013; Duvergé and Jones, 1994; Fonderflick et al., 2015; Froidevaux et al., 2017). In addition, in agricultural landscapes with few hedgerows left, roadside verges are often the only remnants of suitable semi-natural habitats providing corridors and foraging opportunities for a large number of taxa in the immediate roadside vicinity (Augusto et al., 2016; Davies and Pullin, 2007; Penone et al., 2012; de Redon et al., 2015).

4.1.2. Underpass use

In accordance with our prediction that bat use of road underpasses would increase with surrounding forest cover and total hedgerow length, we found that forest cover significantly increased the use of underpasses by *Myotis* spp and *B. barbastellus*. In landscapes with low forest cover, wooded elements are reduced to small patches or tree lines, where bats depend on edge effects between trees and open habitat matrix (and potentially so in the vicinity of underpasses) for foraging or commuting without the need of crossing a road, contrarily to forest landscapes with sharp edges acting as corridors (Roemer, 2018). Previous works studying the effect of landscape context on bat mortality (Lesiński, 2008, 2007, Lesiński et al., 2011a, 2011b; Medinas et al., 2013), on bat collision risk related to vehicle collisions (Roemer, 2018) or on bat activity at road verges (Berthinussen and Altringham, 2012a; Medinas et al., 2019) have shown that bats are much more likely to cross roads (and therefore to use underpasses) in forest-dominated landscapes. These landscapes actually host more specialist bat species such as *Myotis* spp or *B. barbastellus*, both for roosting and foraging (Charbonnier et al., 2016; Dietz et al., 2009; Lesiński, 2007). Thus, even if the proportion of individuals flying in the vicinity of underpasses does not vary among different landscapes, an increase in forest cover would augment the proportion of individuals flying through road underpasses (Kerth and Melber, 2009; Lesiński, 2007). We also found that along the gradient of forest cover, and unlike *B. barbastellus*, the proportion of *Myotis* individuals crossing roads through underpasses was always higher than around underpasses, which was congruent with previous studies (Abbott et al., 2012a, 2012b). Most of the *Myotis* spp actually forage at low flight heights in forest understory whereas *B. barbastellus* is more an edge specialist (Dietz et al., 2009), for which it is likely that landscape contexts will modulate flight height in a greater extent than for *Myotis* spp (Müller et al., 2013; Roemer et al., 2017).

Contrarily to our initial predictions, we found that increasing the total length of hedgerows in the surrounding landscape decreased the use of underpasses for *Myotis* spp. Although counterintuitive, this observation could result from the fact that in presence of hedgerows, *Myotis* bats would fly higher and therefore use less frequently underpasses to cross roads. The configuration of adjacent matrix habitats, including the presence of hedgerows or small woods, actually influences bats' tendency to fly across open grounds such as roads (Abbott et al., 2012a). As expected, the distance between underpasses and the nearest forest patch also decreased significantly underpass use by horseshoe bats. This result is consistent with the fact that horseshoe bats are reluctant to fly in open fields most of the time (Dietz et al., 2009). It is also congruent with previous studies suggesting that increasing distance to surrounding woody

elements decreased bat crossing frequency (Abbott et al., 2012a; Bennett and Zurcher, 2013; Roemer, 2018; Russell et al., 2009).

4.2. Local road underpass attributes can influence their use and attractiveness for bats

Underpass use by *Rhinolophus* spp decreased with entrance height, in accordance with Abbott et al., (2012b). Horseshoe bats habitually mate or roost in caves and other underground structures during various parts of their life cycle and are thus presumably more confident to predation risk in narrow environments. They also display specific adaptations to use small underpasses in regard to their specific flight maneuverability and echolocation call types (Abbott et al., 2012b; Glover and Altringham, 2008; Mcaney, 1999). While underpass height had no effect on attractiveness compared to adjacent habitats for horseshoe bats, it slightly increased attractiveness in comparison with road sections without underpasses. This suggests that the largest underpasses concentrated more horseshoe bat individuals without improving the safety of road-crossings.

Long-eared bats used underpasses according to the number of road lanes above the structure, especially when roads included four lanes or more. Considering that the number of lanes on roads is a good proxy of traffic volume, such a result could indicate a negative response to an increasing traffic volume which is known to greatly change bat flight behavior (Zurcher et al., 2010). Bats actually avoid the zones with the high collision risk probably because they recognize the danger triggered by vehicles (Roemer, 2018). For instance, Zurcher et al., (2010) found that 60% of bats approaching a road reversed their flight in the presence of a vehicle. Such a result could also come from a direct effect of road width: the wider a road is and the longer the time needed to cross and the higher the risk of vehicle collision or predation for low flying species such as *Plecotus* spp. The absence of similar activity patterns for other gleaning/low-flying species may be explained by *Plecotus* spp being able to cross more often roads without using an underpass in a greater extent of road dimension, while they would preferably use underpasses only at high traffic volume (Abbott et al., 2012b). Thus, our results tend to confirm that road avoidance behavior is bat guild-specific (Medinas et al., 2013).

Although the type of habitat within the underpasses did not influence their use and attractiveness, this environmental predictor had a significant effect on the total activity (all locations of recording points combined) of *Myotis*, *Rhinolophus* and *Pipistrellus/Miniopterus* species. We found that, for these three groups of species, the activity was highest when there was a river within the underpasses, an expected result since that wetlands are known to provide important food resources for bats (Korine et al., 2016; Straka et al., 2016). We also recorded

more activity for these groups when there was an agricultural track rather than a minor road within the underpasses. We explain this by the fact that agricultural tracks provide more food resources through grassy track borders than roads. In addition, roads negatively impact bat activity trough different effects (i.e., direct mortality, higher collision risk with vehicles, disturbance related to light and noise pollution, habitat and food resource loss) making them much more unsuitable than tracks.

4.3. Implications for bat conservation

According to our results, we suggest that taking into consideration habitat composition and configuration at landscape scale should be done systematically in the earliest stages during road construction planning to identify the best locations to set up underpasses and optimize their efficiency for bat conservation purposes (Thorne et al., 2009; van der Ree et al., 2011).

Underpasses are the most attractive and used in the most forested landscapes for *B. barbastellus* and *Myotis* spp (except for the comparison with adjacent habitats for the latter group), in the agricultural landscapes with the lower hedgerow density for *Myotis* spp, and when the underpasses are the closest to a forest patch for *Rhinolophus* spp. Underpasses are therefore useful for bat conservation not only in natural, forest-dominated landscapes, but also in human-transformed landscapes dominated by intensive agriculture. This has important consequences for bat conservation in the current context of worldwide biodiversity loss with agricultural intensification (Newbold et al., 2015). We especially showed that when underpasses are accurately located in landscapes, they provide a useful tool for maintaining landscape connectivity and reducing road collisions for threatened bat populations (Voigt and Kingston, 2016). As the underpasses studied here were already settled for at least four years (see Table 1), and bats are long-lived mammals with very good knowledge of their home-ranges (Dietz et al., 2009), we suggest that the patterns of bat underpass use and attractiveness observed during our study actually resulted both from a previous behavioral adaptation of individuals living around roads, as well as from previous mortality events occurring during road early establishment. Yet, bat individuals may need a sufficient time lapse to learn which commuting routes are the safest to cross a new road when established, especially in forest-dominated landscapes where bat species pool, including threatened species such as *Myotis* spp and *B. barbastellus*, is the richest compared to agricultural habitats (Abbott et al., 2012b, Charbonnier et al. 2016). In other words, it is not because underpasses in forest landscapes seem to be more efficient to enhance local bat mobility through road network, that the existing populations in these landscapes have not experienced a previous decline related to road construction

(Zimmermann Teixeira et al., 2017). Furthermore, Roemer (2018) and Lesiński (2007) respectively showed that the proportion of bat low-height flights synonym of high collision risk with vehicles, and the incidence of road casualties were higher in the more forested contexts for most bat species. Thus, it should be preferable to limit road construction across continuous forests as much as possible, but if it is inevitable, the creation of underpasses should be systematic. Finally, the best conservation measure to improve connectivity for most bats as well as other taxa is to vary the dimensions of underpasses for a given road in different landscape contexts, with a particular attention to high-traffic road sections in large forests (Abbott et al., 2012b; Carr et al., 2002; Bhardwaj et al., 2017).

Previous studies have shown that roads and their verges can become ecological traps increasing the risk of road kills for some species (Bernes et al., 2016), leading some authors to recommend to create suitable habitats for bats away from roads (Berthinussen and Altringham, 2012b; Medinas et al., 2019). According to our results, we could recommend to conserve hedgerows only when occurring close to underpasses in agricultural landscapes. Yet, it is likely that underpasses could act as an ecological trap or, at least, could increase the ecological trap effect of a road, especially in particular landscape contexts. As demonstrated in this study, underpasses can be largely attractive for bats, thus questioning the fact that, by enhancing landscape connectivity for bat movements, bat mortality would be systematically and significantly reduced. Furthermore, our results have shown that the same landscape or local features may have opposite effects on underpasses attractiveness and use.

Actually, the attractiveness of underpasses in comparison with adjacent habitats can depend on either a local effect of resource accumulation (Villemey et al., 2018), a barrier effect, or a convergence effect to use underpasses to access required habitats. Further studies including e.g., BACI experiments and long-term temporal monitoring of bat mortality, landscape genetics and acoustic trajectography, are now needed to assess the potential ecological trap effect created by the attractiveness of underpasses for bats (Carr et al., 2002; Claireau et al., 2019a), especially to assess the spatial extent at which underpass attractiveness acts. Despite using only two recording points per landscape to assess attractiveness, we already found significant effects which make our results likely conservative. In addition, the effectiveness of underpasses to reduce population-level road impacts and ensure their viability is still unknown but remains one of the fundamental measures of mitigation success, irrespective of how many individuals actually cross a road through an underpass (Carr et al., 2002; van der Ree et al., 2011, 2007). To improve conservation recommendations for road establishment and landscape planners, further empirical studies are also needed to quantify the separate effects of traffic mortality and

landscape connectivity loss on population persistence (Carr et al., 2002). For instance, Jackson and Fahrig (2011) found, by simulations, that mitigation measures that minimize mortality on roads (such as fences) should more effectively promote genetic diversity and so population viability than measures that attempt to promote connectivity (such as underpasses).

5. CONCLUSIONS

Our study is the first to demonstrate the preponderant influence of landscape context on underpass efficiency to maintain landscape connectivity for bats, for a wide range of road dimensions. By disentangling underpass use from attractiveness, we provide detailed knowledge on how building an underpass can impact bat activity and mobility in space, thus highlighting the importance of incorporating a landscape-scale approach in the decision-making process of underpass location during road project planning. We finally suggest that underpasses should be established in a wide range of landscapes with a particular attention on forest and intensive agricultural landscapes where they seem to be the most efficient to safely facilitate bat movements. Wooded elements such as forest patches and hedgerows are the key components of the landscape to be taken into account for road location planning scheme. Although underpasses are rarely built primarily for animal conservation, we advocate for searching the best trade-off between human and wildlife needs when selecting their optimal establishment in mosaic landscapes.

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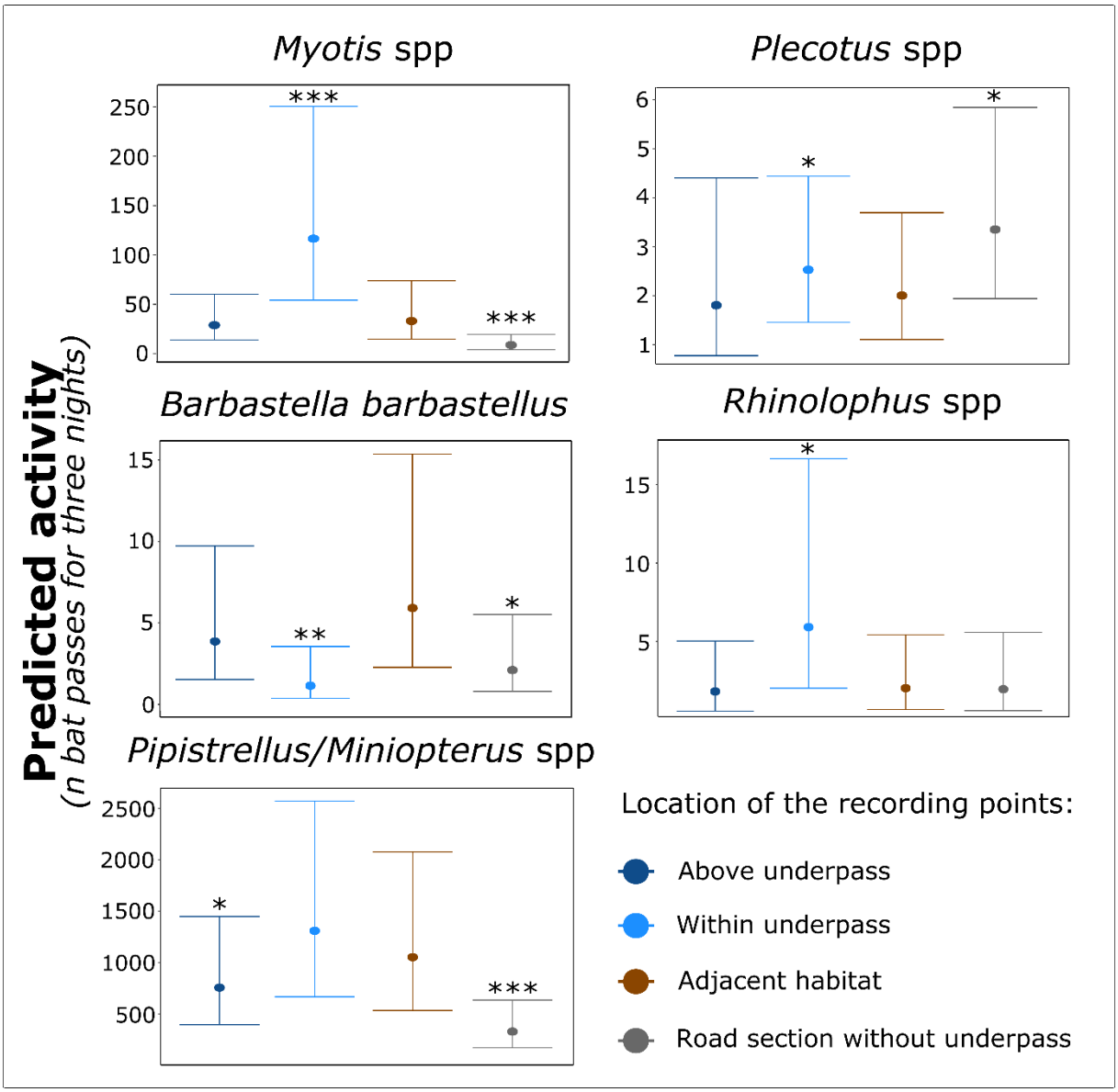
Appendix 4

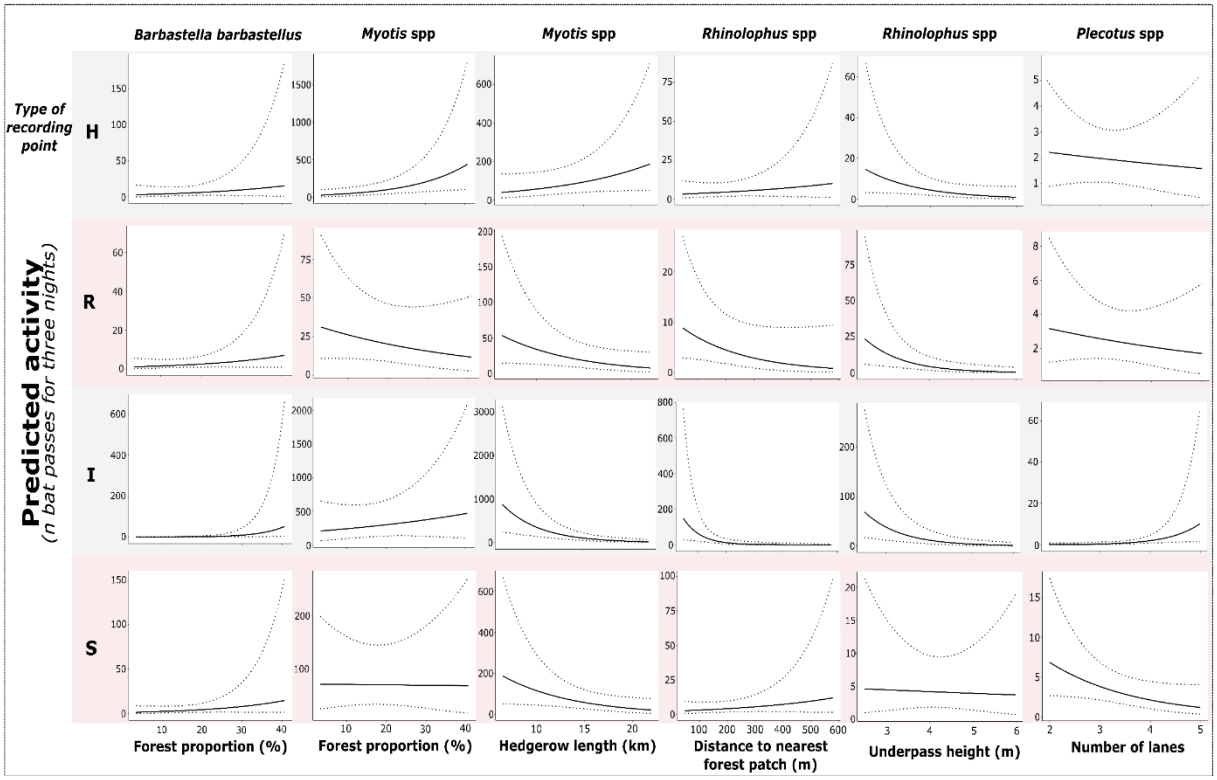
Appendix A.

Boxplots of predicted bat activity for three consecutive nights at each of the 4 locations of recording points. Predictions were obtained from Generalized Linear Mixed Models (GLMMs) fitted with a negative binomial error distribution and a log link function. Dots represent means and error bars show 95% confidence intervals. Bat activity at adjacent habitats were used as the reference (i.e. intercept) in each model (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$).



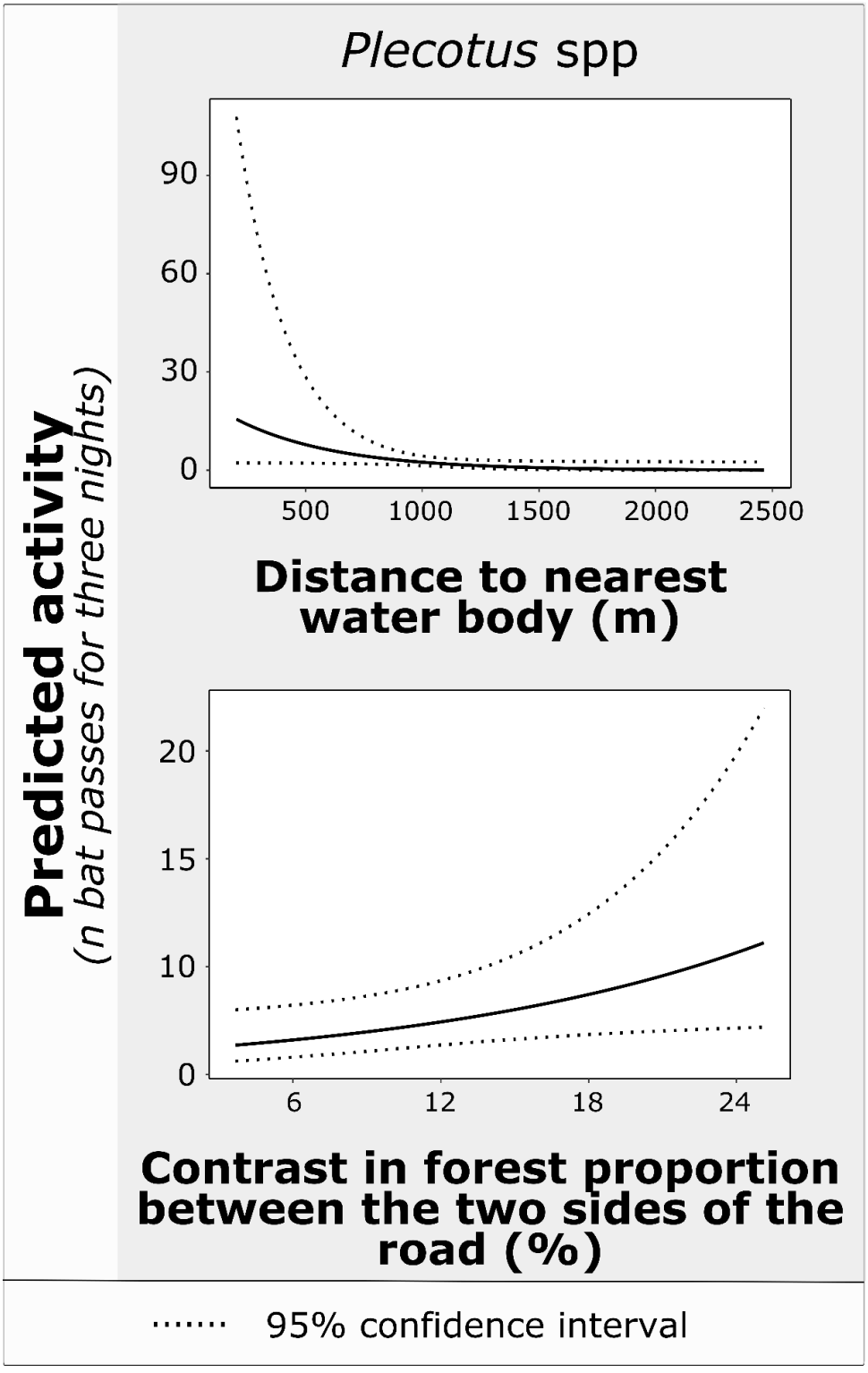
Appendix B.

Response curves for predicted bat activity at each location of recording points for three nights along the different studied environmental gradients (dotted lines represent the 95 % confidence intervals). Predictions were obtained from Generalized Linear Mixed Models (GLMMs) fitted with a negative binomial error distribution and a log link function.



Appendix C.

Response curves for predicted global long-eared bat activity (all locations of recording points combined) for three nights along two landscape gradients: distance to nearest water body from a given underpass ($P < 0.001$) and the contrast in forest proportion ($P < 0.05$). Predictions were obtained from Generalized Linear Mixed Models (GLMMs) fitted with a negative binomial error distribution and a log link function.



GENERAL DISCUSSION

1. Bat responses to multiple drivers of anthropization

1.1. Impacts of roads on bats

In the present work, I documented for the first time that road network (i.e., road density) can act as an environmental filter by significantly reducing functional and phylogenetic bat diversity in temperate landscapes. This environmental filter caused by road network has also been documented on other taxa such as invertebrates, fishes and birds (Carpio et al., 2009; Dambros et al., 2013; Laurance, 2004; Maitland et al., 2016; Schlacher et al., 2008; Vander et al., 2008). I also showed that bat communities are likely to be affected by road density in a wide range of landscapes and ecosystems, even in the most urbanized landscapes (chapter 3). The present work therefore contributes to strengthen the scientific evidence suggesting that road density contributes to the overall biotic homogenization of the biodiversity related to landscape anthropization (Devictor et al., 2008; Gámez-Virués et al., 2015; McKinney, 2006).

However, I showed that road density impacts bat activity differently depending on the amount and fragmentation of forests (chapter 1). Furthermore, the analysis I conducted at the species-level revealed that road density has a positive or neutral effect on open- and edge-space species but a negative effect on clutter-space species, i.e. forest specialists. Several likely underlying processes and mechanisms could explain these patterns. First, road expansion is likely to affect bats according to species traits and therefore modify interspecific interactions (e.g., competition for food). For example, open- and edge-space species may be able to take advantage of insect-prey accumulation above and more generally in the vicinity of roads (due to light and higher dusk temperature of paved surfaces) more than clutter-space species (Claireau et al., 2019). However, this food accumulation is unlikely to compensate habitat loss induced by road network, even for the most generalist species. Alternatively, road expansion may result in a larger decrease in the amount of foraging areas for clutter-space species than for open- and edge-space species (Mathews et al., 2015). Second, as clutter-space species fly lower and slower, they are more vulnerable to mortality caused by vehicle collision when crossing a road (Fensome & Mathews, 2016). Thus, road density may have a higher impact on survival and population size for clutter-space species than for open- and edge-space species. Third, I showed in chapter 1 that barbastelle bats were more abundant in sites further away from a road, suggesting that roads may act as a barrier effect to bat movement, as previously shown for other European bat species (Berthinussen & Altringham, 2012b; Claireau et al., 2019; Medinas et al., 2013, 2019). Finally, I showed in chapter 4 that road underpasses can be markedly used and attractive, which confirms once again that roads represent a threat during bat movement and

thus a potential barrier effect. Unfortunately, the analysis of the published radio-tracking data from Europe and North-America did not confirm such behaviours (i.e., movements deducted from acoustic data gathered at different locations) and the suggested barrier effect (see Chapter 2). However, we should be cautious with this last result as landscapes included in this review covered a gradient of road density probably too narrow to detect any effects. Recent publications bring some support to the barrier effect hypothesis. For instance, Voigt et al. (2019) recently found that GPS tracked common noctules, an open-space insectivorous species, commuted most often far away from roads (> 500 m) regardless of the level of illumination or vegetation.

1.2. Impacts of light pollution on bats

In chapter 3, I documented three very distinct response of bat species to light pollution: positive, negative and hump-shaped response. Like road density, ALAN (i.e., Artificial Light At Night) seems to favour open- and edge-space species at the expense of clutter-space species (Blake et al., 1994; Russo & Ancillotto, 2015; Rydell, 1992; Threlfall et al., 2011). At the lamp scale, because of their relatively fast and high flying, open- and edge-space species can access more easily to high concentration of prey resources in open spaces (Polak, Korine, Yair, & Holderied, 2011; Zeale et al., 2018). Where light-opportunistic species are advantaged, competition for food might contribute to the decline of light-averse species with similar diets (Arlettaz, Godat, & Meyer, 2000). ALAN could therefore alter the balance of species interactions in lit environments (Davies, Bennie, Inger, de Ibarra, & Gaston, 2013), generating temporal and spatial asynchronies between lit and unlit areas of prey and predator activity among ecosystems and landscapes (Eisenbeis, 2006; Stone et al., 2015). This could cause top-down and bottom-up trophic effects as demonstrated, e.g. on invertebrate populations (Bennie et al., 2018). The present work therefore contributes to strengthen the scientific evidence suggesting that ALAN (i.e., Artificial Light At Night) may be a driver of biotic homogenization of bat communities (Mathews et al., 2015).

ALAN is known to have distinct effects on bats depending on the scale considered. For instance, although some bat species, such as *Pipistrellus pipistrellus*, *Nyctalus noctula*, *Vespertilio murinus* and *Eptesicus nilssonii*, can take advantage of outdoor lightings, at least when foraging (Blake et al., 1994; Russo & Ancillotto, 2015; Rydell, 1992), the same species bypass illuminated commuting routes (Hale et al., 2012, 2015) and drinking sites (Russo et al., 2017) and respond negatively to light pollution at the landscape scale (Azam et al., 2016). Thus,

ALAN can substantially reduce habitat quality and disconnect habitats (Hale et al. 2012, 2015; Mathews et al., 2015) even for the most urban-adapted species, whereas they can take advantage for foraging locally. It thus suggests that the main negative impact of ALAN on bats may be due to landscape connectivity reduction. Chapter 3 offers potential avenues to mitigate this negative impact by showing that lowering illumination may re-establish landscape connectivity for bats. This seems to be particularly true in urban areas, where ALAN is most prevalent with an annual growth rate of 6% per year (Hölker, et al., 2010) and where bats still persist, facing numerous different threats (Russo & Ancillotto, 2015).

So far, information from behavioural studies assessing the effect of light pollution on bat movement is scarce, because following individual movement in the most urbanized landscapes is challenging (Voigt et al., 2019). In chapter 2, I tried to explore the effect of the Human Footprint Index (that takes into account and thus is correlated with light pollution) on bat movement. However, during the exploratory analysis of the review chapter, we realized that the great majority of radio-tracking studies on temperate bats occurred in the least light-polluted landscapes. This probably explains why I could not find any effect of the Human Footprint Index on bat movement. However, it is important to note that a study recently published using GPS loggers in the Berlin metropolitan area on 20 equipped individuals of common noctule bats (*Nyctalus noctula*) has managed to test two predictions developed in the article presented in chapter 3: (1) light reduction may re-establish habitat connectivity for bats in urban landscapes; and (2) open-space species may take advantage of the illuminated areas in an urban context (Voigt et al., 2019). They found that common noctules tolerated ALAN only when foraging next to bodies of water or « well vegetated areas », but avoided ALAN when commuting. Furthermore, they demonstrated that dark corridors were used by common noctules for commuting and thus likely improved the permeability of urban landscapes. In conclusion, they confirmed that dark corridors are key for connecting patchily distributed foraging areas in the urban matrix, as previously suggested by article presented in chapter 3.

1.3. Forest habitat: an opportunity to improve mitigation measure for bats

In chapters 1 and 2, I provided new evidence for the strong relationship between landscape structure and bat diversity and movement, respectively. This relationship has been the postulate for methodological approaches used in the two other chapters. Indeed, we hypothesized that landscape would play a significant role in the efficiency of conservation measures such as

wildlife crossings (chapter 4) and wildlife-friendly lighting schemes (chapter 3). These two chapters allowed filling knowledge gaps previously identified in the literature. For instance, previous studies on the influence of light reduction on bats had focused on the distance effect, illuminance thresholds (Azam et al., 2018) or emission spectra (Kuijper et al., 2008; Zeale et al., 2018) but none had focused on the potential importance of the landscape context. Similarly, previous work on road underpass use by bats addressed the importance of structure dimensions (e.g., height and width), structure type (e.g., bridges vs culvert) (Abbott et al., 2012; Bhardwaj et al., 2017) and the local vegetation presence at the entrance (Berthinussen & Altringham, 2012a) but none assessed whether these effects were influenced by the landscape context. By integrating ecological processes at the landscape level, the present work provided knowledge that will contribute to better predict the efficiency of mitigation measure and to improve bat conservation.

This work also provided new evidence on the key role of forest habitat for bat communities. I have shown very important relationships between forest habitat and bats, and more particularly the numerous benefits of forest for bats. These relationships may represent an opportunity to reduce and limit the negative influence of urban-related factors such as road and light on bats. First, preserving intermediate amount of forest habitat and intermediate number of forest patches within landscapes could help maintaining optimal taxonomic, functional and phylogenetic diversity. This may help mitigating the biotic homogenization of bat communities induced by road density, as suggested in chapter 1. Second, increasing the amount of forest habitat at the landscape level may reduce distances between bats roosting and foraging sites and therefore may reduce the mortality risk from roads, the increasing predation risk in lit open areas and ultimately the cost of stressful movement across the landscape matrix. Third, forest habitat may improve the efficiency of conservation measures by reducing the financial cost while optimizing their benefits to bats. For instance, work conducted in chapter 3 revealed that reducing light in urban woodlands is one of the most efficient strategy to improve landscape connectivity. Indeed, tree cover can amplify the negative effect of street lamps, and species most dependent on forests are also the most light-averse species (Straka, Wolf, Gras, Buchholz, & Voigt, 2019). Work conducted in chapter 4 showed that road underpasses are all the more attractive and used when they are located in a landscape mainly covered by forests, as tree cover provides excellent commuting routes to access underpasses (Boughey et al., 2011).

However, the interactive effects of forest habitat and road network on bats may be complex. On the one hand, I have shown that forest habitat (both its amount and configuration) can reduce

the negative road density effect on bats. On the other hand, I have shown that road density may modify bat communities within forest patches, suggesting that road network could alter forest ecosystem functioning (Laurance, 2004). First, roads can change insect-prey communities (Carpio et al., 2009; Dambros et al., 2013). Second, by favoring aerial hawkers at the expense of gleaner bats (i.e., forest-specialized species), roads may contribute to alter species-interactions at forest patches, reduce regulation of defoliating insects by gleaner bats (Charbonnier, Barbaro, Theillout, & Jactel, 2014), and ultimately the vegetative dynamics of the forest habitats. However, I did not find significant interactions between the road network and the amount and/or configuration of the forest (landscape scale) on bat diversity, suggesting a complex threefold interaction between road network, forest amount/configuration at the landscape scale, and the habitat type at forest patch (for instance, forest edge and interior). Regarding road underpasses, other studies have shown that the behavior (flight height) of bats above tree-lined roads was more at risk of collisions with vehicles (Roemer, 2018). Although this may primarily apply to the road network, which directly and routinely causes mass mortality among bats (Fensome & Mathews, 2016), it is necessary to ensure that roads and their related-structures (e.g., underpasses) do not act as an ecological trap in specific landscape contexts such as forests.

Similarly, research on the effect of light pollution on bats also highlights complex and interactive links between ALAN and forest cover. For instance, Straka et al. (2019) found that tree cover dampened the negative effect of street lamps (without UV) on open-space bats of the genera *Nyctalus, Eptesicus*, and *Vespertilio*, yet it amplified the preexisting negative or positive effect of street lamps (with or without UV) on *Pipistrellus pipistrellus*, *P. pygmaeus*, and *Myotis* spp. Furthermore, Voigt et al., (2019) helped clarifying these different response patterns, revealing that common noctule bats (i.e., open-space species) were foraging in areas with high levels of ALAN but that these were also well vegetated (and water bodies). This pattern may be explained by the fact that tree cover offsets the increased predation risk associated with light conditions, or the fact that lamps adjacent to trees are particularly insect-rich (Voigt et al., 2019). Alternatively, there could be other benefits from flying close to trees, such as favourable microclimate, which could outweigh any disadvantages associated with lighting (Mathews et al., 2015). However, while urban woodlands are crucial for urban bats (i.e., for roosting, foraging and commuting) not all bat species can take advantage of these sites for foraging when they are lit (Straka et al., 2016; Voigt et al., 2019). This underpins the importance of minimizing artificial light at night close to vegetation, to reduce additional key habitat loss particularly for

bats adapted to spatial complexity in the environment (i.e., clutter-space species), and to increase dense vegetation in urban landscape to provide, besides roosting opportunities, protection against ALAN for open-space bats to commute in city landscapes (Hale et al., 2012, 2015; Straka et al., 2019).

To summarize, this thesis advocates for minimizing road construction and street lamps where tree cover is preponderant, in any type of landscapes. However, when social, economic and political priorities will overpass conservation purposes, measures such as underpasses, friendly-street lamps (e.g., emission spectra, illuminance and direction) or friendly-lighting schemes should be considered, in particular close to forest, tree lines or isolated trees. More generally, the present work points out the low value of heavily anthropized areas for bat, even for open-space bat species (Gili, Newson, Gillings, Chamberlain, & Border, 2019; Voigt et al., 2019). Thus, urban expansion accompanied by strategies such as protecting and creating bat-friendly habitat could provide mitigation for the negative effects of urbanization. Any opportunities to increase dark woodland surface, even discontinuously, should be encouraged. This would especially contribute to the development of sustainable urban expansion for bats (Gili et al., 2019; Mimet, Kerbiriou, Simon, Julien, & Raymond, 2020). Landscape anthropization and its different components (e.g., urban expansion, roads and lighting) are likely to contribute to biotic homogenization on bat communities but probably not by providing more favorable conditions for common/generalist species, such as pipistrelles, as previously and commonly proposed (Arlettaz et al., 2000), but by affecting less detrimentally generalist species than habitat-specialists (Mathews et al., 2015).

2. Research perspectives and conservation challenges

2.1. Further steps to improve road mitigations

When roads have to be built, the location of the road and associated underpasses should be chosen in order to increase the highest mitigation level. This requires knowledge of the relevant landscape context, identification of involved processes as well as information on distribution and movement of species of concern (Carr et al., 2002). Work conducted in chapter 4 provided one of the first evidences for the importance of properly locating underpasses within the landscape. However, further work should be conducted to improve our understanding of the role of landscape influence on underpass efficiency. Further studies should include additional predictors such as forest configuration (e.g., number of forest patches) and the Shannon

diversity of the matrix, both known to facilitate landscape complementation, a key process for bats (Ethier & Fahrig, 2011). This will help identify landscapes in which underpasses construction is most important. Furthermore, it is very likely that landscape context influences underpass use and attractiveness at a greater extent than 1 km (the only scale tested in chapter 4) and at different spatial scales regarding species movement capacity (Ethier & Fahrig, 2011). Furthermore, empirically estimating the scale of effect using a multi-scale study design would contribute to improving future conservation efforts (Jackson & Fahrig, 2015; Moraga, Martin, & Fahrig, 2019), but also our capacity to assess at what extent underpass attractiveness applies to bats. This would help to better apprehend the effectiveness of underpasses to reduce population-level road impacts, which remains one of the fundamental measures of mitigation success, irrespective of how many individuals actually cross a road through an underpass (Carr et al., 2002; van der Ree, Jaeger, van der Grift, & Clevenger, 2011; van der Ree et al., 2007). GPS and radio-tracking designs could be useful to refine the potential attractive effect from underpasses and its spatial extent, and should be ideally tested in a large range of landscape types. Investigating the extent of spatial attraction of underpasses to bats could help to derive an optimal mitigation strategy, such that landscape connectivity could be restored for the largest number of species at the lowest possible cost (i.e., the smaller number of underpasses for a specific road). The goal would be to predict the optimal distribution of underpasses for a given set of species, a given type of road and a given landscape context, while avoiding ad hoc solutions from complex multispecies and multi-scales planning strategy for each road development (Carr et al., 2002). Furthermore, in a socio-political context of restricted funding allocated to biodiversity conservation, it is urgent to assess the number and density of wildlife crossings needed to maintain landscape connectivity and population viability in landscapes fragmented by roads. Thus, future studies should take into account underpass density along roads as a comprehensive landscape predictor.

Studies conducted on different types of roads (from highways to minor roads) all found that bat activity increased with distance to the nearest road (Berthinussen & Altringham, 2012b; Claireau et al., 2019; Medinas et al., 2016, 2019). This suggests that roads induce a barrier effect regardless of the traffic level, probably because bats recognize the danger triggered by vehicles (Roemer, 2018; Zurcher, Sparks, & Bennett, 2010). However, vehicle traffic density is likely to influence the barrier effect induced by roads on bat movement. Similarly, the type of roads and whether roads are impervious to individual bat crossings is likely to have an effect too. Traffic is expected to be a better predictor than road density because it integrates the road

sizes as well as the traffic volume on those roads (Carr et al., 2002). As a result, further studies should take into account the direct effect of traffic density on bats whenever data are available. Disentangling pure road effects from pure traffic effects and their relative importance on bats should improve our global understanding of mechanisms underlying the impact of road expansion on bat communities. From a conservation perspective, it would allow predicting the traffic threshold above which underpasses would be particularly efficient as conservation measures. For instance, in chapter 4, I found that *Plecotus* spp. used underpasses primarily when the above-road included four lanes or more, suggesting that underpasses are used according to the traffic volume. Under what conditions would the impact of one large road be less important than that of several smaller roads? Or under what conditions would the impact of one road with high traffic volume be less detrimental to bats than that of several similar roads with low traffic volume? The answers to these questions would certainly depend on the road-effect zone, which is known to vary among species and landscapes. Building a new road rather than expanding an existing road to improve road traffic flow may be more costly but resulting in more-efficient human travel (Carr et al., 2002). Scientific studies on whether avoiding new road construction is an overall benefit to regional bat populations are sorely needed (van der Ree et al., 2011).

2.2. Towards a more holistic vision for bat conservation

Road expansion and light pollution each have dramatic impacts on bat communities, as well as interactive effects. Additionally, they are often combined with other complex landscape changes resulting from increased human density. The synergistic effects of road expansion and light pollution must now be considered alongside other threats that operate simultaneously, such as habitat loss, habitat fragmentation, agricultural intensification, and increased urbanization (Mathews et al., 2015; van der Ree et al., 2011). For instance, while we know that landscape context can modulate collision risk with vehicles for bats (Roemer, 2018), we do not know how additional road lightings would magnify or mitigate that risk. Yet, bats appear to rely on vision in lit conditions despite their limited capability for fine spatial resolution in bright light: experiments have shown that bats to have an increased propensity to collide with objects in light compared with dark conditions, even though there was no change in their echolocation patterns (Mathews et al., 2015; Orbach & Fenton, 2010). Furthermore, Voigt et al. (2019) found that the common noctules selected dark areas when commuting close to roads, suggesting interactive effects of roads and lights on bat activity, both depending on the landscape context.

Recent advances in conceptual background in landscape ecology have advocated for a more holistic view of the landscapes when studying synergistic or antagonistic effects of habitat loss and fragmentation processes on biodiversity (Fahrig, 2017; Fletcher et al., 2018; Presley et al., 2019). The positive or negative effects of fragmentation on biodiversity remains deeply debated (Fahrig, 2019; Püttker et al., 2020). Previous research has confirmed that matrix quality can strongly influence biodiversity in fragmented landscapes, and suggests that managing the matrix to benefit biodiversity could be surprisingly straightforward (Ruffell, Clout, & Didham, 2017).

Road expansion and light pollution as well as other components of global changes influence multiple dimensions of bat communities, populations, and individual behaviours. Exploring the importance of intra-specific and heterospecific social information and biotic interactions on population and communities dynamics, and how they are affected by land use changes, represents a very promising avenue to improve our global understanding of the effects of global changes on bats (Brambilla et al., 2019; Gil, Hein, Spiegel, Baskett, & Sih, 2018). Since insectivorous bats constantly emit ultrasonic species-specific echolocation calls when flying, they provide a constant flow of inadvertent social information to others who can decode that acoustic information (Lewanzik et al. 2019). For instance, Lewanzik et al. (2019) started to reveal valuable mechanisms within social information and inter- and intra-specific interactions. First, they found that activity reduction is a very widespread response to high conspecific activity, performed by most insectivorous bats while high feeding acoustic activity indicates large insect-prey density (Gager, 2019; Racey & Swift, 1985). This suggests that high conspecific activity makes dense prey clusters unprofitable due to pronounced intraspecific competition. Second, they demonstrated that increased competition for prey cannot be the only reason for social information effects on bat activity because bats also reduced activity when broadcasting calls from species of other foraging guilds that feed on different prey species than the eavesdropping bat. A comprehensive understanding of how bats incorporate social information into their decision-making will help researchers explaining species distribution patterns and unravelling mechanisms of communities structuring (Gil et al., 2018; Lewanzik et al., 2019). There are also indications of heterospecific attraction depending on prey and/or bat density, and transmission of foraging strategies between adult and young bats in field conditions have not been fully studied to date. Thus I would also briefly advocate here for studying potential positive and indirect social interactions (i.e., non-feeding interactions) between and within bat species (Kéfi et al., 2012). Furthermore, a detailed knowledge about the multifaceted

intra- and interspecific interactions within bat communities is highly relevant for conservation measures and ecosystem management because social information can have demographic consequences and alter population as well as community dynamics (Gil et al., 2018; Lewanzik et al., 2019). Particularly in a context of rapid and widespread anthropization of landscapes, social transmission of information about resources or danger can influence how populations respond to environmental change (Gil et al., 2018; Lewanzik et al., 2019). For instance, understanding how artificial lighting influences intra- and inter-specific interactions among bats is of particular importance to know to what extent bat community and diversity are altered (Zeale et al., 2018).

2.3. Evidences for bat population persistence

Consequences of the barrier effect induced by roads and lights on individual movements has been a long standing issue in ecology, especially their consequences on long-term bat population future (Altringham & Kerth, 2015; Carr et al., 2002; van der Ree et al., 2011, 2007). Indeed, barrier effect and their consequences are of major concern for bat conservation. Roads and lights, by acting as a barrier to movement, may limit the flow of individuals between populations with two major consequences. First, barriers may slow the recovery of local populations after a sharp decline since recruitment of individuals from neighboring populations ("rescue effect") will be reduced and this will further increase the probability of local extinction (Brown & Kodric-Brown, 1977; Opdam, 1991; Wilcove, McLellan, & Dobson, 1986). Secondly, barriers may also reduce gene flow between populations and increase inbreeding, reducing individual fitness and increasing the risk of local extinction (Kindlmann & Burel, 2008; Turner, 2005). A genetic isolation such as this can only occur with very low levels of natal dispersal. These factors may only be significant for rare bat species that already have small and fragmented populations, whatever the exact driver of their rarity (Sykes, Santini, Etard, & Newbold, 2019). Genetic isolation as a direct result of roads and lights has not been studied in bats, although they may be important drivers of evolutionary change (Tomassini, Colangelo, Agnelli, Jones, & Russo, 2014). In several other (but non-flying) mammal species, an effect of roads on genetic population structure has been found (Frantz et al., 2012). For example, Gerlach & Musolf (2000) have shown that populations of bank vole are genetically different either side of a four-lane highway. However, even in bat species such as Bechstein's bat (*Myotis bechsteinii),* for which barrier effects of motorways have been shown to occur in the summer habitat (Kerth & Melber, 2009), local populations living in an area with several motorways

show only weak genetic differentiation (Kerth, Mayer, & Petit, 2002; Kerth & Petit, 2005). Furthermore, population genetic studies on other temperate zone bats typically found no or very little evidence for genetic isolation at the regional scale (Moussy et al., 2013; Tournayre et al., 2019), despite the dense road network and high levels of light pollution in Europe and North America. Although previous studies suggested, at least in the temperate zone, that roads probably have no significant effect on gene flow in most bat species, further studies are clearly needed to clarify this (Altringham & Kerth, 2015). ALAN has rarely been considered as a driver of evolution (Hopkins et al., 2018) but few recent studies suggested that it may be an important genetic force and thus a driver of evolutionary change for bats (Tomassini et al., 2014) but also for moth species (Altermatt & Ebert, 2016), a key prey item for bats (Ter Hofstede & Ratcliffe, 2016). As a consequence, ALAN has the potential to explain broad patterns of population differentiation across landscapes (Altermatt & Ebert, 2016; Hopkins et al., 2018).

2.4. A conservation research directed towards practitioners and society

Temporal variations in bat activity following road expansion need to be urgently addressed to truly assess whether conservation measures can maintain long-term landscape connectivity for populations. Furthermore, to fully distinguish the pure road effect from the pure traffic effect, long temporal surveys of the effect of road traffic variations on bat activity are urgently needed (for instance, it is expected that road traffic is the highest during the summer, when bats are also the most active and mobile). However, this critical research need has never been addressed to date, probably because such large temporal scales (i.e., several years) are not compatible with most postgraduate programs, i.e., MSc or PhD theses, or short-term research contracts (van der Ree et al., 2011). To remedy to the time-constrained research context and conduct research at the relevant time-scale, partnerships between conservation research and conservation practitioners (as the "Conservatoire d'Espaces Naturels de Midi-Pyrénées", CENMP for instance) represent a unique opportunity (Laurance et al., 2012). During my PhD, I benefited from several opportunities to work with bat specialists from the CENMP to improve their bat sampling designs and adjust their field protocols to their specific questions. For instance, the CENMP is actually involved in a long-term survey of temporal bat activity during every steps of road constructions and after roads are put into service, as an offset measure funded by road agency and piloted by government policy makers in the framework of an Environmental Impact Assessment (EIA). Yet, long-term impact of roads has never been studied by the scientific community to date. Furthermore, much conservation action is still

guided by personal intuition and guesswork more than by scientific evidence (Milner-Gulland et al., 2012; Sutherland, Pullin, Dolman, & Knight, 2004). Thus, such partnerships should provide more scientifically rigorous studies for conservation practitioners and produce more valuable data for conservation researchers, i.e. a win-win relationship. This kind of relationship should be particularly valuable because, in far too many cases, the EIA process for road developments is too weak and potentially flawed and detrimental to bat conservation (Fearnside, 2007; Laurance et al., 2012).

After reviewing the conservation assessment literature and then conducting a survey with the authors, Knight et al. (2008) concluded that two-thirds of the conservation assessments published in the peer-reviewed scientific literature did not deliver any true conservation action. The majority of conservation scientists are in academic positions and have limited interactions with conservation practitioners and managers that furthermore have generally no time to keep connect with the new results constantly published (Laurance et al., 2012; Milner-Gulland et al., 2010). To improve the relationship between scientists and wildlife managers, PhD theses funded in the framework of specific programs of collaborations between research laboratories and private companies, governmental organizations or NGOs (e.g., CIFRE program in France) represent an interesting and efficient tool. Obviously, multiplying diverse tools and approaches to reconnect between 'what is interesting' (conservation research needs) and 'what is important' (conservation practitioners and political decision maker's needs) is needed to broaden both the scope and impact of conservation research. Furthermore, reducing the negative influence of landscape anthropization on bats and overall biodiversity will only be possible if novel approaches to engage citizens is achieved (Kobori et al., 2016; van der Ree et al., 2011). Citizen science, by allowing data collection at spatial and temporal scales unachievable otherwise, and by engaging the public in authentic and collaborative science, can (1) improve our capacity to understand and thus to respond to environmental challenges such as biodiversity loss and ecosystem degradations; and (2) allow citizens to better support community decisions and societal change (Kobori et al., 2016). In the case of bats, citizen science has already permitted to gather enough new data and to make scientists able to better specify population trends and spatial distributions (Barlow et al., 2015; Newson, Evans, & Gillings, 2015) and to study the effects of broad scale urban expansion (Gili et al., 2019) and light pollution (Azam et al., 2016). Citizen science programs such as the French national bat-monitoring program 'Vigie-Chiro' have therefore a great potential for improving bat conservation. In order to contribute to this ambitious large-scale bat-monitoring program, all acoustic data gathered during this PhD thesis

were integrated to the program. In 2018, this data represented about 10 % of the national database.

Regarding, the effect of light pollution, ALAN is related to multiple social, economic and political uses (e.g. security enhancement of goods and people, activities of the night-time economy, architectural aestheticism, city marketing and promotion). The negative effects of ALAN on biodiversity are therefore at the heart of complex interactions between wildlife conservation and human societies (i.e., "conflict of interests"; Challéat et al., In Prep.; see Appendix 5). The concept and development of dark ecological networks, connected areas without artificial lighting across the landscapes (Lacoeuilhe et al., 2014), has often been expressed as necessary and relevant for bat conservation (Azam et al., 2016; Mathews et al., 2015; Zeale et al., 2018). It now requires a more integrated conservation and interdisciplinary approaches, paying attention to the multiple uses, both human and non-human, of nocturnal space and time (Challéat et al., In Prep.; see Appendix 5) for successful conservation (Campbell, 2005). Indeed, the routine protection of darkness for its contribution to biodiversity, through the dark ecological network, will always be confronted to "the real world" and therefore needs a social-ecological approach, which aims to (re)define the nocturnal living space that a society agrees to share with biodiversity. A new approach is emerging, which brings together the tradition of ecological research with that of sociology and geography (Barreteau et al., 2016; Campbell, 2005). In other words, experimental sciences and social sciences are making progress in bringing their analytical questions and methods closer together (Challéat et al., In prep.; see Appendix 5). This scientific emergence has the potential to bring new horizons to develop required ecological solidarity within our societies (leading to a more general appropriation of ecological transition and biodiversity protection policies) and a profound consideration "of the community of destiny between human, society and his environment" (Mathevet, Thompson, Folke, & Chapin, 2016); essential to ensure the coexistence of humans and biodiversity in an increasingly anthropized world.

« *L'utopie n'est pas l'irréalisable mais l'irréalisé.* »

Théodore Monod

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Appendix 5

The dark ecological network as a socio-ecological framework to limit the impacts of artificial light at night on biodiversity: objectives and challenges

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ABSTRACT

Artificial light at night (ALAN) is nowadays recognized as a major anthropogenic pressure on the environment on a global scale, which is reflected in the notion of light pollution. Through its attractive or repellent effects, and its disruption of the biological clock on many animal and plant species, ALAN is emerging as a factor in the spatial and temporal fragmentation of ecosystems. Preserving the different components and interactions of ecosystems, therefore, requires that the spatial and temporal dimensions of the effects caused by ALAN be included in biodiversity conservation tools. The ecological network, i.e. the physical and functional sum of the natural elements which promotes landscape connectivity, provides a framework for integrated conservation of the darkness for its contribution to the ecological quality of the environment, paying attention to the multiple functions of use of nocturnal space and time, by humans and non-humans alike. Here we present the notion of a "dark ecological network". We demonstrate its ability to stem the effects of habitat loss and fragmentation caused by ALAN, its ability to integrate the temporalities of ecological processes into biodiversity conservation planning, and its vocation to trivialize the protection of darkness in land use planning. From an operational point of view, the challenge will be to translate the levers for reducing the impacts already identified into a political method for its 'territorialisation'. To achieve this objective, we propose a course of action that consists in building an interdisciplinary repertoire of knowledge (e.g. impacts on wildlife, human-lightscape relationship, existing legal tools), in order to deduce practical supports for the governance of the dark ecological network in response to societal and ecological issues.

KEYWORDS

Artificial light at night (ALAN); Darkness; Ecological network; Light pollution; Conservation sciences; Land-use planning; Social-ecological systems; Participatory processes

1. INTRODUCTION

The destruction, reduction, transformation or isolation of habitats profoundly affects the dynamics of populations, communities and ecosystems, as well as the viability of all ecological processes and therefore the level of biodiversity in environments [Soulé & Orians, 2001]. Based on this observation, many studies have highlighted the need to redirect the traditional conservation objectives of some remarkable sites and species towards more holistic concerns, both from the point of view of the species concerned and from the spatial point of view [Margules & Pressey, 2000; Hansen & DeFries 2007; Thompson et al., 2011]. To enable the landscape to function ecologically, the scale of ecological planning must be large enough to allow for the inclusion of connectivity [Fischer & Lindenmayer, 2007]. The concept of an ecological network has emerged in response to this need for renewed conservation policies and spatial forms of protection [Opdam et al., 2006; Boitani et al., 2007]. Its objective is to maintain or restore the ecological conditions necessary for ecosystems and populations to survive in a fragmented landscape. The strength of this concept, developed on the basis of the theories of island biogeography [MacArthur & Wilson, 1967] and population dynamics [Levins, 1969], is to allow "a shift away from the 'topologic' approach to conservation, involving only protected areas, and to the landscape 'chorological' approach, involving the whole territory" [Battisti, 2003, p. 241].

It is therefore essential to approach ecological networks from a twofold pragmatic perspective and within the framework of integrated conservation [McShane & Wells, 2004]: to combat the homogenization and fragmentation of habitats on the one hand [Jongman, 2002], and to integrate conservation theories into landscape and land use planning practices on the other hand [Opdam et al., 2006]. On this last point, Battisti [2003, p. 241] insists that "this planning must take into account the 'real world', whose interpretation needs a multidisciplinary approach [Haila, 1985; Soulé, 1986]: applied ecologists and wildlife managers will have to interact with landscape planners and politicians, although their languages are different."

In this perspective, the concept of the ecological network has established itself in the field of nature conservation [Bischoff & Jongman, 1993]. While debates on the effectiveness of ecological networks exist within the scientific community [Levêque, 2017], the concept has nevertheless achieved unprecedented social and political success [Jongman, 1995], particularly in Europe in a landscape context under strong human domination [Vimal et al., 2012]. The Pan-

European Biological and Landscape Diversity Strategy was thus initiated in 1995 by the European Ministers of the Environment in association with the United Nations and the Council of Europe [Jongman et al., 2004], with the primary objective of creating a Pan-European Ecological Network [Jongman & Pungetti 2004], i.e. a homogeneous and coherent network from a geographical and ecological point of view, consisting of core areas, corridors, restoration areas and buffer zones. Since the late 1990s, many European Union (EU) Member States have implemented a national ecological network planning policy [Jongman & Kristiansen, 2001; Bennett & Wit, 2001]. The EU is now seeking to harmonize these national policies and is working on the establishment of a Green Infrastructure (GI), defined as "a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services. It incorporates green spaces (or blue if aquatic ecosystems are concerned) and other physical features in terrestrial (including coastal) and marine areas. On land, GI is present in rural and urban settings [European Commission, 2013]." Like many current biodiversity conservation policies, those currently trying to implement ecological networks are based on a compromise between scientific knowledge on the one hand, and political and social issues related to the territories of action on the other hand [Alphandéry et al., 2012].

Current approaches to build ecological networks do not explicitly integrate the temporal dynamics of ecosystems: they are based only on material criteria with a daytime perception. However, if their planning claims to takes into account the "real world" [Battisti, 2003], ecological networks must necessarily consider the nocturnal dimension. Indeed, in this "real world" and to repel the daily arrival of darkness, societies deploy specific techniques, such as artificial light at night (ALAN) and more particularly lighting of outdoor spaces [Brox, 2015]. ALAN is a space planning tool that responds to multiple social uses — e.g. security enhancement of goods and people, activities of the night-time economy, architectural aestheticism, city marketing and promotion — but the degradation of the darkness it generates in and around urban areas is nowadays understood as a source of pollution in its own right, known as "light pollution" [Riegel, 1973]. The negative effects of ALAN are therefore at the heart of the complex interactions between the environment and societies that occur within anthropized nocturnal space-time.

Strongly linked to urbanization, outdoor lighting has grown by between 3 and 6% per year during the second half of the 20th century [Hölker et al., 2010]. Even today, light pollution is increasing in most parts of the world. Between 2012 and 2016, Earth's artificially lit outdoor

area have increased by 2.2% per year, with a radiance growth of 1.8% per year, and the brightness of continuously illuminated areas has increased by 2.2% per year [Kyba et al., 2017]. De facto, light pollution affects 23% of the global land surface, including 88% of the European surface area [Falchi et al., 2016]. Under the influence of aerosols suspended in the atmosphere, ALAN spreads beyond urbanized areas to protected areas and biodiversity hotspots [Guetté et al., 2018]. This growing anthropogenic pressure, therefore, contributes to global environmental change through multiple mechanisms, energetic, health, cultural and ecologic. Artificial lighting represents an important part of global energy consumption, with 20% of global electricity consumption and, on the same scale, 6% of CO2 emissions [UNEP, 2012] and about 3% of global oil demand [UNEP, 2017].

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

In sociocultural terms, the loss of natural darkness deteriorates several scientific [Riegel, 1973] and cultural amenities [Gallaway, 2010; Stone, 2017; Challéat & Poméon, 2019]. ALAN "closes the window" on the starry sky [Isobe et al., 1998] — one-third of humanity no longer sees the Milky Way [Falchi et al., 2016] — and makes opportunities for direct contact with a naturally dark environment rare events. In this, ALAN contributes to the extinction of the experience of nature [Pyle, 1978; Miller, 2005; Soga & Gaston, 2016] and fuels generational environmental amnesia [Kahn, 2002]. Cultural geography studies emphasize the extent to which darkness allows original forms of conviviality and intimacy, occupation of public spaces and perception of the world through senses other than sight [Edensor, 2013, 2015; Shaw, 2018].

In other words, and whatever the types of space in question, the darkness preservation provides access again to an array of experiences for the sensorial apprehension of the world.

Finally, ALAN produces many ecological disturbances [Rich & Longcore, 2006] and constitutes one of the least understood sources of perturbation affecting biodiversity [Gaston et al., 2015]. Altering the natural patterns of light and dark in ecosystems, especially day/night rhythm [Longcore & Rich, 2004; Navara & Nelson, 2007; Gaston et al., 2017], ALAN impacts a wide range of taxa from the scale of molecules to ecosystems, interactions between species and regulatory processes [Bennie et al., 2018; Knop et al., 2017; Hölker et al., 2010]. ALAN plays a large role in the activity and energy metabolism of birds and amphibians by altering the energy expenditure [Welbers et al., 2017; Touzot et al. 2019]. This physiological consequence of ALAN may have a long-term negative effect on the fitness of populations [Touzot et al. 2019]. ALAN also fragments landscapes, altering the ability of animals to move into and out of artificially lit areas [Hale et al., 2015]. Such fragmentations due to ALAN have genetic implications which have been recently proposed as a driver of evolution contributing to population differentiation across urban-rural landscapes [Hopkins et al., 2018]. The response of species to ALAN strongly depends on spatial scale, with e.g. positive effects on some bat species activity at the light scale [Blake et al., 1994; Azam et al., 2015, 2018] while strong negative effects of the radiance at the national scale. It was even shown that ALAN constitutes a threat for these taxa equivalent to other ones such as urbanization and agricultural intensification at large scale [Azam et al., 2016]. Such spatial and temporal perturbation of habitats and species could profoundly affect the dynamics of populations, communities, and ecosystem functioning as a whole.

At present, these effects, expressed through the fragmentation of natural habitats, are urgently needed to be taken into account in existing ecological planning tools as largely highlighted by recent studies [Azam et al., 2016, 2018; Pauwels et al., 2018; Laforge et al., 2019]. Among these planning tools, the ecological network is relevant but needs to be enriched by integrating the night dimension of ecological processes, and by articulating the scales of ecological processes and the institutions that are responsible for managing. These difficulties, traditionally encountered in the treatment of environmental problems [Cumming, Cumming & Redman, 2006], are accentuated because of the diffuse nature of light pollution, the plurality of its effects, but also the uncertainties that remain in the scientific knowledge of these effects at certain geographical scales and/or ecological levels. This results in a mismatch between scales of knowledge and scales of action. The concept of a dark ecological network provides a relevant

framework for pragmatic action, which "requires establishing and organizing social relationships, communicating and discussing the values, ends and means" [Mathevet, 2012, p. 150, translated by us] that underlie the geographically situated action. It allows for the deployment of integrated conservation of darkness, paying attention to the multiple uses — both human and non-human — of nocturnal space and time.

The purpose of this article is twofold. Based on the conceptual framework of the ecological network, the first objective is to present the notion of the dark ecological network and to clarify its aims, particularly from an ecological and geographical point of view. The second objective is to highlight the challenges involved in translating the dark ecological network from a network defined by scientists into a territorial project. In other words, we are discussing the transition from a scientific method to an unavoidable political compromise for the territorialisation of the protection of darkness.

2. THE INTERTWINING OF SPATIAL AND TEMPORAL DIMENSIONS OF ALAN'S ECOLOGICAL EFFECTS

Habitat fragmentation constitutes a central concern about ALAN effects on biodiversity. The first purpose of the dark ecological network is to be able to identify levers to mitigate impacts. The fragmentation effects on biodiversity due to ALAN occurs following two main mechanisms. The first is the spatial barrier effect, which can be produced following physical or temporal impacts. Specifically, ALAN can generate lighted gaps in urban areas low crossed by biodiversity, e.g. for bats [Hale et al., 2015] and toads [van Grunsven et al., 2016]. ALAN also generate asynchronies inducing mismatches between lit and unlit areas in the timing of sexual signalling and sleeping, e.g. for singing birds [Da Silva et al., 2014, 2015; Raap et al., 2015], as well as the timing of emergence for bats [Downs et al., 2003; Boldogh et al., 2008] or the timing of grass species flowering later under artificial light [Bennie et al., 2018] and producing less fruits [Knop et al., 2017]. Such temporal asynchronies can thus induce spatial differentiation between populations and ultimately a spatial barrier, and losses of habitats in avoided areas. The second main mechanism through which ALAN cause habitat fragmentation is its attractiveness on biodiversity. Light sources promote the accumulation of individuals of many species, such as arthropods under light sources [Rydell, 1992] and their depletion in unlit areas [Eisenbeis, 2006]. Artificial light thus also attracts indirectly predators such as

insectivorous bats [Stone et al., 2015] or seabirds [Rodríguez et al., 2017] and could cause top-down and bottom-up trophic effects as demonstrated e.g. on invertebrate populations [Bennie et al., 2018]. Another facet of ALAN attractiveness is the migration disrupting, altering fly path, migration activity [Doren et al., 2017] and migratory stopover selection by birds [McLaren et al., 2018]. Such attractive effects can thus generate modifications in the spatial use of habitats.

ALAN may thus alter optimal timing of biological cycles in lit and unlit areas that could induce spatial and temporal isolation of populations, and could even ultimately promoting regulation of gene flow and genetic drift [Hopkins et al., 2018]. However, many pieces of knowledge have already been developed to reduce these impacts. Indeed, lights that contain the most blue and UV wavelengths (i.e. high and low-pressure mercury, metal-halide and white light-emitting diodes) attract the most arthropods [van Langevelde et al., 2011], and in turn light-attracted bat species [Stone et al., 2015], while low and high-pressure sodium are less attractive ([Perkin et al., 2014] but 27 times more than dark conditions). Spectrum-dependent responses are also known for taxa such as birds [de Jong et al., 2015], reptiles [Witherington et al., 1991], toads [van Grunsven et al., 2016] and mice [Bird et al., 2004]. It was also shown that red spectrum lights were equivalent to dark conditions for insectivorous bats [Spoelstra et al., 2017] and that even high-pressure sodium lamps known to less attract insects negatively impacts edge bat commuting [Stone et al., 2009]. However, although measures modifying streetlight attributes are useful, they cannot be enough without the development of a larger scale night environment requiring a territorial strategy. Indeed, it has been shown that light pollution can remain a concern for natural ecosystems far away from city centres through the light halo phenomena, which can be exacerbated in periods of cloudy nights [Secondi et al., 2017]. Furthermore, following the example of bats, despite some positive effects at a local scale for some species, ALAN shows a strong negative effect at larger spatial scales for all European guilds [Azam et al., 2016]. Maintaining and increasing unlit areas remain likely the most efficient solutions: reducing the trespass of lighting could keep habitat heterogeneity which provides dark refuges, as well as decreasing in lighting intensity which limits skyglow and impacted areas [Gaston et al., 2012]. Some studies, however, found that current lighting schemes using switch off strategies were not a promising way for bats because not match with peaks of activity [Azam et al., 2015], while more drastic options — i.e. using lamps switched off between 00:00 and 04:00 am — were not fully effective although reducing the number of taxa impacted for grassland invertebrate assemblages [Gaston et al., 2017]. At a conurbation scale, Laforge et al. [2019] tested different light-reduction scenarios and found that their

efficiency to improve landscape connectivity for bats depends more on the type of land use — i.e. habitat — where we apply light reduction than on the total area impacted by it. These result, implemented by the other studies previously mentioned, has two main consequences. First, it provides a lever for action in order to find the best trade-off between biodiversity conservation and social/political acceptability — for instance, light-reduction measures are likely to be better accepted by inhabitants in small zones around watercourses than in large areas in city centres. Secondly, it reminds that ALAN effects on biodiversity also depend on environmental contexts and that associated mitigation measures (such as light reduction/extinction) efficiency is likely optimal at maintaining landscape connectivity in suitable (semi-)natural areas in regard to other factors. For instance, it was recently shown that the probability of crossing a gap in an ecological corridor — e.g. a hedgerow — of greater horseshoe bat strongly decreased from 38 meters [Pinaud et al., 2018], which constitutes a key knowledge to mix with lighting schemes. In addition, it has been recently demonstrated that bats avoid streetlight at up to 50 meters [Azam et al., 2018], which coupled with knowledge about landscape connectivity such as Pinaud et al. [2018] could help the implementation of an efficient dark ecological network. Thus, existing ecological network, such as TVB in France, represent the most promising framework to develop dark ecological ones.

Beyond temporal asynchronies generated between lit and unlit areas generating spatial segregations developed in the previous part, different scales of temporality in ALAN impacts constitute important concerns as well. First, as explained in the introduction part, species depend on regular alternance of day and night which shapes their daily biological cycle. Perturbations of daily light cycles impact biological events such as singing for birds, daily movements, foraging, sleep and recovery, documented for a wide range of taxa [Gaston et al., 2017]. Then, peak of species abundance, foraging activity and breeding periods strongly depend on seasons [e.g. Newson et al., 2015; Salvarina et al., 2018; Lučan et al., 2010], this is why species are affected by artificial lighting differently according to time of year — e.g. response of avian daily rhythms to light intensity [de Jong et al., 2016]. Monthly and seasonal regimes of lunar sky brightness also shape biological timings and spatial repartition of species — e.g. for vertical migrations of zooplankton — and can be masked or even strongly negatively impacted by the skyglow generated by the extent of artificial lighting sources [Ludvigsen et al., 2018; Davies et al., 2013]. Finally, ALAN can generate durable impacts in the long-term. Indeed, impacts of lighting can change community assemblages including diurnal ones and independently of the time of day — e.g. for invertebrates [Davies et al. 2012, 2017] — and even

exert a genetic force as shown for a moth species in which individuals from lit areas had reduced flight-to-light behaviour compared to unlit areas ones [Altermatt et al., 2016]. Concerning solutions to mitigate such impacts, no studies to our knowledge tested the efficiency of lighting schemes focused on durable and seasonal impacts. However, accurately include long-term temporal processes in decision-making to establish dark ecological network thus appears essential to ensure the coexistence of humans and biodiversity in an increasingly urbanizing world [Secondi et al., 2017].

3. THE DARK ECOLOGICAL NETWORK, OR THE RETICULAR THINKING APPLIED TO THE PROTECTION OF DARKNESS

The analysis of nocturnal time in town planning and urban development studies [Gwiazdzinski, 2009; Shaw, 2015] highlights the concept of "chronotopia" to show how urban projects incorporate patterns of variation in the uses of places. This urbanistic concept is akin to the geographical concept of "nocturnal territoriality" [Raffestin, 1988], which underscores the role of night-time darkness in the change in our daily relations with the places we experience. To know nocturnal territorialities is to know in a situated way the daily practices and uses *in* and *of* the night-time [Challéat & Lapostolle, 2018]. Taking into account an area's specific nocturnal characteristics means partially moving away from technocratic prescriptions of what spaces should be, by giving back a role to do-it-yourself approaches with a view to adding other knowledge and experiences — i.e. other than those of experts — into the mix. This is essentially a form of democratization of urban planning which, in addition to defining space in terms of the production of figures and procedural standards, takes account of actual uses and experiences of the city. The knowledge of nocturnal territorialities enables to move towards the "right lighting", a new doctrine of urban lighting that seeks a settlement between our needs for artificial light and the set of needs of darkness — ecological, health-based, and socio-cultural [Challéat, 2019].

From the public lighting policies point of view, it is important to note that the consideration of nocturnal territorialities is not in itself a fight against light pollution, but rather a fight against unnecessary expenditure — financial and energy savings [Franchomme et al., 2019]. However, the "right lighting" is proving to be a frame of reference for action permeable to new environmental considerations. In other words, if considering night-time territorialities does not necessarily mean placing the fight against light pollution at the foundation and heart

of the renewal of lighting practices, it nevertheless opens the way to integrating this issue into the production of tomorrow's urban lighting. It is in this frame of reference that the new public lighting regulation practices come to coil up. In the early 2010s, local-authority budget cuts in France and pressure to meet energy-transition targets placed new constraints on urban lighting. As a result, an increasing number of municipalities — most often in rural areas, but also, increasingly, in (peri-)urban areas — have been reducing or switching off public lighting at certain times of the day and/or certain times of the year. But these actions remain spatially scattered, and politically uncoordinated: there is no inter-territoriality for their implementation or, in other words, no articulation between the different organisational levels of action.

At the international level, the fight against light pollution is carried out in different ways, supported by different actors. In its most advanced territorial form today, it can be seen in the protection of the starry sky through new zoning built on the classic centre-periphery logic. This is the case with the dynamics of the development of "dark sky places" [Charlier & Bourgeois, 2013; Bénos et al., 2016] which is the most significant marker of this process. Initiated in 1993 in the United States with the creation of the Dark Sky Preserve at Lake Hudson (Michigan), this territorial dynamic really took off at the end of the 2000s. It is based on a logic of labelled zoning, supported by various associations from the "Dark sky movement" [Challéat & Lapostolle, 2014; Challéat, 2019], at the forefront of which is the International Dark-sky Association. Just over 140 territories are currently labelled by the latter. Its "International dark sky places" (IDSP) initially made it possible to distinguish high places of astronomical observation, and are now sought by conventional protected areas according to IUCN typology, which thus extend to the starry sky the scope of their protection measures [Collison & Poe, 2013; Charlier & Bourgeois, 2013]. The main labelling criterion here is the existence of a remarkable starry sky, which can be easily mobilised in different valorisation strategies, e.g. "dark sky tourism" development and other territorial marketing strategies that can lead to a purely utilitarian apprehension of the "starry sky" as a new assessable economic good [Mitchell & Gallaway, 2019]. Although the lines are currently moving, this aesthetic criterion still often obscures the ecological and health stakes of preserving darkness as a resource. Moreover, no reticular thinking presides over the implementation of these IDSP-type zoning: they are not networked, connected, and can, therefore, be read as islands of protection scattered within a larger space in which the overall logic that underlies our conception of lighting does not change much. From the point of view of the preservation of darkness as an ecological asset and more broadly an environmental and sociocultural good, this consideration is important.

De facto, moving from the only reduction of energy costs and/or from the only starry sky protection to the preservation of all the benefits of darkness requires mobilizing a holistic protection tool such as the ecological network. In what is thus becoming a "dark ecological network", IDSPs are "macro-reservoirs of darkness", i.e. core areas of darkness among others, linked by the others structural components of the network: "dark landscape corridors", "dark linear corridors", "dark buffer zones" and "dark stop-over sites" (fig. 1). In addition, the multi-scale structure of the dark ecological network allows it to protect the darkness needed for ecological processes by capturing the multiple effects of ALAN at different scales, from the light footprint generated by a sole luminaire to the one generated by the skyglow of megacities.

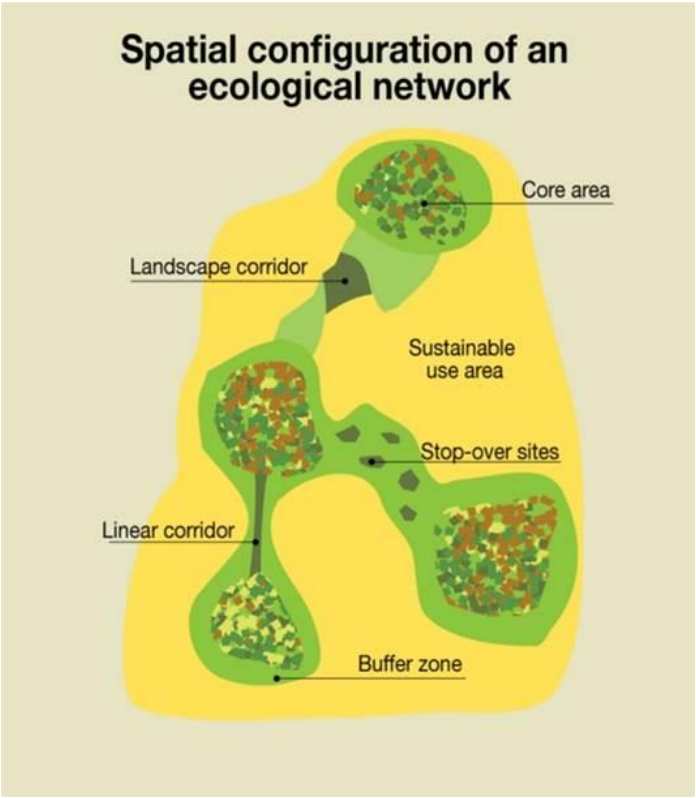

Figure 1 - Conceptual schematization of the dark ecological network according to the theoretical framework of the ecological network

Unlike IDSP-type zoning, the network has no centre or periphery, no clear boundary between inside and outside, but relies on the connexity and connectivity of its components. This structural characteristic provides it with lability, a property that is particularly effective in terms of preserving darkness. The fragmentation of habitats by ALAN differs from the physical obstacles of linear transport infrastructure: the obstacle can be temporarily removed by

switching off the lights. Thus, some elements of the dark ecological network, such as dark corridors, can be activated according to temporary issues, such as the passage of migratory birds particularly sensitive to ALAN [Horton et al., 2019]. Given this network's lability, isolated and scattered actions that already exist could be linked to the dark ecological network, such as Houston Audubon's Lights Out Action Alerts in the USA. This operation consists in generating alerts for individuals, businesses and communities to turn off the lights during the passage of migratory birds. For and through the implementation of the dark ecological network, it is, therefore, a question of deepening and extending the protection of darkness. Faced with the urgent need to preserve biodiversity, the dark ecological network enriches the tools for territorial action in the fight against light pollution. In other words, it is no longer just a question of protecting the starry sky or a few remarkable species, but of protecting ordinary biodiversity. Extending the fight against light pollution means spreading the protection of biodiversity beyond protected areas alone — symbolically represented by areas overhung by an exceptional starry sky —, even in ordinary areas. The reticular approach proposed via the dark ecological network goes in this double ecological and geographical direction: it aims to make the protection of the darkness/biodiversity couple a new guiding principle for land-use planning.

The concept of a dark ecological network is therefore no less than a reframing of the fight against light pollution. It is a shift in the view of conservation from a vertical landscape — the artialized starry sky, contemplated like a moving painting, in a way that is dissociative from the self — to a horizontal landscape — a boundary object [Brand & Jax, 2007] between the modality of scientific analysis and the modality of public action. This is the challenge of the "territorialisation" of the dark ecological network, whose practical implications stem from this holistic and geographically situated approach of the nocturnal socio-ecological systems. According to Dessein et al. [2015], "we use the notion of 'territorialisation' to describe the dynamics and processes in the context of regional development that are driven by collective human intentionality; these stretch beyond localities and fixed regional boundaries." De facto, any territorialisation process involves multiscalar, multiactor and multi-sector approach.

4. FROM A SCIENTIFIC CONCEPT TO AN ACTION-ORIENTED TOOL: FACING THE TERRITORIALISATION CHALLENGE

BUILD REPOSITORIES OF CONTEXTUALISED SCIENTIFIC KNOWLEDGE

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

Thinking about the protection of biodiversity beyond protected areas alone poses the difficulty of confronting the multiple nocturnal uses and the planning choices that have been made at different territorial scales. The transition from a scientific concept to a territorial — and political — project is therefore a problematic situation in that it puts under tension scientific and territorial constraints. Negotiations and arbitrations — particularly in terms of artificial lighting management, respect for human uses and choice of species to be protected — preside over the production of the dark ecological network and reflect its socio-ecosystemic complexity. The territorialisation and operationalisation of the dark ecological network require an effort of reflexivity on the part of both scientists and territorial actors, which is reflected in a change in practices on both sides. These changes illustrate the observational effect [Devreux, 1980] and contribute to the redefinition of dialectics. In this process, the social sciences play a catalytic role in creating a framework that respects acceptable trade-offs. For example, asking the question of the species to be protected, beyond quantitative measures, is like questioning the very scope of protection. Indeed, the use of living organisms as indicators results from differentiated relationships with Nature [Devictor, 2015], some of which are expressed even in scientific tools — e.g. the metrology of light pollution, its modelling, the choice of control species or even experimental devices in life sciences.

The mapping of the dark ecological network — an operational extension of this setting of indicators of the living world — is also the subject of a consensus based on the convergence between “knowledge, techniques and realities of the territory in order to organize the transition from the concept to the development of concrete projects” [Vimal & Mathevet, 2011]. In concrete terms, the cartographic definition of the ecological network must integrate value

systems and representations linked to the historical, social, economic, political and symbolic dimensions of the territories [Mascia et al., 2003; Blicharska et al., 2016]. Social sciences tools and methodologies make it possible to probe this territorial thickness by analysing the connections of spaces and actors involved in the protection of the darkness/biodiversity couple [Challéat & Lapostolle, 2014], the mediation logics at work in local redefinitions of lighting policies [Lapostolle et al., 2015], the integration of biodiversity issues into public controversies and debates, social, economic and scientific issues related to the protection of nocturnal spaces and species, or pioneering practices that foreshadow new forms of organization of nocturnal socio-ecosystems.

However, if objective knowledge of territorial specificities is necessary to inform the action, it is not enough. The experiential relationships to nature expressed by inhabitants and users — i.e. vernacular knowledge — must be integrated into the repertoire of situated scientific knowledge, in order to guarantee balanced governance of the dark ecological network.

THE NATURE EXPERIENCE AS THE BASIS OF THE GOVERNANCE OF THE DEN

Public policy decision-making is based on different knowledge repositories. In the perspective of classical Evidence-based policy making, the repertoire of objective knowledge predominates. But since we wish to territorialise public environmental policies, several recent studies show that it is necessary to integrate into their governance the actors holding other knowledge repositories: citizens, resource users, policymakers and practitioners for example [Cornell et al., 2013; Leach et al., 2013; Díaz et al., 2015]. This is the challenge of the Multiple evidence base approach developed by Tengö et al. [2014, 2017], which recognizes as complementary the different knowledge systems with distinct epistemic properties and aims to link them in action. This approach requires a broader construction of the publics of the problem [Dewey, 1927] and the creation of the conditions for participation in its governance [Zask, 2011]. This “common decision-making process” is the meaning we give to the dark ecological network as a political method to recognize the diversity of nature experiences [Skandrani & Prévot]. Thus considered, the dark ecological network is no longer just a scientific concept, but becomes the preferred vehicle for restoring the experience of darkness within the everyday life [Miller, 2006] of ordinary territories, even in (peri-)urban territories.

The work of cultural geography underscores the extent to which darkness allows for original forms of conviviality and intimacy, the investment of public spaces and the perception

of the world by other senses than sight [Edensor, 2013, 2015; Shaw, 2014]. In other words, and whatever the types of spaces considered, the preservation of darkness gives access to a range of experiences that allow a sensitive understanding of the world. This sensitive understanding of the world is permeable to environmental issues. Thus and even in urbanized spaces, night appears as the daily scene of multiple experiential dimensions of nature and biodiversity [Bogard, 2008, 2013; Challéat, 2019], as well as to oneself — emotional dimensions (including some of our atavistic fears [Painter, 1996; Schaller et al., 2003; Koslofsky, 2011]), sensory, memory, analogue or utilitarian dimensions [Prévot et al., 2016]. These experiences are a tangible basis for debating artificial light at night facing of darkness. These multiple dimensions make darkness a multifaceted resource — e.g. naturalistic, poetic, literary, philosophical, religious, landscape, scientific or artistic — that participates as much in our individuation and in the constitution of our relationship to the world as in the fabric of the territories [Challéat et al., 2018]. It thus gives meaning to places [Barreteau et al., 2016]. However, the governance of artificial light at night, by neglecting these different meanings of the resource, spatially and temporally erodes darkness and impoverishes the relationships that our societies maintain with the nocturnal environment. In this way, it deprives itself of a number of levers to preserve the darkness and to support consensus on how to preserve it at the local level.

In order to act, this holistic, integrated and situated approach of the conservation of darkness must be built within hybrid forums [Callon et al., 2001] allowing the expression of the plurality of experiential relationships. The teachings and learnings on the difficulties encountered in the territorialization of other forms of public environmental actions or policies must be heard [Franchomme et al., 2013]. In France, for example, when identifying biodiversity reservoirs and ecological corridors at the territorial level as part of the TVB policy, several studies have highlighted the difficulty of involving field actors alongside modeling experts. The mobilization of the latter's sophisticated tools has not been accompanied by the consideration of other forms of knowledge or a contradictory debate despite the criticisms and limitations pointed out by the actors in the field about the method used [Alphandéry & Fortier, 2012].

Moving beyond the technical approach to the problem and initiating a real project approach [Janin *et al.*, 2011] around the conservation of darkness can, for example, involve transdisciplinarity, which makes it possible to (re)integrate research, action, and policy. By creating the conditions for participation, transdisciplinarity brings together researchers, residents, politicians, practitioners, user groups, environmental associations, and experts. Citizen science programmes are another avenue for action, which can be complemented by the

previous one. On the condition that these programmes go beyond — but do not rule out — the mere mobilization of "experts amateur" and the sole purpose of producing scientific knowledge at a reduced cost [Reed, 2008]. These programmes can only provide a pragmatic basis for regulating this public action, which addresses scientific and technological issues, if they allow, on the one hand, the involvement of a diverse public in the local production of the dark ecological network and, on the other hand, the involvement of researchers in the democratic and political process [Lewenstein, 2004]. It is then a question of not abandoning a method that establishes facts and recognizes the singularity of territories [Vimal, Mathevet & Thompson, 2012] without giving way to the performative dimension of public policy instruments in general, and of the dark ecological network in particular.

5. CONCLUSION

Building on the ecological network framework, the dark ecological network aims to consider artificial light at night as a factor in habitat fragmentation, to further integrate the temporal dynamics of ecological processes into biodiversity conservation planning, and to deepen and extend the fight against light pollution towards ordinary biodiversity and within ordinary areas. The success of the dark ecological network is therefore dependent on the inclusion of the logic of preserving darkness in the common law of environmental planning and development of all territories. This banalization of the protection of darkness for its contribution to biodiversity, its pragmatic confrontation with "the real world" — i.e. the everyday life of territories with a historical, social and political depth and struggling with situated value systems and representations — gives rise to new needs. In particular, it requires ecological solidarity [Mathevet et al., 2016], a profound consideration of the "community of destiny between human, society and his environment" [Mathevet et al., 2010]. This approach of the protection of darkness can only be deployed within a relational thinking framework that, within preservation of living diversity systems, puts in interaction ecological systems on the one hand, and social systems on the other. In other words, the banalization of the protection of the darkness/biodiversity couple through the dark ecological network is a radically socio-ecosystemic approach, which aims to (re)define the nocturnal living space that a society agrees to share with the non-humans among whom it evolves.

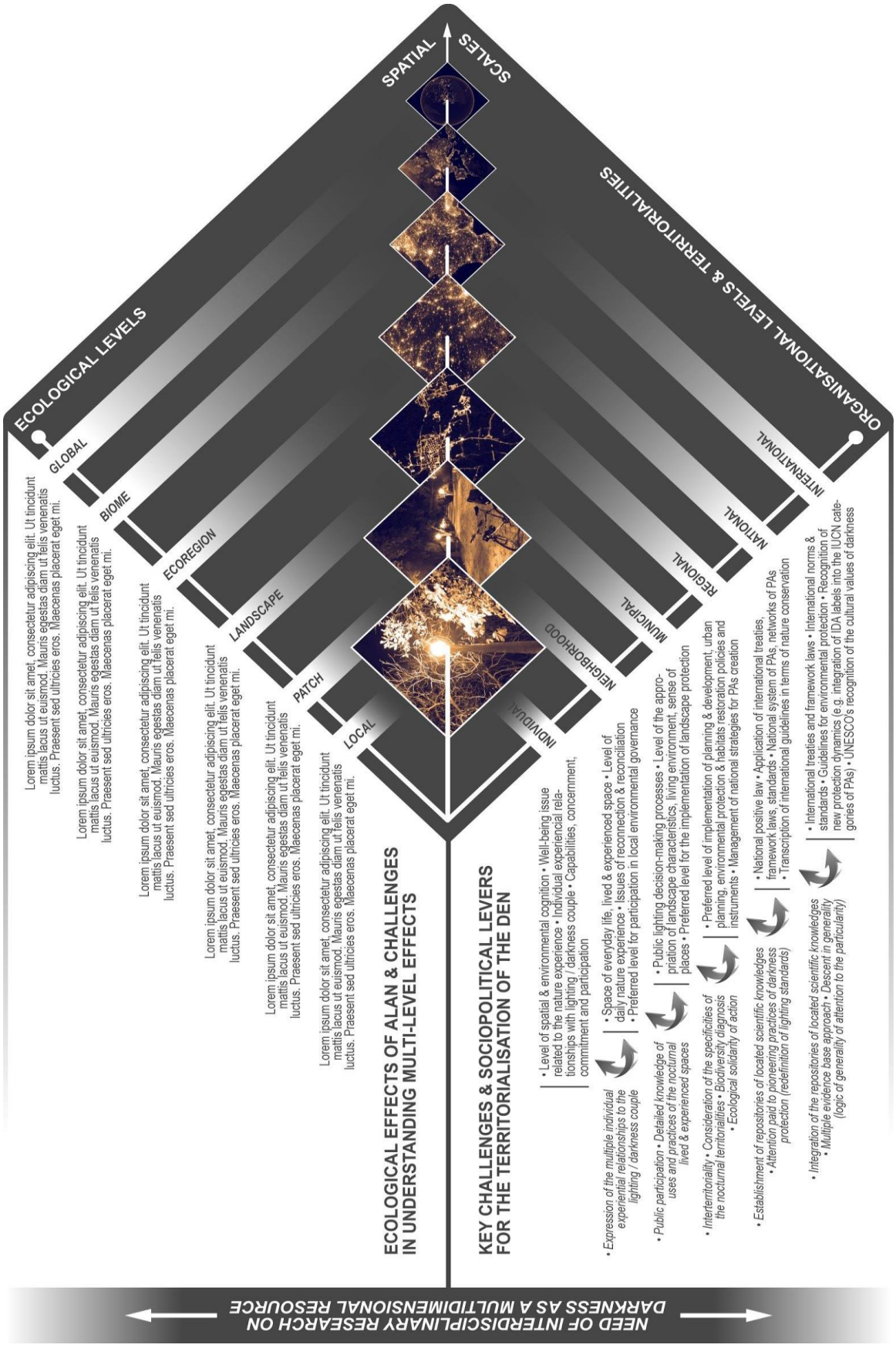

Figure 2 - Synthesis diagram pointing out the multilevel effects of ALAN and the challenges of articulating organisational levels for a bottom-up approach of the dark ecological network.

Various experiences of defining and implementing the dark ecological network in France show that issues of protecting darkness to meet biodiversity challenges are gradually being taken into account in land-use planning policies [Challéat et al., 2018; Franchomme et al., 2019]. But from these experiments in a few pioneering territories to their transcription into the common planning law of all territories, the road is long. It requires a rethinking of both the terms of the analysis of the relationship between societies and the environment and the conditions of land-use planning. A serious approach is emerging, which brings together the tradition of ecological research with that of social geography in the territories [Barreteau et al., 2016]. In other words, the experimental sciences and social sciences are making progress in bringing their analytical questions and methods closer together. Interdisciplinary socio-ecosystem approaches are emerging as a new scientific paradigm. But the difficulty remains the "how to do", i.e. the application of these analyses in territorially situated planning policies. Here, the methods of knowledge production (participatory sciences, citizen sciences, action research, engaged research) shake up — because they question them — the social significance of scientific knowledge and the practical experience of land-use planning professionals. In doing so, they highlight the need for a more general appropriation of ecological transition and biodiversity protection policies. It is a paradigm shift that requires recognizing that scientific controversies and "sustainability [are] political issue[s] and as such requires an inclusive debate and a plurality of voices" [Leach et al., 2013].

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ABSTRACT

Landscape anthropization through habitat loss and fragmentation is one of the main threats to biodiversity. This PhD (CIFRE funding) was carried out in at INRAE Toulouse (Dynafor lab) in collaboration with the Conservatoire des Espaces Naturels de Midi-Pyrénées (CENMP). It aimed at a better understanding of the impacts of light pollution and road expansion on bats, two major and inevitable elements of anthropization, using a landscape ecology framework applied to bat conservation. This work is structured in 4 sections: (i) by means of an exhaustive review of bat telemetry studies in Europe and North America, I explored how landscape anthropization influenced bat mobility through mean home range sizes and commuting distances; (ii) using simultaneous acoustic sampling of bat communities at both edge and interior forest patches in 172 landscapes varying in terms of forest amount and road density, I analyzed how forest fragmentation and road network shaped the taxonomic, functional and phylogenetic diversity of bat communities at multiple spatial scales; (iii) by developing models of species distribution and connectivity (least-cost path) at the scale of a large urban area, I assessed the effect of different street lighting extinction scenarios on landscape connectivity for three bat species; and (iv) using a field experiment, I tested the influence of landscape context around road underpasses on their use by bats and the efficiency of these structures in maintaining landscape connectivity while reducing the risk of collision with vehicles. While the first two sections of the PhD seek to better understand the mechanisms underlying the effects of landscape anthropization on bats, the last two axes are applied to their direct conservation by demonstrating how landscape ecology can contribute to improve existing measures.

RÉSUMÉ

L'anthropisation des paysages à travers la perte des habitats naturels et leur fragmentation est une des premières menaces sur la biodiversité. Cette thèse Cifre effectuée à l'INRA Dynafor de Toulouse en collaboration avec le Conservatoire des Espaces Naturels de Midi-Pyrénées a pour fondement de mieux comprendre les impacts de la pollution lumineuse et du réseau routier, deux éléments majeurs et inévitables de cette anthropisation, sur les chauves-souris. Les approches, concepts et méthodologies provenant de l'écologie du paysage ont été mobilisés à des fins appliquées à la conservation des chiroptères. La thèse se structure en 4 axes de recherche: (i) à travers une revue exhaustive des études de télémétrie en zone tempérée, nous avons cherché à comprendre comment l'anthropisation des paysages influence la mobilité des chiroptères via la taille des domaines vitaux et les distances de déplacement; (ii) grâce à un échantillonnage simultané des communautés de chiroptères en lisière et à l'intérieur de fragments forestiers dans 172 paysages variant en termes de proportion de forêt et de densité du réseau routier, nous avons étudié comment la configuration forestière, la composition de la matrice paysagère et le réseau routier façonnent la diversité taxonomique, fonctionnelle et phylogénétique des communautés de chiroptères à différentes échelles spatiales; (iii) en développant des modèles de distribution d'espèces et de connectivité (chemins de moindre de coût) à l'échelle d'une grande agglomération nous avons pu évaluer l'effet de différents scénarios d'extinction de l'éclairage public sur la connectivité du paysage en faveur de trois espèces de chiroptères; et (iv) par une expérimentation in situ, nous avons testé l'influence du contexte paysager autour des passages routiers inférieurs sur leur usage par les chiroptères et l'utilité de ces ouvrages à maintenir une connectivité du paysage tout en réduisant le risque de collision avec les véhicules. Alors que les deux premiers axes de la thèse cherchent à mieux appréhender les mécanismes sous-jacents aux effets de l'anthropisation du paysage sur les chiroptères, les deux derniers axes sont appliqués à leur conservation en cherchant à montrer les apports de l'écologie du paysage pour améliorer des mesures déjà existantes.