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Tipping the scales: Bats' response to artificial light on a local and national scale

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Resumo

Com o crescimento da população humana, aumenta também o uso da luz artificial à noite que se torna uma ameaça emergente à biodiversidade noturna. Os morcegos são particularmente vulneráveis a esta ameaça e podem ser afetados de maneira distinta em diferentes escalas. Numa escala local, espécies de voo rápido alimentam-se de insetos atraídos pela luz, enquanto espécies de voo lento evitam áreas iluminadas. Numa escala mais abrangente, demonstrou-se que ambos os grupos tendencialmente evitam áreas iluminadas. Assim, procurámos perceber como a atividade, a ocorrência e a composição das comunidades de morcegos se alteram num gradiente de luz artificial em diferentes escalas, tendo em conta variáveis ambientais e de vegetação. A amostragem local realizou-se em três áreas florestadas no centro de Portugal. Para a análise nacional usámos dados do Atlas dos Morcegos de Portugal Continental. Localmente, a atividade total dos morcegos e do grupo de voo rápido diminuiu com a distância à luz. *Plecotus sp.* foi o único do grupo de voo lento a ser afetado pela distância à luz, com uma diminuição da atividade. No estudo local, a atração parece ocorrer em maior escala que a repulsão. Evidenciando a escala do efeito de repulsão, a preferência do grupo *Plecotus sp.* por zonas próximas da luz está condicionada pela preferência por zonas com menos luminância, revelando um *trade-off* entre o risco de predação e a abundância de presas. No estudo nacional, espécies de ambos os grupos preferiram zonas menos iluminadas, demonstrando a importância da escala em estudos de luz artificial. Espécies que beneficiam da presença de luz artificial a uma pequena escala mostram um padrão contrastante em escalas maiores. Com o aumento global de luz artificial à noite, este estudo salientou que a investigação dos impactos da luz artificial a várias escalas é crucial para a conservação da biodiversidade noturna.

Palavras-chave

Atividade de morcegos; Composição de comunidades de morcegos; Luz artificial à noite; Poluição luminosa

Abstract

As the human population grows, so does the use of artificial light at night (ALAN), which is becoming an emerging threat to nocturnal wildlife. Bats, who are particularly vulnerable to this threat, can be affected in distinct ways at different scales. On a local scale, fast-flying bat species hunt insects attracted to light sources while slow-flying species avoid artificially lit areas. Both groups have been shown to avoid artificial light on a larger scale. Therefore, we sought to understand how bat activity, occurrence and assemblage composition change in a gradient of artificial light at different scales, considering other environmental and vegetation variables. Our local sampling took place in three forested areas in central Portugal. We defined linear transects in a gradient of light and sampled bats with ultrasound recorders. We used presence-absence data from the Atlas dos Morcegos de Portugal Continental for the national analysis. On a local scale, bat activity decreased with distance to light. The vast majority of the fast-flying bats showed the same pattern. *Plecotus sp.* was the only group of slow-flying species affected by distance to light, showing decreased activity. Locally, the attraction to light seems to occur on a larger spatial scale than the repulsion. Attesting to the scale of the repulsion effect, *Plecotus sp.*'s preference for places closer to light sources is conditioned by a preference for low luminance values, which suggests a trade-off between predation risk and high prey abundance. On the national analysis, species from both groups preferred less lit areas, illustrating the importance of scale in ALAN studies. Species who benefit from ALAN at a local scale exhibit a contrasting pattern at a larger scale. In conclusion, with the global increase of ALAN, this study revealed that researching ALANs impacts at several scales is pivotal for the conservation of nocturnal biodiversity.

Keywords

Bat activity; Bat assemblage composition; Artificial light at night; Light Pollution

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1 Introduction

As the human population grows, so do urbanised areas with high population densities. In these areas, the use of artificial light at night (ALAN) is ever-increasing to address the needs of the population (Hölker et al. 2010a; Cravens & Boyles 2019) and is becoming an emerging threat for nocturnal wildlife (Hölker et al. 2010b; Cravens & Boyles 2019).

Light pollution is defined in Rowse et al. (2015) as the change of natural light levels in nocturnal landscapes through artificial lighting sources. The type of light pollution with direct ecological effects is called ecological light pollution (Longcore & Rich 2004). Some phenomena that cause ecological light pollution are glare, over-illumination, light clutter, light trespass and skyglow (Gaston et al. 2013; Kyba & Hölker 2013; Rowse et al. 2015).

The effects of artificial light are scale-dependent (Stone et al. 2009, 2012; Mathews et al. 2015; Azam et al. 2016), with most studies focused on the local response of organisms to direct light (Rich & Longcore 2006; Stone et al. 2012; Azam et al. 2015; Pauwels et al. 2019). ALAN is known to impact several aspects of nocturnal animals, such as their physiology, behaviour, reproduction, and predator-prey interactions (Longcore & Rich 2004; Cravens & Boyles 2019). It is also known to alter animal assemblages (Longcore & Rich 2004; Rich & Longcore 2006; Hölker et al. 2010b, 2010a; Gaston et al. 2013; Voigt et al. 2017). However, recent studies have also focused on uncovering the larger scale impacts of ALAN, which are crucial to infer its long-term effects on population dynamics and species distribution (Gaston & Bennie 2014; Azam et al. 2016, 2018).

A group of nocturnal animals that can be significantly affected by this threat are bats. Bat populations have been declining since the 60s, particularly in Europe (Hutson et al. 2001). There are 27 known bat species in Portugal, nine of which are considered threatened (Hutson et al. 2001; Cabral et al. 2005). Being long-lived, slow to reproduce and having a low birth rate, bats are particularly vulnerable, requiring a long time to recover from population declines (Stone et al. 2015a).

Biological circadian rhythms are directly connected to the natural light-dark cycle, which controls the activity and behaviour patterns of most organisms exposed to the daily sunlight fluctuations (Stone et al. 2015a). In the case of bats, this cycle regulates emergence time from roosts and foraging activities (Stone et al. 2015a) which can be disturbed by artificial light in foraging and roost areas. Therefore, light pollution can impact bats in several ways, including foraging, commuting, emergence, roosting, breeding and hibernation (Stone et al. 2015a; Cravens & Boyles 2019).

On a local scale, ALANs' effect on bats is species-dependent (Stone et al. 2015a). The differences relate to each species' foraging strategy and flight pattern (Jones & Rydell 1994). Bats of temperate zones, being mostly insectivorous species, are highly affected by changes in prey availability. Typically, fast-flying species, such as the *Pipistrellus*, *Nyctalus* and *Eptesicus* genus, are known to tolerate higher artificial light levels and hunt insects attracted to UV-emitting light sources (Azam et al. 2015; Voigt et al. 2017). This attraction, described as a flight-to-light behaviour, is highly dependent on the spectral output of the light source (Rowse et al. 2015). Artificial light can also cause a 'dazzling effect' in many insects, rendering them immobile when approaching a lamp and forcing them to rest, becoming less able to evade predation (Rich & Longcore 2006; Rowse et al. 2015). In contrast, slow-flying species, such as *Rhinolophus*, *Myotis* and *Plecotus*, adapted to densely vegetated habitats, are known to avoid highly lit areas, despite the higher prey availability, due to the increased predation risk (Stone et al. 2009, 2012, 2015b; Mathews et al. 2015; Lewanzik & Voigt 2017; Voigt et al. 2017). *Tadarida teniotis*, a powerful and fast flyer, hunts in straight flight at heights up to 300 meters, taking advantage of a large habitat spectrum (Rainho et al. 2013; Dietz & Kiefer 2016). Despite being a fast flyer, it wasn't included in the fast-flying group due to its distinct use of habitat and foraging patterns.

A crucial factor that can enhance or dampen the effects of ALAN on bat species is the habitat type and vegetation. Tree cover can mitigate the negative effects of ALAN on some species by reducing light trespass and skyglow or enhance that same effect on other species by increasing the edge effect (Mathews et al. 2015; Straka et al. 2019). Environmental factors such as cloud cover or moonlight can also affect night sky brightness and skyglow. Clouds have reflective proprieties and in artificially lit areas, they can increase skyglow by more than an order of magnitude due to reflecting artificial light (Kyba & Hölker 2013; Hänel et al. 2018). This can increase luminance levels and, therefore, impact bat night activity.

With the advancement of lighting technologies and increasing urbanisation, the number and extension of urban areas with high levels of artificial light is expanding, giving rise to large permanently illuminated areas (Falchi et al. 2019). Studies show that species that benefit from artificial light on a streetlamp scale might suffer deleterious effects from artificial light on larger scales (Stone et al. 2015a; Azam et al. 2016). ALAN on a landscape scale can reduce habitat connectivity for all species. Particularly for light-sensitive species, it can reduce the availability of suitable dark roosting sites, essential for bat reproduction (Azam et al. 2016).

Artificial light can ultimately favour one group of species over another, changing community composition, bat activity and distribution patterns on several spatial scales (Arlettaz et al. 2000; Rowse et al. 2015). It is thus vital to the conservation of these species to understand the community effects of ALAN. For this purpose, this thesis's main objective was to understand how bat activity, occurrence and community composition change with a gradient of increasing artificial light on a local and national scale. More specifically, on a local scale, we intend to ascertain the influence of distance to light on bat species' night activity and how it relates to (a) environmental and (b) vegetation variables. We also aim to understand if (c) bat assemblages' composition changes with increasing distance to light. On a national scale, we intend to (d) determine the influence of artificial light level and other environmental and landscape variables in the distribution of bat species.

According to Rowse et al. (2015), insect abundance is presumed to increase near light sources and decrease with distance to light. On a local scale, we expect fast-flying species' activity to exhibit a similar pattern due to prey availability patterns (Voigt et al. 2017). Slow-flying species, described as light-averse by Stone et al. (2015a), are expected to show a contrasting pattern, absent from lit environments. Their activity increases with increasing distance to light. With the presence of vegetation, we expect the effects of distance to light to be mitigated for slow-flying species and augmented for fast-flying species (Mathews et al. 2015; Straka et al. 2019). In conclusion, we expect the change in bat community composition to be gradual, with species richness increasing with the distance to artificial light. On a national scale, we expect to see an exclusion of light-averse species from areas with high radiance levels and a contrasting pattern from some light-tolerant species (Azam et al. 2016), with the possibility of an adverse effect of radiance across all species and groups.

2 Methods

2.1 Local analysis

2.1.1 Study area

The three areas chosen for this study were Mata Nacional dos Medos (Figure 2.1a) and Mata Nacional da Machada (Figure 2.1b), located in the Setúbal district, and Companhia das Lezírias (Figure 2.1c) located in the Santarém district, in central Portugal. Mata Nacional dos Medos is a protected site comprising 338 ha of coastal maritime pine (*Pinus pinaster*) forest (ICNF 2013). Mata Nacional da Machada has an area of 387 ha, with an arboreal community of maritime pine (*P. pinaster*) and cork oak (*Quercus suber*) (Autoridade Florestal Nacional 2011). Lastly, Companhia das Lezírias is a state-run agriculture and forestry company covering 18 thousand ha. Our sampling in this area was predominantly in *montado,* an extensive silvopastoral system consisting of grasslands, with a tree cover of holm oak (*Quercus rotundifolia*) or cork oak (*Q. suber*) (Companhia das Lezírias 2016).

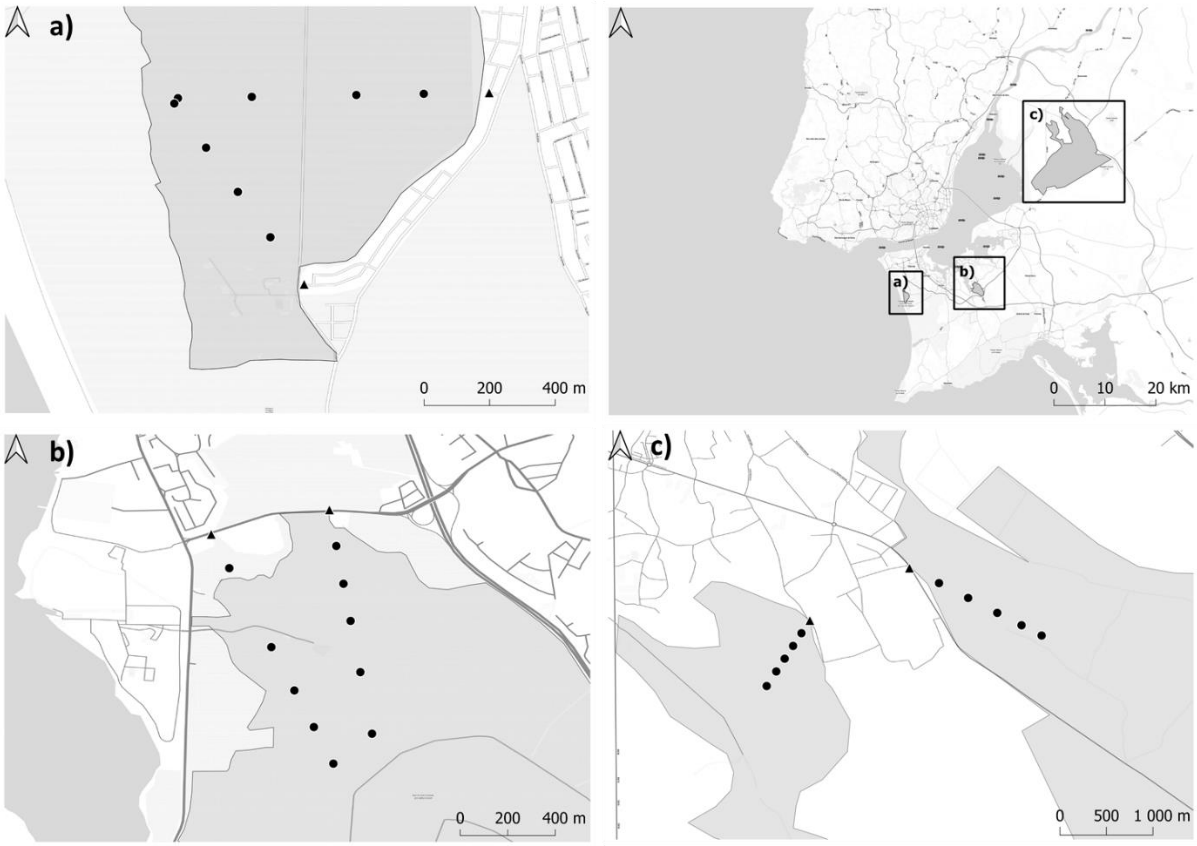

Figure 2.1 – ***Maps of the study areas with transect points*** *- Mata Nacional dos Medos (a), Mata Nacional da Machada (b) and Companhia das Lezírias (c) with the respective transects: □ - Study area locations; ▲ - Streetlamps; ● - Sampling points (200m-800m and 200m-1000m); Study area boundaries shaded in grey.*

2.1.2 Bat sampling

We recorded the GPS coordinates of all the lamps surrounding each study area, including streetlamps, spotlights, and smaller house lamps. Using QGIS software (QGIS.org 2022), we mapped the lamp locations. We defined two transects per area, with a maximum length between 800 and 1000 m. In each transect, we established sampling points spaced consecutively by 200 m form the light sources (Ongole et al. 2018). All transects started at a streetlamp, the closest light source to all sampling points. Mata Nacional da Machada and Mata Nacional dos Medos were sampled in August and September of 2020, and Companhia das Lezírias was sampled in May 2021.

In each sampling point, we deployed an acoustic automatic recording device, AudioMoth (Hill et al. 2019), on a tree at approximately 2 to 2,5 m from the ground (Linley 2017), with the microphone pointing away from the light source. The devices stayed in place for a minimum of four consecutive nights (Carmo 2011). The AudioMoths were set with a sampling rate of 256 kHz, with a cyclical recording of 5 s and a 10 s interval, with a high-pass filter of 10 kHz to eliminate low-frequency noise. Sampling began 30 min before sunset and ended 30 min after sunrise.

2.1.3 Environmental and vegetation variables

Artificial light was measured in each sampling point, in the form of luminance, determined through a single exposure photograph taken with a digital camera, Nikon D3300, fitted with an 18 mm lens, an f of 3,5, an ISO of 1600 and a 30 s exposure time. Photographs were taken during a new moon on cloudless nights to reduce the influence of other light sources (Hänel et al. 2018). In the QGIS software (QGIS.org 2022), based on the raw image's RGB colour bands, we calculated the mean value for each RGB band per sampling point. The values corresponding to the colour green (G) were chosen to represent each site's luminance (Hänel et al. 2018).

Species' presence varies greatly with the type of vegetation and habitat available. To account for that variation, we characterized the vegetation at each sampling point using the following metrics: habitat type, tree composition, percentage of canopy cover, tree and shrub height, percentage of soil covered (herbaceous, shrub and trees) and bare ground.

We measured prey abundance at each sampling point by counting every insect crossing the light beam of a handheld lantern with an LED white light (30 lm) pointing up for 60 s. Insect counts were replicated four times at each site with 60 s intervals between counts. The four replicas were divided into sets of two which were temporally spaced, when possible, to avoid the bias of differential insect activity during the night. We identified and mapped the nearest freshwater sources using cartographic maps (S.C.E. 1971, 1972, 1992b, 1992a; I.G.E 1993b, 1993a), validated with the satellite imagery available at Google Earth (www.google.com/earth/). Companhia das Lezírias provided the location of the freshwater sources in the area. Using the QGIS software (QGIS.org 2022), we measured the distance of the closest available freshwater source to all sampling points.

Additionally, we retrieved weather variables such as wind speed, cloud cover, humidity, and moonlight available at World Weather Online (www.worldweatheronline.com). The AudioMoths recorded the temperature values for each sampled night. All variables are described in Table 2.1. Detailed methods for selected variables are described in Annexe 1.

2.1.4 Sound analysis and species identification

We used Kaleidoscope Pro 5.2.1 with the Bats of Europe 5.2.1 classifier (Wildlife Acoustics, Concord, MA, USA) for the first analysis of the recorded files. This software automatically classifies the bat calls in each file. Files with no bat calls were classified as noise and excluded from the analysis. The signal detection parameters were set to a minimum of 10 kHz and a maximum of 128 kHz for the frequency range, a minimum of 2 ms and a maximum of 500 ms for the length of detected pulses and a minimum number of one pulse per file.

All files filtered by Kaleidoscope were then run through SonoBat 3.1 (Arcata, CA, USA) to obtain various metrics for each recorded bat call. A maximum of eight pulses per file was measured, with an acceptable call quality of 80% and skipping calls below the quality of 20%, with a high-pass filter of 20 kHz.

We then used the BatSound 4.2 software (Pettersson Elektronik, Uppsala, Sweden) to confirm the automatic classification. This software was also used to manually measure the frequency of maximum energy (FMaxE) and call duration in files where pulses were not measured automatically in SonoBat. To measure these parameters, we selected a minimum of three pulses. We retrieved the value from the power spectrum and the spectrogram. Lastly, the previous software could not correctly classify files containing more than one bat species. These were manually classified when possible.

To validate automatic classifications and identify the bat species, we used an identification key to the vocalizations of bats of mainland Portugal (Rainho et al. 2011). All recordings were classified to the species level when possible. Otherwise, they were classified as genus (ex. *Pipistrellus sp.*) or phonic groups (ex. *Myotis myotis / blythii*). Some species with very similar vocalizations were grouped due to difficulties in the classification process, which resulted in the following groups: *Plecotus sp., Nyctalus lasiopterus / Nyctalus noctula, Nyctalus sp., Nyctalus leisleri / Eptesicus sp., Eptesicus sp., Hypsugo savii / Pipistrellus kuhlii, Myotis sp.* and *Pipistrellus sp.*

Table 2.1 - ***Local variable table with environmental and vegetation variables*** *- Description of the variables used for the local models, with range, units, and source. Variables were measured per sampling point and night/day when applicable.*

Name	Description	Range and Units	Source
Distance to light	Distance to all light sources in the vicinity of the study area	0 - 1000 m	This study
Vegetation variables			
Habitat	Habitat type in classes (*Montado*, Eucalyptus, Mixed Forest; Pine Forest; Riparian)	7 habitat types	This study
Canopy	Percentage of canopy	0,5 - 80%	This study
Canopy height	Median of all tree species heights	5 - 18 m	This study
Vegetation	Predominant type of vegetation (Bush, Herbaceous or Unoccupied soil)	3 vegetation types	This study
Tree composition	Tree species present in each sampling point	5 tree species	This study
Bush height	Height of bush species	0,2 - 2,5 m	This study
Environmental variables			
Insects	Median of the number of insects	0 - 30,5	This study
Luminance (G)	Median G value in RGB of raw image	2,314 - 221,939	This study
Distance to water	Distance to the nearest freshwater source	0 - 762,2 m	Companhia das Lezírias and Cartographic maps (S.C.E. 1971, 1972, 1992b, 1992a; I.G.E 1993b, 1993a)
Temperature	Temperature measured at 21h each night	17,7 - 31,7 ºC	AudioMoth
Humidity	Median humidity value per day	43,75 - 75,25%	www.worldweatheronline.com
Cloud coverage	Median cloud coverage value per day	0 - 37,13%	www.worldweatheronline.com
Wind	Median wind speed value per day	7,75 - 30,38 km/h	www.worldweatheronline.com
Moon light	Percentage of visible moon	48 - 97%	www.worldweatheronline.com

2.1.5 Statistical analysis

We plotted accumulation curves for all transects to assess if our sampling effort was sufficient to accurately describe the bat assemblage present in each sampled area. Due to the reduced number of observations (n < 10), *Barbastella barbastellus* and *Hypsugo savii* were excluded from the individual species analysis, and *H. savii* / *P. kuhlii* and *N. lasiopterus* / *N. noctula* could only be modelled with distance to light. However, these four species and groups were included in the analysis of species richness and beta diversity.

We conducted an exploratory graphical analysis of the data, plotting the inherent variation and covariation of independent variables with bat activity (total and per species) and the species richness. Afterwards, we ran a correlation analysis selecting only variables with a Spearman correlation below 0,7 (Tabachnick & Fidell 2007).

Species richness and bat activity (in the form of bat passes) were modelled as a function of distance to artificial light, site luminance, vegetation cover, insect abundance, distance to freshwater sources and meteorological parameters. The study area, transect and night/month were included in all models as random effects. We used generalized linear mixed-effects models (GLMMs) with the Negative Binomial family and link log (Lewanzik & Voigt 2017), fitted using the 'glmer.nb' function from the package lme4 v. 1.1-6 (Bates et al. 2015) in R v. 4.1.2 (R Core Team 2021). Significance was set at $p < 0,05$.

First, we modelled the relationship between individual species, species richness and total bat activity, and each independent variable in univariate GLMMs. All univariate models were tested with various forms of rescaling for each variable (log, square root, squared and scaled between 0-1) and compared with Akaike's information criterion (AIC) (Burnham & Anderson 2002). The scaling from the model with the lowest AIC value, when $\Delta i > 4$, was used in the multivariate GLMM models. Even after treatment and rescaling, the variables in which the models' returned errors were excluded.

Due to the high number of variables, we used a model reduction procedure, excluding all descriptors with $p > 0,1$ in the univariate models. In the multivariate GLMMs, we fitted models (a) including ALAN and environmental variables and (b) including ALAN and vegetation-related variables. Variables were further reduced based on the p-value. Non-significant or less significant variables were discarded from the model. Variables were also excluded if correlated in the model outputs, selecting the variable with more ecological significance. We excluded insect abundance, cloud coverage, and tree composition with these procedures. Distance to light was the only variable kept in all the models due to its importance for this study's main objective.

All models were subjected to goodness of fit tests through the package DHARMa v 0.4.4 (Hartig 2022) residuals diagnostic to assess their ability to predict and explain the patterns in the data. Lastly, we plotted each model's partial effects of relevant descriptors using the package effects v 4.2-0 (Fox 2003).

We calculated the beta diversity for each transect using the betapart v 1.5.4 package (Baselga et al. 2021). Based on each species' number of bat passes, we computed a dissimilarity matrix accounting for the dissimilarity derived from unidirectional abundance gradients. We then fitted a negative exponential and power-law function through GLMs, to describe the gradient of assemblage dissimilarity with distance to light.

2.2 National analysis

2.2.1 Dataset

We used data from a national bat survey of Continental Portugal for this analysis. The data consists of bat observations, identified to the species level, when possible, collected for the *Atlas dos Morcegos de Portugal Continental* (Rainho et al. 2013) between 2010-2012. Some species also include historical observations gathered from the available bibliography. The data was collected through various sampling methods, including netting, acoustic detectors, and roost inventory. For the species that are hard to identify acoustically and strictly cave-dwelling such as *Miniopterus schreibersii, Myotis blythii, Myotis myotis, Rhinolophus euryale* and *Rhinolophus mehelyi*, the data consists mainly of observations in roosts.

2.2.2 Landscape and environmental variables

To represent artificial light, we used the VIIRS nighttime lights (2012), containing radiance data (radiant flux reflected or emitted by a given surface) in nanoWatts/cm^2/sr (Baugh et al. 2013; Azam et al. 2016). VIIRS is a composite raster, with a resolution of 1 km^2, collected by the Suomi NPP-VIIRS Day/Night Band in 2012 on new moon nights without cloud coverage. It contains lights from sites with persistent lighting, in which transient events have been removed.

We used the Latitude with UTM coordinates to represent the regional preferences of the different species, given Portugal's significant variation in climatic and habitat types on a latitude scale. We also used the *Carta de Uso e Ocupação do Solo de Portugal Continental* from 2010 (COS10) (DGT 2021). The COS10 composite consists of a thematic map detailing soil occupation with a resolution of 0,01 km^2. We used the second classification level, joining compatible classes into nine classes of land use. Freshwater and urban classes in COS10 were used to derive the variables distance to water and urban areas, as these landscape features can significantly promote and deter a species presence. Altitude and slope were derived from the European Digital Elevation Model (EU-DEM) version 1.0 (Bashfield & Keim 2011), a digital surface model (DSM), with a 25 m resolution (EU GMES/Copernicus programme). As an indicator of the cover greenness, we used the Normalized Difference Vegetation Index (NDVI) version 3 (Straka et al. 2020; Toté et al. 2020), generated by the Global component of the Land Service of Copernicus, the Earth Observation programme of the European Commission. We used the data corresponding to the middle of August 2010, a composite raster of 10 days derived from SPOT/VEGETATION and PROBA-V daily orbit reflectance values. We chose the month of August, the lowest value of NDVI, to highlight the differences in productivity between the dry and wet areas. Climate variables were retrieved from the WorldClim Historical Climate Data version 2.1, climate data for 1970-2000 (Razgour et al. 2011; Fick & Hijmans 2017). From this dataset, we used the data for minimum, mean, and maximum temperature and precipitation for August, with a resolution of 1 km^2. All variables are detailed in Table 2.2.

2.2.3 Statistical analysis

Species with fewer than 10 observations - *Eptesicus isabellinus, Myotis mystacinus, Nyctalus noctula* and *Nyctalus lasiopterus* - were excluded from the analysis. We generated absence data, pseudo-absences, for each species selected. These consisted of random points similar to the number of observations (max 1,5x the number of presences). Pseudo-absences were distributed outside a radius of 1 km^2 from presences. Data were pooled to a 1 km^2 grid to reduce spatial autocorrelation issues.

We conducted an exploratory graphical analysis of the data, plotting the inherent variation and covariation of independent variables with bat occurrence per species. Afterwards, we ran a correlation analysis selecting only variables with a Spearman correlation below 0,7 (Tabachnick & Fidell 2007).

Each species' occurrence was modelled as a function of radiance, soil occupation, distance to water and urban areas, altitude, slope, NDVI and climatic variables. We used generalized linear models

(GLMs) with the Binomial family and link logit (Ancillotto et al. 2019), fitted using the 'glm' function from the package stats v 4.1.2 in R v. 4.1.2 (R Core Team 2021). Significance was set at $p < 0,05$.

First, we modelled the relationship between all bat species and independent variables in univariate GLMs to select the relevant variables for each species, excluding all descriptors with $p > 0,1$. Then, we modelled all species with the relevant independent variables in multivariate GLMs. Variables were again selected based on the p-value. Due to the similarity of effects and correlation, we chose the average temperature as the representative variable from the temperature variables. Radiance, as the variable corresponding to the main objective of this study, was kept in all models regardless of its significance.

All models were subjected to goodness of fit tests through the package DHARMa v 0.4.4 (Hartig 2022) residuals diagnostic to assess their ability to predict and explain the patterns in the data. We also used the Area Under the Receiver Operator Characteristic Curve (AUC) calculated in the 'roc' function in the package pROC v 1.18.0 (Robin et al. 2021) to establish the explanatory capacity of the model. Lastly, we plotted the effects, using the package effects v 4.2-0 (Fox 2003), of the variables in the models that had a significant or important relationship.

Table 2.2 – ***National variable table with landscape and environmental variables*** *- Description of the variables used for the national models, with range, units, and source.*

Name	Description	Range and Units	Source
Radiance	Radiance values measured from a satellite on new moon nights without cloud coverage	0 - 63 nanoWatts/cm2/sr	VIIRS nighttime lights (Baugh et al. 2013)
Latitude	Latitude in UTM 29N coordinates	4098673 - 4658833 m	This study
Soil occupation	Map of soil occupation classes at the second level of detail (Urban areas; Mining, construction and waste disposal sites; Agricultural and agro-forestry areas; Permanent pastures; Forests; Open forests, shrub and herbaceous vegetation; Naked soil or sparsely vegetated; Wetlands; Marine and coastal waters)	9 classes	COS10 (DGT 2021)
Distance to water	Distance to the closest large freshwater body	0 – 16845,73 m	COS10 (DGT 2021)
Distance to urban areas	Distance to the closest urban areas	0 – 10633,76 m	COS10 (DGT 2021)
Elevation	Distance from sea level to the highest point	-1,230141 – 1863,058 m	EU-DEM (Bashfield & Keim 2011)
Slope	Angle of slope between terrain levels	0 – 58,7 º	EU-DEM (Bashfield & Keim 2011)
NDVI	Dimensionless index used to estimate the density of green on an area of land	24 – 255	Copernicus NDVI (Toté et al. 2020)
Mean temperature	Medium temperature of August 2010	16,6 – 25,1 ºC	WorldClim (Fick & Hijmans 2017)
Maximum temperature	Maximum temperature of August 2010	21,3 – 33,1 ºC	WorldClim (Fick & Hijmans 2017)
Minimum temperature	Minimum temperature of August 2010	11,4 – 18,6 ºC	WorldClim (Fick & Hijmans 2017)
Precipitation	Amount of precipitation of August 2010	3 - 39 mm	WorldClim (Fick & Hijmans 2017)

3 Results

3.1 Local analysis

We sampled 34 points and obtained 50191 calls belonging to 14 species/groups of species. The most common species recorded was *Pipistrellus pipistrellus* (18031 calls), followed by *Pipistrellus sp.* (17417), *N. leisleri* / *Eptesicus sp.* (4389), *Pipistrellus pygmaeus* (3705), *Pipistrellus kuhlii* (3464), *Nyctalus sp.* (1167), *Eptesicus sp.* (887), *Plecotus sp.* (296) , *T. teniotis* (292), *Myotis sp.* (141), *H. savii* / *P. kuhlii* (69), *N. lasiopterus* / *N. noctula* (50), *B. barbastellus* (9) and *H. savii* (4).

All 14 bat species/groups were present in Mata Nacional dos Medos, and all but *H. savii* were present in Companhia das Lezírias. Mata Nacional da Machada had 11 of the bat species/groups present, excluding *B. barbastellus*, *N. lasiopterus / N. noctula* and *T. teniotis*. The number of bat passes per species/group for all study areas is detailed in Annexe 2.

The accumulation curves for both transects in Mata Nacional da Machada didn't stabilize after six sampling points. For Mata Nacional dos Medos and Companhia das Lezírias, only one transect per area stabilized after five and six sampling points, respectively (Annexe 3). This suggests that for Mata Nacional da Machada, our sampling efforts may not have been sufficient to accurately represent the bat community composition of this area, probably due to the low abundance of bats. The bat richness of the other two study areas seems to be better sampled.

3.1.1 The influence of distance to light and environmental variables in bat activity

Distance to light proved to be a significant driver of bat activity for the two species groups modelled solely with this variable, *N. lasiopterus / N. noctula* (*p-value* = 0,002) and *H. savii / P. kuhlii* (*p-value* = 0,009). Both groups showed a significant decrease in activity with increasing distance to light, despite the low number of calls recorded.

Artificial light in the environmental models (Table 3.1) is represented by distance to light and site-specific luminance (G), independent of distance to light. Distance to light showed a significant negative effect on the activity of half the species and groups in these models, *P. pipistrellus* (*p-value* = 0,001), *N. leisleri* / *Eptesicus sp.* (*p-value* < 0,001), *Nyctalus sp.* (*p-value* = 0,001), *Eptesicus sp.* (*p-value* < 0,001), *Plecotus sp.* (*p-value* = 0,018) and total bat activity (*p-value* < 0,001) (Figure 3.1).

*Table 3.1 – **Environmental models summary table** - Summary of the results of the environmental multivariable GLMMs, with variable significance (*** < 0,001; ** < 0,01; * < 0,05; . < 0,1; n.s. > 0,1) shaded in a gradient of grey (darker tones are more significant), and relationship signal (+/-).*

	Eptesicus sp.	*H. savii / P. kuhlii*	*Myotis sp.*	*N. lasiopterus / N. noctula*	*N. leisleri / Eptesicus sp.*	*Nyctalus sp.*	*P. kuhlii*
Distance to light	- ***	- ***	+ n.s.	- **	- ***	- ***	+ n.s.
Luminance (G)	- ***						
Distance to water					- ***	- .	- ***
Temperature					+ ***		
Wind speed			- ***			- ***	- ***
Moon light	- .				- .	- .	

	P. pipistrellus	*P. pygmaeus*	*Pipistrellus sp.*	*Plecotus sp.*	*T. teniotis*	*Bat passes*	*Species richness*
Distance to light	- **	- n.s.	- n.s.	- *	+ n.s.	- ***	+ n.s.
Luminance (G)				- ***			+ .
Distance to water	- *	- ***	- **			- ***	
Temperature	+ ***	+ **					
Wind speed			- .			- ***	- *
Moon light	- *				- ***	- *	- .

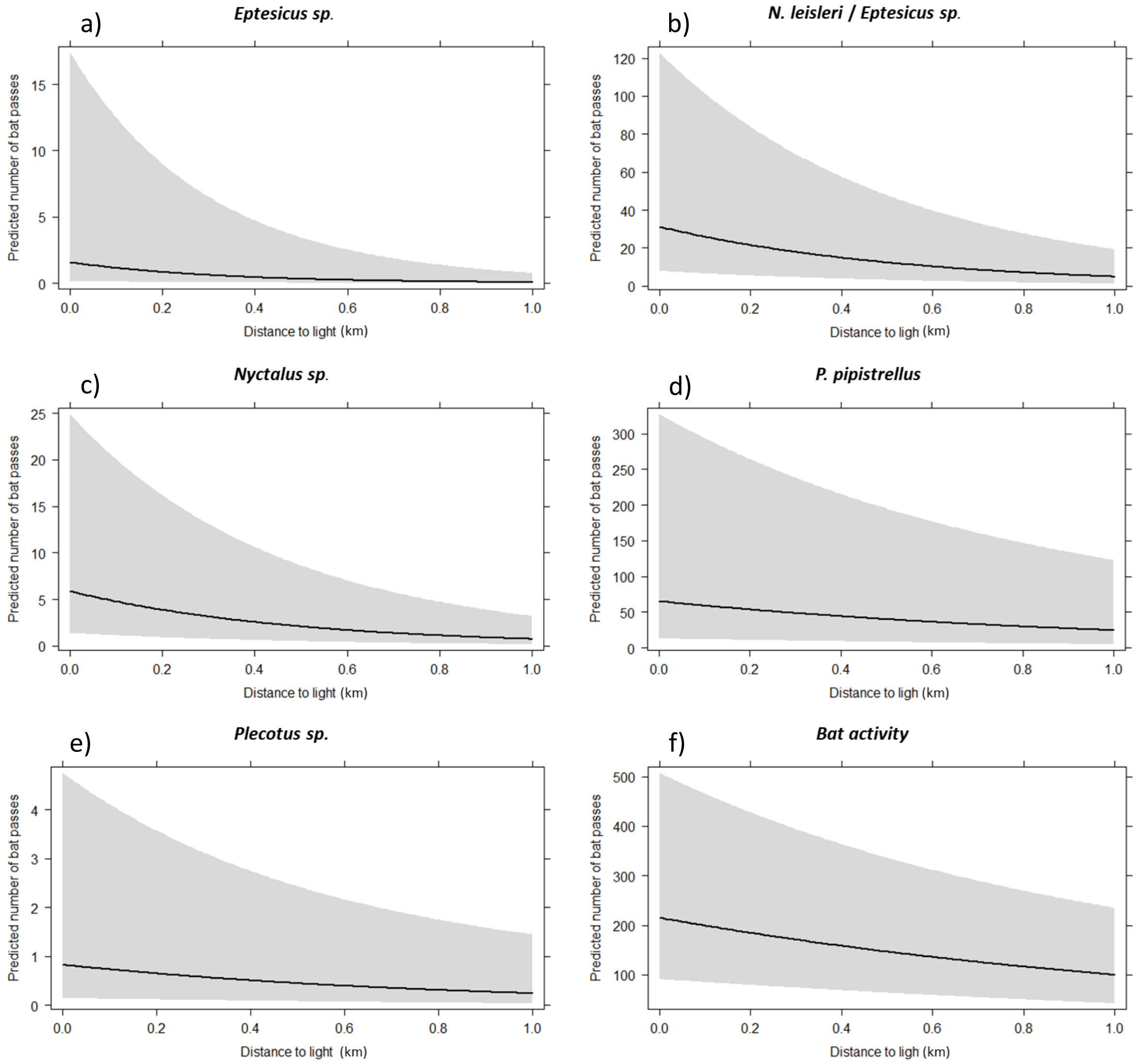

Figure 3.1 - ***Environmental models effects of distance to light*** *- Model partial effects of distance to light on the estimated bat activity: Eptesicus sp. (a), N. leisleri / Eptesicus sp. (b), Nyctalus sp. (c), P. pipistrellus (d), Plecotus sp. (e) and total bat activity (f). Models include other descriptors summarized in Table 3.1. Shaded areas represent 95% confidence intervals.*

Luminance was a significant variable only for two groups (Figure 3.2), *Eptesicus sp.* (*p-value* < 0,001) and *Plecotus sp.* (*p-value* < 0,001). Both species exhibit a decrease in activity with increasing luminance levels, a contrasting relationship to the one shown by these species with distance to light. The effect of the remaining environmental variables in these models are summarised in Table 3.1 and detailed in Annexe 4.

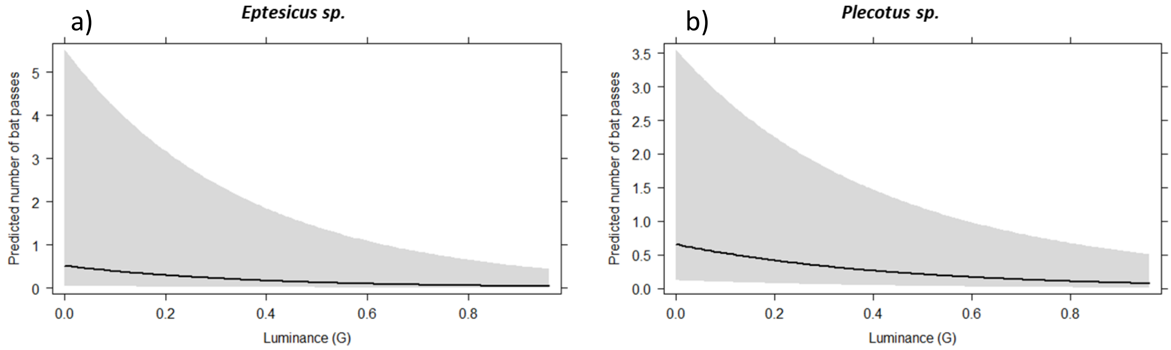

Figure 3.2 - ***Environmental models effects of luminance (G)*** *- Model partial effects of luminance on the estimated bat activity: Eptesicus sp. (a) and Plecotus sp. (b). Models include other descriptors summarized in Table 3.1. Shaded areas represent 95% confidence intervals.*

3.1.2 The influence of distance to light and vegetation variables in bat activity

In the vegetation models (Table 3.2), the effects of distance to light were coherent with the environmental models. An exception to this was the model of the activity of *Plecotus sp.* that showed that distance to light had no effect once vegetation variables were considered. Also, *P. pygmaeus* (Figure 3.3) shows a significant (*p-value* < 0,001) increase in activity with distance to light.

Table 3.2 – ***Vegetation models summary table*** *- Summary of the results of the vegetation multivariable GLMMs, with variable significance (*** < 0,001; ** < 0,01; * < 0,05; . < 0,1; n.s. > 0,1) shaded in a gradient of grey (darker tones are more significant), and relationship signal (+/-). For the habitat variable, the reference class is the lamp edge, and for the vegetation variable the reference class is the bush cover.*

		Eptesicus sp.	*Myotis sp.*	*N. leisleri / Eptesicus sp.*	*Nyctalus sp.*	*P. kuhlii*	*P. pipistrellus*
Distance to light		- **	+ n.s.	- ***	- *	+ n.s.	- **
Habitat	*Montado*			+ **		+ *	
	Eucalyptus			+ ***		- ***	
	Mixed forest						
	Pine forest			+ *		- ***	
	Riparian					- **	
Vegetation	Herbaceous	- **			- ***		
	Unoccupied soil	-	- .				+ *
Canopy				- **	- **		
Canopy height		+ *			+ .	+ *	

		P. pygmaeus	*Pipistrellus sp.*	*Plecotus sp.*	*T. teniotis*	*Bat passes*	*Species richness*
Distance to light		+ ***	- n.s.	- n.s.	+ n.s.	- **	- n.s.
Habitat	*Montado*				- .		
	Eucalyptus	- ***	- ***			- ***	- ***
	Mixed forest				- .		
	Pine forest	- ***	- *				
	Riparian						
Vegetation	Herbaceous		- .	- *			
	Unoccupied soil			- *			
Canopy		- *					
Canopy height		+ .	+ *	+ *			

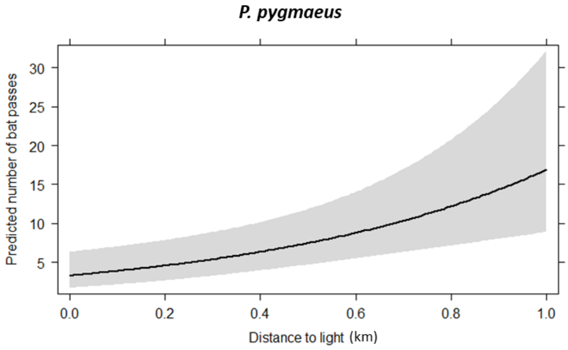

Figure 3.3 - ***Vegetation models effects of distance to light*** *- Model partial effects of distance to light on the estimated bat activity of P. pygmaeus. Models include other descriptors summarized in Table 3.2. Shaded areas represent 95% confidence intervals.*

The remaining vegetation variables' effect on each species activity is summarised in Table 3.2 and detailed in Annexe 5.

3.1.3 Changes in bat assemblages' composition with increasing distance to light

In both models, distance to light was not a significant variable to explain differences in species richness (Tables 3.1, 3.2). However, as this analysis doesn't account for species substitution, only the variation in species number, we calculated the beta diversity for all transects.

Based on the beta diversity for each transect, only one transect in Mata Nacional dos Medos showed significant assemblage composition differences with increasing distance to light (Figure 3.4). For the other transects, we detected no significant differences in assemblage composition (Annexe 6).

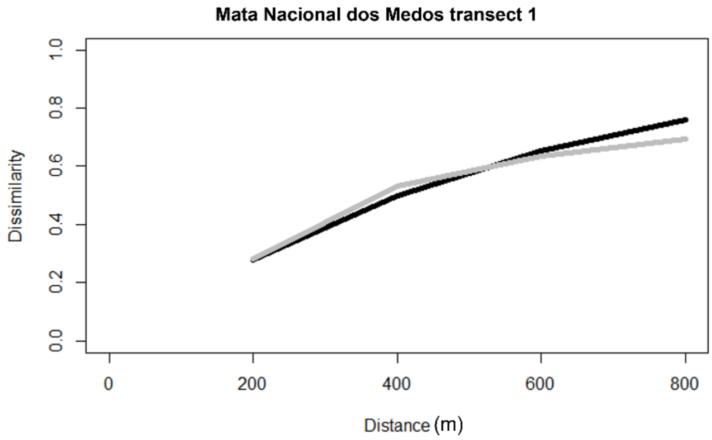

Figure 3.4 - ***Bat assemblage composition dissimilarity*** *- Dissimilarity of bat assemblage composition based on a negative exponential (black) and power-law function (grey) in a gradient of distance to light for Mata Nacional dos Medos transect 1.*

3.2 National analysis

We had a total of 3354 presences from 22 species/groups of species. Radiance significantly affected *H. savii* (*p-value* < 0,001), *M. blythii* (*p-value* = 0,042), *N. lasiopterus / N. noctule* (*p-value* = 0,033), *P. kuhlii* (*p-value* < 0,001) and *Rhinolophus hipposideros* (*p-value* = 0,007) (Figure 3.5). Furthermore, radiance showed a near-significant effect on *Nyctalus leisleri* (*p-value* = 0,053) and *Rhinolophus ferrumequinum* (*p-value* = 0,081) (Figure 3.5). Most species showed a pattern of lower probability of occurrence with increasing radiance, except *N. leisleri*, with a higher probability of occurrence in illuminated areas. For *M. schreibersii, P. kuhlii* and *P. pygmaeus,* these results are based on less-than-ideal models with poor predictive power (AUC < 0,65). The effects of the remaining variables in the models are summarised in Table 3.3 and detailed in Annexe 7.

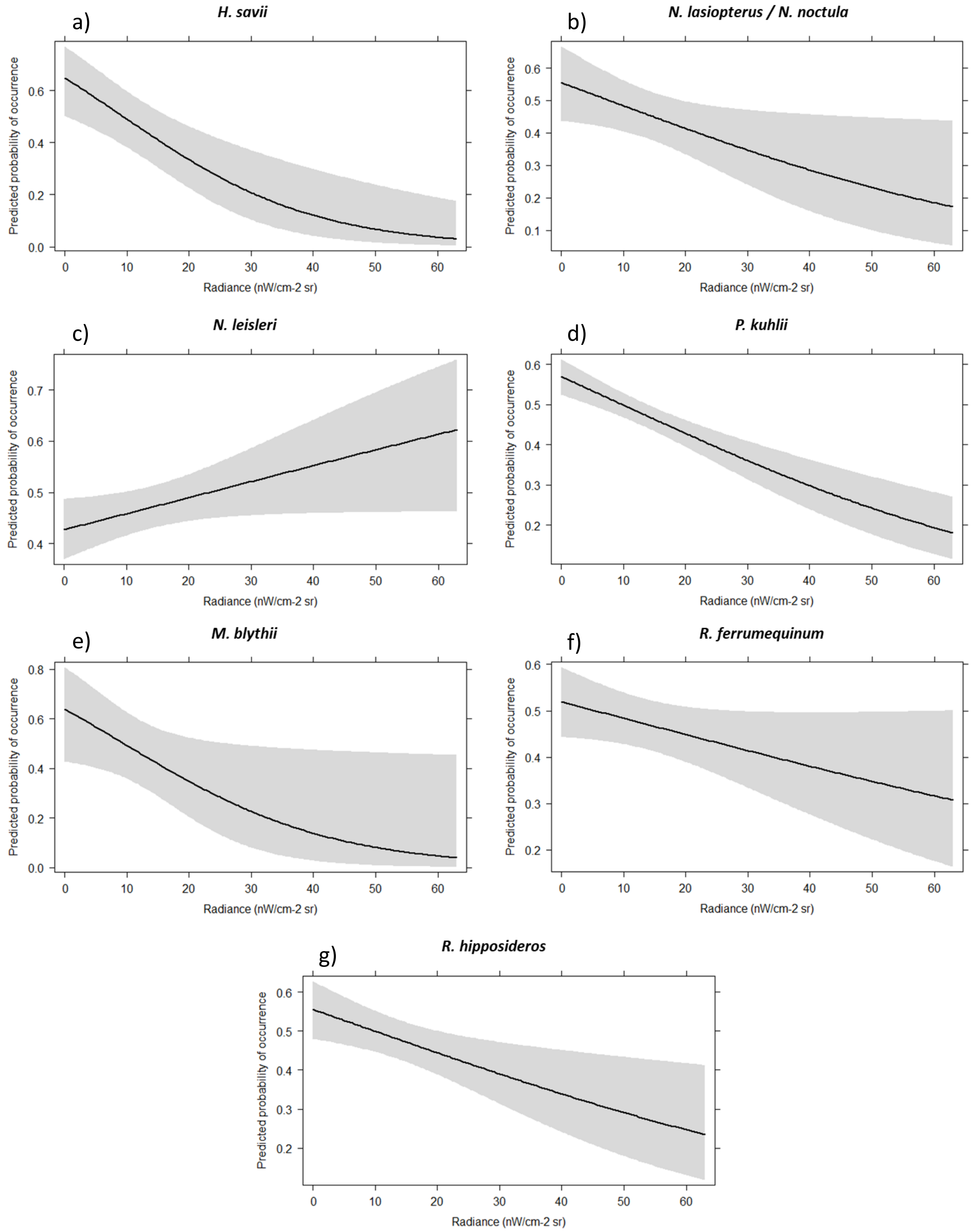

Figure 3.5 - ***National models effects of radiance*** *- Model partial effects of radiance on the estimated bat occurrence: H. savii (a), N. lasiopterus / N. noctula (b), N. leisleri (c), P. kuhlii (d), M. blythii (e), R. ferrumequinum (f) and R. hipposideros (g). Models include other descriptors summarized in Table 3.3. Shaded areas represent 95% confidence intervals.*

Table 3.3 – ***National models summary table*** *- Summary of the results of the national multivariable GLMs, with variable significance (*** < 0,001; ** < 0,01; * < 0,05; . < 0,1; n.s. > 0,1) shaded in a gradient of grey (darker tones are more significant), and relationship signal (+/-). For the soil occupation variable, the reference class is the urban areas. In this table are represented only the classes of soil occupation that showed a significant effect on bat species occurrence. Soil occupation classes: AAF - Agricultural and agro-forestry areas; PP – Permanent pastures; F – Forests; OFSH - Open forests, bush and herbaceous vegetation; NS - Naked soil or sparsely vegetated.*

		B. barbastellus	*E. serotinus*	*H. savii*	*M. schreibersii*	*M. bechsteinii*	*M. blythii*	*M. daubentonii*	*M. emarginatus*	*M. escalerai*	*M. myotis*	*N. lasiopterus / noctula*
AUC		0,807	0,924	0,859	0,602	0,783	0,845	0,706	0,823	0,773	0,708	0,705
Radiance		- n.s.	+ n.s.	- ***	- n.s.	- n.s.	- *	- n.s.	+ n.s.	- n.s.	- n.s.	- *
Latitude		+ ***					- ***	+ ***			+ *	
Distance to water							+ **	- **	+ *			
Distance to urban areas							- *				- *	- **
Elevation			+ ***				+ *					
Slope		- **	- *						- **	- .		- **
NDVI		+ ***	+ **		+ *	+ *			+ *	+ ***		
Precipitation												
Average temperature				- ***								
Soil occupation	AAF		- ***									
	PP											
	F		- **									
	OFSH		- ***									
	NS		- *									

		N. leisleri	*P. kuhlii*	*P. pipistrellus*	*P. pygmaeus*	*P. auritus*	*P. austriacus*	*R. euryale*	*R. ferrumequinum*	*R. hipposideros*	*R. mehelyi*	*T. teniotis*
AUC		0,724	0,639	0,699	0,624	0,777	0,726	0,820	0,738	0,723	0,817	0,814
Radiance		+ .	- ***	+ n.s.	+ n.s.	- n.s.	- n.s.	+ n.s.	- .	- **	+ n.s.	+ n.s.
Latitude									+ ***			
Distance to water												
Distance to urban areas			- *	- **						- **	- *	
Elevation		+ ***		+ ***				+ ***			+ **	+ *
Slope		- **	- *						- **	- ***		- ***
NDVI		+ ***	+ ***	+ ***	+ ***				+ *			
Precipitation		- **			- ***						- ***	
Average temperature						- ***	- **					- ***
Soil occupation	AAF	- *	- *	- *						- *		
	PP		- **							- *		
	F	- .	- **	- *	- *					- .		
	OFSH		- **	- *								
	NS		- .							- **		

4 Discussion

4.1 Local analysis

4.1.1 The influence of distance to light with environmental and vegetation variables in bat activity

As proposed by our first hypothesis, we found that total bat activity in both models is higher near the light sources. Most bat passes recorded were classified as *P. pipistrellus* and *Pipistrellus sp.* (70% of bat passes). The total bat activity is thus mainly represented by these two species/groups. The habitat type was the only significant vegetation driver of total bat activity, which revealed a significantly lower activity in eucalyptus areas than the lamp site. This might be due to the low tree variability of this habitat type in our study area, making them less attractive for bat species in general.

Also consistent with our hypothesis, most species from the group of fast-flying bats exhibited a significant decrease in activity with distance to light in both models. These results attest that open-space and edge foragers are the most light-tolerant species and benefit the most from insect aggregations at artificial light (Rowse et al. 2015; Stone et al. 2015a). From these groups and species, the night activity of *Eptesicus sp.* was the only one that showed a significant effect both of luminance and distance to light. Against expectations, this groups' activity decreases with higher luminance values. Azam et al. (2018) described a negative effect of very low and very high levels of luminance on *E. serotinus*, which could explain why *Eptesicus sp.* has higher activity levels near light sources and lower activity levels in areas with more luminance. Luminance increases the predation risk of nocturnal species (Jones & Rydell 1994) thus, the response of this group might indicate a trade-off between prey availability and increased predation risk.

For *Eptesicus sp.* and *Nyctalus sp.*, the effects of distance to light in the vegetation models were coherent with the environmental models but became less significant. Vegetation variables explained some variation attributed to distance to light in the environmental models. The fast-flying group comprise various species with different ecologies: woodland species that hunt just above or below the canopy, open areas and canopy foragers that prefer forest edges, and city dwellers. The choices displayed by the different species in the vegetation models show the multiplicity of ecologies present in this group (Rainho et al. 2013; Dietz & Kiefer 2016).

Unlike other species in the fast-flying group, in the vegetation model *P. pygmaeus* revealed a significant increase in activity in areas further away from the light sources, contrasting with the lack of effect in the environmental model. When vegetation is accounted for, the effect of distance to light for this species is much more prevalent. We expected to see a similar pattern to *P. pipistrellus*, given this genus has a relatively uniform documented response of attraction to artificial light (Stone et al. 2015a). However, this species is more dependent on vegetated and riparian foraging habitats, especially during maternity season (Straka et al. 2019). This behaviour might explain the preference for more densely vegetated habitats, with less dense and higher canopies, further away from where artificial lights are installed. Eucalyptus and pine woods have significantly less activity than the lamp edge in our research despite this preference. Pine and eucalyptus forests in our study area have low tree richness and, therefore, seem less attractive to this species even when compared to artificially lit areas with less vegetation.

Furthermore, from the slow-flying bats group, *Plecotus sp.* was the only group exhibiting a significant effect of distance to light, only in the environmental model. Several studies (Rydell 1992; Stone et al. 2015a; Barré et al. 2022) showed that this genus avoids areas close to artificial light. Contrary, our results show that these species' activity decreases with distance to light. On the other hand, luminance displays a very significant negative effect in the night activity of this group, providing support to the previously described pattern of light avoidance. *Plecotus sp.* could be taking advantage of the insect concentration in areas closer to artificial light sources, the flight-to-light effect (Rowse et al. 2015) but with lower luminance levels tolerable for these species. The luminance level is highly dependent on vegetation cover, more densely vegetated areas reducing light trespass (Straka et al. 2019) while also being the most suitable areas for these species (Rainho et al. 2013; Dietz & Kiefer 2016). For *Myotis sp.*, probably due to the low sample size, distance to light showed no effect on bat activity in both models.

As expected, the species from the slow-flying group also showed a preference for more densely vegetated areas. *Myotis sp.* exhibited a near-significant negative effect of unoccupied soil, and *Plecotus sp.* also preferred areas with more bush cover and higher canopies. Forest dwellers, like small *Myotis* and *Plecotus* species, are adapted to slower, more precise flights and shorter-ranged echolocation calls to manoeuvre and forage in denser vegetation environments (Rowse et al. 2015; Stone et al. 2015a). Their limited flight speed makes them more dependent on vegetation as a cover to avoid predation. Therefore, they are less adapted to open spaces where artificial lights tend to be installed. These species also tend to emerge later from their roosts to avoid predation from diurnal animals (Rowse et al. 2015). They are, therefore, intrinsically more light-averse (Rowse et al. 2015; Stone et al. 2015a; Straka et al. 2019). This light aversion and the slower flight explain these species' absence from illuminated areas and the surrounding habitats affected by light trespass.

T. teniotis is a species with distinct commuting and foraging patterns, not included in the previously described groups. As it forages very high above the ground (Marques et al. 2004; Rainho et al. 2013), artificial light might not be a driver of night activity for this species. This was reflected in our models, where the distance to light was not a significant variable to explain this species' activity. Also, due to its high-flying behaviour, it does not select habitats while foraging (Marques et al. 2004; Rainho et al. 2013). Therefore, as expected, vegetation variables in our models showed no influence in its activity.

Besides distance to light, other environmental variables affected bat activity in these areas. Distance to water, wind speed, and moonlight negatively affect bat activity. It's well documented that water is an essential and determinant resource for bats. Their presence is highly dependent on the proximity of freshwater sources (Ancillotto et al. 2019). The effect of moonlight is also well documented (Appel et al. 2017). Despite not being a significant variable for the slow-flying species, it negatively influences the bat activity of the remaining species. The wind is a deterring factor for bat activity, constraining flight dependent activities such as foraging and commuting (Blake et al. 1994). It also influences detectability and introduces noise in the recordings. Lastly, temperature is crucial for bat activity, which increases with higher temperatures (McCain 2006).

4.1.2 Changes in bat assemblages' composition with increasing distance to light

As shown in our accumulation curves, our sampling may not be sufficient to accurately describe the bat richness in the study areas, particularly Mata Nacional da Machada. This suggests that the following analysis might not truly represent the pattern of change in bat assemblage composition in each study area.

Both local species richness models have dispersion and distribution problems, probably due to the low number of species or groups of species identified. Therefore, any inferences or analysis based on these models must be carefully considered. Both models – environmental and vegetation – had non-significant effects of distance to light on bat richness. Furthermore, according to the beta diversity of each transect, there seems to be no defined pattern of change in assemblage composition with an increasing gradient of distance to light. Only one transect in Mata Nacional dos Medos showed a significant difference. The pattern might be more evident in longer transects, increasing the differences between lit and unlit areas, and longer sampling periods, including several seasons. Furthermore, bat captures may be necessary to increase the taxonomic level in bat classification. More studies are thus needed to shed light on this matter.

4.2 National analysis

Radiance significantly affected five species and groups, three fast-flying and two slow-flying. All these species/groups had a lower probability of occurrence with increasing radiance levels. Radiance not having a significant effect on more species might be due to the low number observations.

In the fast-flying group, the three species with a significant effect of radiance, *H. savii*, *N. lasiopterus / N. noctula,* and *P. kuhlii,* showed a preference for areas with lower radiance values. Only *N. leisleri* exhibited a near-significant positive effect of radiance. For *N. leisleri*, despite being near-significant, our results are concurrent with other studies at a landscape scale, depicting a pattern of attraction to artificial light by this species (Mathews et al. 2015). Although fast-flying species typically show a preference for illuminated areas, as shown in our local study for *H. savii* and *N. lasiopterus / N. noctula*, other studies reveal a negative or neutral effect of artificial light at a landscape scale for fast-flying species (Mathews et al. 2015; Azam et al. 2016; Pauwels et al. 2019). Despite the lack of effect in our local study, *P. kuhlii* also shows a strong pattern of avoidance of artificial light at a landscape scale. Azam et al. (2016), described the same pattern of large-scale light avoidance in this species. However, distance to urban areas negatively affected *N. lasiopterus / N. noctula* and *P. kuhlii*. In fact, when analysing land-use preferences, *P. kuhlii* exhibits a pattern of preference for urban areas over all other habitat types. These results counter the significant negative effect of radiance on these species. Still, they concur with the effect of distance to urban areas and the known behaviour of *P. kuhlii*. According to several studies (Ancillotto et al. 2015; Russo & Ancillotto 2015; Salinas-Ramos et al. 2021), *P. kuhlii* is mainly observed foraging around artificial light sources and is most abundant in urban habitats. Therefore, these species' results demonstrate two opposing patterns. This might be explained by a preference for peri-urban or small-scale urban habitats with less artificial light prevalence. However, our predictions for *P. kuhlii* in the national study are based on models with poor predictive power (AUC < 0,65). They need to be interpreted with careful consideration.

In the slow-flying group, *M. blythii* and *R. hipposideros* display the significant expected pattern of avoidance to higher radiance levels. *R. ferrumequinum* also demonstrates a near-significant radiance effect with the expected avoidance pattern. This attests to the fact that the negative effect of artificial light on these species may be felt on all scales, affecting their distribution on a national level. However, distance to urban areas showed a negative effect on all species of this group, for which it is a significant factor. Most being cave-dwelling species, roost location can explain this result. Additionally, soil occupation was an important driver of occurrence mainly for *R. hipposideros,* showing a preference for urban areas. Again, this was unexpected when accounting for the effect of radiance but concurred with the effect of distance to urban areas. However, this species tolerates relatively high levels of light and is known to roost in buildings (Rainho et al. 2013). A significant proportion of the data comes from roosts, which can attest to the pattern in land cover usage and distance to urban areas.

Our results may not faithfully describe the effect of radiance on cave-dwelling bats as *M. schreibersii*, *M. myotis*, *M. blythii*, *R. euryale,* and *R. mehelyi*. Most data for these species comes exclusively from roosts. Thus, the modelled variables have much less explanatory power, given that the most critical factor for these species' occurrence is the presence of suitable roosts.

Similar to what was observed in the local models, radiance does not significantly affect the occurrence of *T. teniotis*. This species is a powerful, fast flyer in open spaces, flying at great altitudes. It takes advantage of a broad habitat spectrum, utilizing both illuminated and dark areas (Marques et al. 2004; Rainho et al. 2013).

4.3 Conclusions

In conclusion, our results show that artificial light shows stronger signs of attraction at a local scale by light-tolerant species rather than repulsion by light-sensitive species. This might be due to the scale of the effect, suggesting that light aversion takes place at smaller scales for these species, its effects being reduced with distance and vegetation cover (Azam et al. 2018; Straka et al. 2019). Furthermore, the attraction phenomena might happen on a larger scale due to the "vacuum cleaner" effect (Rich & Longcore 2006), which significantly reduces insect abundance in areas further from artificial light. Traditionally light-sensitive species such as *Rhinolophus sp.* were absent or not recorded in all study areas and could not be included in the local analysis. *Myotis sp.* and *Plecotus sp.* were present, albeit in smaller numbers than almost all other species. In accordance with behavioural patterns described for these species (Stone et al. 2015a), there was a notorious exclusion from the directly lit sampling point and an increase in activity on the next sampling point. This attests to the pattern of avoidance being more prevalent in smaller scales closer to the light source or directly illuminated areas.

On a national scale, only five species were significantly affected by radiance. Even so, all of them demonstrated a decreased probability of occurrence with increasing radiance levels. The lack of effect on some species could be due to the small number of observations or the data source. Nonetheless, species identified as light-avoidant in smaller scales exhibited the same pattern on a national scale. Some species described as light-tolerant showed a pattern of avoidance on a national scale. This might indicate the importance of scale regarding artificial light's effect on bat species. Small-scale emissions of artificial light can be beneficial for light-tolerant species (ex. *Pipistrellus sp.*) or mitigated for light-avoidant species (ex. *Plecotus sp.*) (Straka et al. 2019). However, on a national scale, large concentrations of artificial light could cause a large-scale avoidance effect for both light-tolerant and avoidant species (ex. *N. lasiopterus / N. noctula*, *Rhinolophus sp.*). With the global increase of ALAN and the innovation of lighting techniques, this study reveals it would be relevant to study the long-term impacts of artificial light on several scales, essential for the conservation of all nocturnal biodiversity.

Finally, this study didn’t find a significant effect of artificial light on bat assemblage composition for most transects, likely due to the low number of species detected. To better describe this effect, longer transects and longer sampling periods would be needed, increasing the differences between lit and unlit areas and the effects of season on bat species. Furthermore, with acoustic identification, various bats could only be classified in phonic groups. Therefore, bat captures would be more appropriate, increasing taxonomic identification to better describe bat assemblage composition.

5 References [1]

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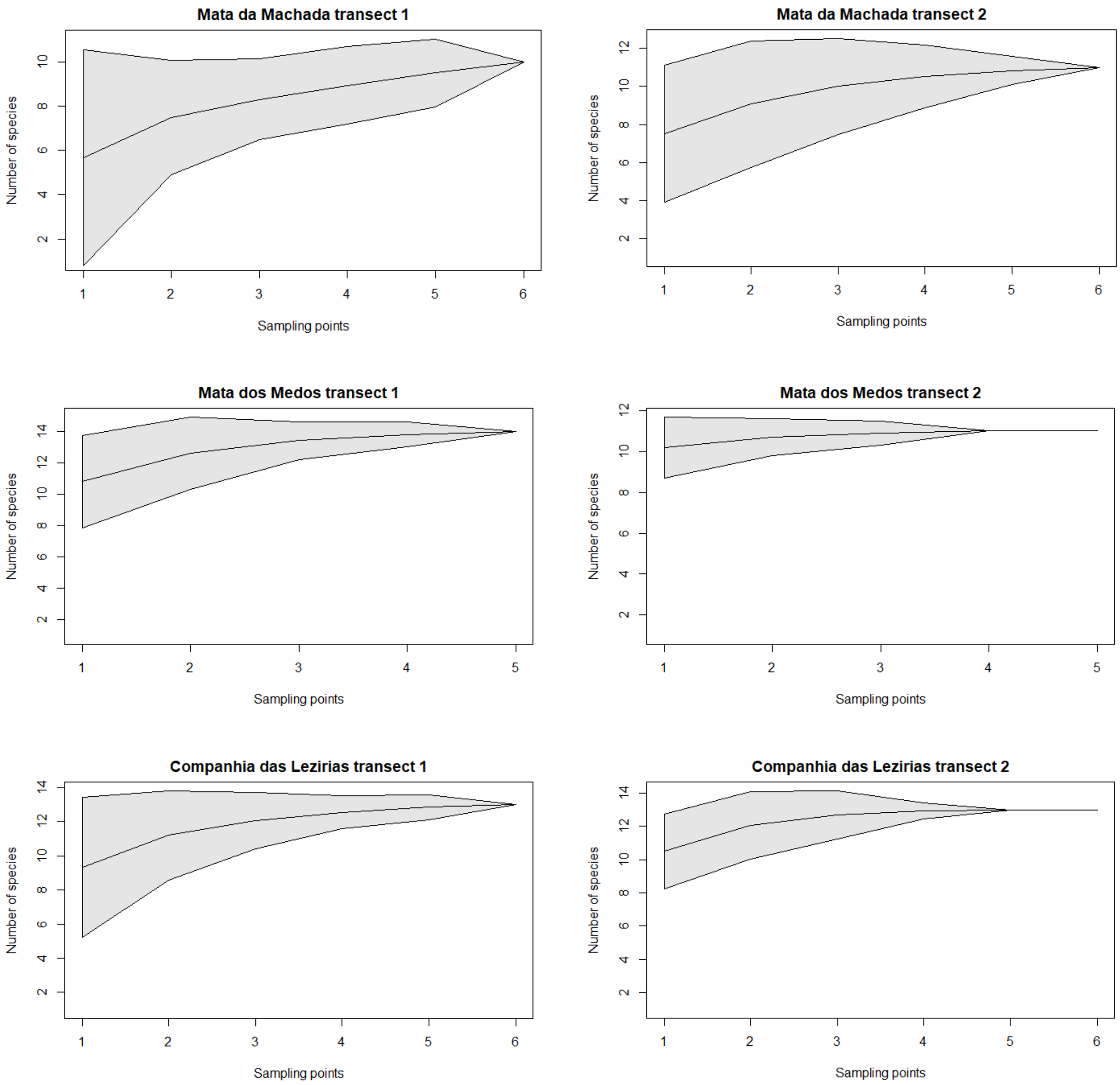
Annexe

Annexe 1 - ***Local scale variable details*** *– Detailed methods for Distance to light, Insects and Vegetation metrics.*

Variable	Details
Distance to light	We recorded the GPS coordinates of all the lamps inside and surrounding the perimeter of each study area. Most light sources were streetlamps, but spotlights and smaller house lamps were also included. Using QGIS software, we mapped the lamp locations and created buffers to all light sources in increments of 200 m. Then, we defined two transects per area, in which we established sampling points that intersected the previously created buffers. All transects start at a streetlamp and have a maximum length of 1000 m, except for Mata Nacional dos Medos with a maximum transect length of 800 m. Overall, two transects of six sampling points were defined for Companhia das Lezírias, and Mata Nacional da Machada and two transects of five points for Mata Nacional dos Medos.
Insects	Using a handheld lantern with a LED white light (30 lm) pointing up for 60 s, we counted every insect that crossed the light beam. Insect counts were replicated four times at each site with 60 s intervals between counts. The four replicas were divided into sets of two which were temporally spaced, when possible, to avoid the bias of differential insect activity during the night. The first set took place at the time of recovery of the recording devices and the second set took place on the return after all the devices had been collected. This sampling took place in August and September 2020 and May 2021.
Vegetation metrics	We characterized the vegetation by describing various metrics in the immediate vicinity of each sampling point. The habitat type was described according to the predominant tree cover and vegetation type. We conducted a visual estimate of the percentage of canopy cover, tree and shrub height, percentage of soil covered (herbaceous, shrub and trees) and bare ground. Lastly, all tree species were recorded in the variable tree composition. All metrics were recorded standing in the AudioMoth placement site and encompassing the nearest visible area on a 360º radius from the sampling point.

Annexe 2 - ***Bat passes per species/group for each study area*** *– Raw number of bat passes per bat species/group for Mata Nacional da Machada, Mata Nacional dos Medos and Companhia das Lezírias.*

	Mata Nacional da Machada	Mata Nacional dos Medos	Companhia das Lezírias
B. barbastellus	0	2	7
Eptesicus sp.	3	869	15
H. savii	1	3	0
H. savii / P. kuhlii	38	25	6
Myotis sp.	10	105	26
N. lasiopterus / N. noctula	0	7	43
N. leisleri / Eptesicus sp.	465	2693	1231
Nyctalus sp.	99	131	937
P. kuhlii	625	1985	854
P. pipistrellus	766	10961	6304
P. pygmaeus	724	389	2592
Pipistrellus sp.	1236	10928	5253
Plecotus sp.	11	271	14
T. teniotis	0	128	164



Annexe 3 - ***Accumulation curves per transect*** - *Species accumulation curves, with number of species per sampling point for each transect of all study areas. Confidence intervals shaded in grey.*

Annexe 4 - ***Environmental GLMMs results*** *– Multivariate GLMMs with all significant environmental variables for each species/group with fixed effects, estimate (B), standard error (SE), z-value (z) and p-value (p) with variable significance (*** < 0,001; ** < 0,01; * < 0,05 ; . < 0,1) and random effects, variance explained (V) and standard deviation (SD).*

Eptesicus sp.	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	2.27004	1.45217	1.56300	0.11800
	Distance to light	-3.18150	0.50245	-6.33200	2.42e-10 ***
	Luminance	-2.78456	0.47003	-5.92400	3.14e-09 ***
	Moon light	-0.02079	0.01208	-1.72100	0.0853 .
	Random effects	***V***	***SD***		
	Area	4.10120	2.02510		
	Transect	0.10680	0.32670		
H. savii / P. kuhlii	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	-0.40290	0.67990	-0.59300	0.55351
	Distance to light	-2.93890	0.93820	-3.13200	0.00173 **
	Random effects	***V***	***SD***		
	Transect	0.19530	0.44190		
	Month	0.73060	0.85470		
Myotis sp.	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	3.04130	1.23950	2.45400	0.014142 *
	Distance to light	0.37200	0.50150	0.74200	0.45825
	Wind	-1.46140	0.40240	-3.63200	0.000281 ***
	Random effects	***V***	***SD***		
	Area	0.83500	0.91380		
N. lasiopterus / N. noctula	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	-2.96210	2.51120	-1.18000	0.23818
	Distance to light	-1.82550	0.69640	-2.62100	0.00876 **
	Random effects	***V***	***SD***		
	Area	5.46400	2.33700		
	Month	6.15100	2.48000		
N. leisleri / Eptesicus sp.	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	1.65657	2.29289	0.72200	0.47000
	Distance to light	-1.85056	0.22816	-8.11100	5.03e-16 ***
	Distance to water	-1.19622	0.34001	-3.51800	0.000435 ***
	Temperature	0.24057	0.04235	5.68000	1.34e-08 ***
	Moon light	-0.87279	0.49188	-1.77400	0.076000 .
	Random effects	***V***	***SD***		
	Area	1.19400	1.09260		
	Transect	0.24300	0.49290		
Nyctalus sp.	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	12.16120	3.52810	3.44700	0.000567 ***
	Distance to light	-2.06960	0.31370	-6.59700	4.19e-11 ***
	Distance to water	-0.87050	0.50250	-1.73200	0.083220 .
	Wind	-1.74130	0.36360	-4.78900	1.68e-06 ***
	Moon light	-1.24780	0.73520	-1.69700	0.089659 .
	Random effects	***V***	***SD***		
	Area	1.28750	1.13470		
	Transect	0.25830	0.50820		
P. kuhlii	***Fixed effects***	***B***	***SE***	***z***	***p***
	Intercept	5.90330	0.85440	6.91000	4.86e-12 ***
	Distance to light	0.23340	0.32260	0.72300	0.46900
	Distance to water	-2.03690	0.45880	-4.44000	9.01e-06 ***
	Wind	-0.98880	0.24710	-4.00100	6.31e-05 ***
	Random effects	***V***	***SD***		
	Area	0.33330	0.57730		
	Transect	0.37490	0.61230		

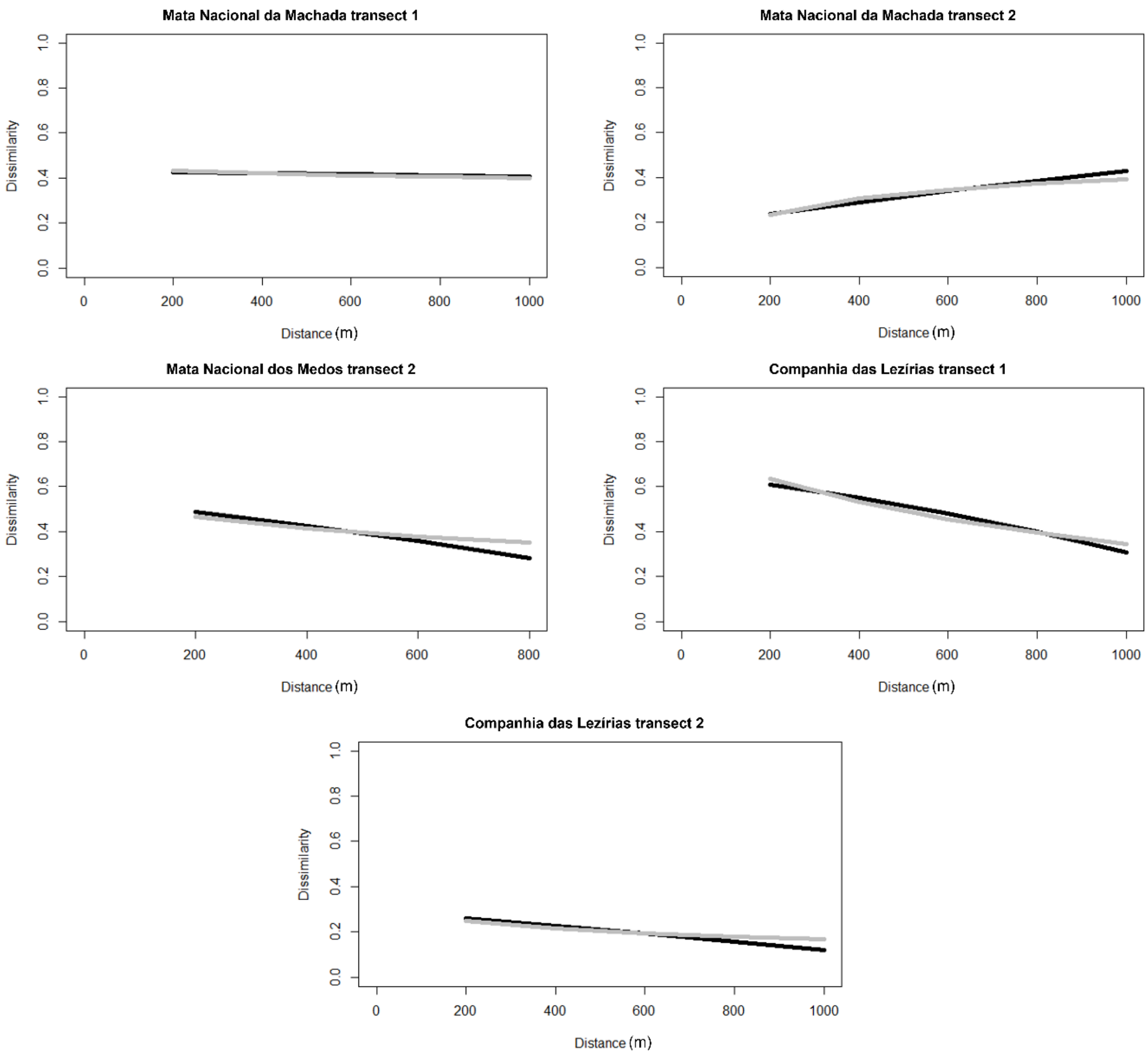
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	4.73660	2.84175	1.66700	0.09556 .
	Distance to light	-0.97657	0.29837	-3.27300	0.00106 **
	Distance to water	-0.14920	0.06755	-2.20900	0.02718 *
P. pipistrellus	Temperature	0.22135	0.05029	4.40200	1.07e-05 ***
	Moon light	-1.22635	0.60322	-2.03300	0.04205 *
	Random effects	***V***	***SD***		
	Area	1.79420	1.33950		
	Transect	0.14070	0.37510		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	-5.92203	4.28012	-1.38400	0.16650
	Distance to light	-0.25301	0.28639	-0.88300	0.37700
P. pygmaeus	Distance to water	-0.62292	0.06299	-9.88900	<2e-16 ***
	Temperature	3.54670	1.28554	2.75900	0.0058 **
	Random effects	***V***	***SD***		
	Area	3.02100	1.73800		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	6.68286	0.95528	6.99600	2.64e-12 ***
	Distance to light	-0.41010	0.26405	-1.55300	0.12039
Pipistrellus sp.	Distance to water	-0.26769	-0.26769	-3.16400	0.00156 **
	Wind	-0.45781	0.23889	-1.91600	0.05532 .
	Random effects	***V***	***SD***		
	Area	0.41020	0.64040		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	0.18270	0.90000	0.20300	0.83910
	Distance to light	-1.21980	0.51380	-2.37400	0.0176 *
Plecotus sp.	Luminance	-2.27430	0.54180	-4.19700	2.7e-05 ***
	Random effects	***V***	***SD***		
	Area	1.85870	1.36340		
	Transect	0.29180	0.54010		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	14.04500	5.18300	2.71000	0.006732 **
	Distance to light	0.12750	0.49830	0.25600	0.79813
T. teniotis	Moon light	-4.08220	1.08800	-3.75200	0.000175 ***
	Random effects	***V***	***SD***		
	Area	13.55000	3.68100		
	Month	4.69000	2.16600		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	10.41922	0.99704	10.45000	< 2e-16 ***
	Distance to light	-0.76658	0.21271	-3.60400	0.000313 ***
	Distance to water	-0.21472	0.06238	-3.44200	0.000577 ***
Bat passes	Wind	-0.97784	0.19274	-5.07300	3.91e-07 ***
	Moon light	-0.01724	0.00723	-2.38200	0.017196 *
	Random effects	***V***	***SD***		
	Area	0.47507	0.68930		
	Transect	0.05207	0.22820		
	Fixed effects	***B***	***SE***	***z***	***p***
	Intercept	2.21806	0.23838	9.30500	<2e-16 ***
	Distance to light	0.00116	0.11593	0.01000	0.99200
	Luminance	0.04823	0.02884	1.67200	0.0945 .
Species richness	Wind	-0.01202	0.00470	-2.55600	0.0106 *
	Moon light	-0.00469	0.00271	-1.72800	0.0839 .
	Random effects	***V***	***SD***		
	Area	0.04038	0.20094		
	Transect	0.00046	0.02146		

*Annexe 5 - **Vegetation GLMMs results** - Multivariate GLMMs with all significant vegetation variables for each species/group with fixed effects, estimate (B), standard error (SE), z-value (z) and p-value (p) with variable significance (*** < 0,001; ** < 0,01; * < 0,05 ; . < 0,1) and random effects, variance explained (V) and standard deviation (SD). For the vegetation variable, the reference class is the bush cover and for the habitat variable the reference class is the lamp edge.*

Eptesicus sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		-1.05004	1.4256	-0.737	0.46139
	Distance to light		-1.64083	0.51992	-3.156	0.00160 **
	Vegetation	Herbaceous	-2.24737	0.73024	-3.078	0.00209 **
		Unoccupied soil	-0.47395	0.4069	-1.165	0.2441
	Canopy height		0.16825	0.07141	2.356	0.01847 *
	Random effects		***V***	***SD***		
	Area		3.936	1.984		
Myotis sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		-0.7773	0.9406	-0.826	0.4086
	Distance to light		0.22	0.5365	0.41	0.6818
	Vegetation	Herbaceous	0.595	0.4964	1.199	0.2306
		Unoccupied soil	-0.786	0.4342	-1.81	0.0702 .
	Random effects		***V***	***SD***		
	Area		1.4805	1.217		
	Month		0.4556	0.675		
N. leisleri / Eptesicus sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		3.5336	0.7171	4.928	8.32e-07 ***
	Distance to light		-2.0882	0.4095	-5.099	3.41e-07 ***
	Habitat	*Montado*	1.5325	0.5328	2.876	0.004023 **
		Eucalyptus	2.0662	0.5771	3.581	0.000343 ***
		Mixed forest	0.1495	0.2999	0.499	0.618119
		Pine forest	0.8504	0.3539	2.403	0.016260 *
		Riparian	-0.7408	0.5658	-1.309	0.190426
	Canopy		-1.2535	0.4401	-2.848	0.004401 **
	Random effects		***V***	***SD***		
	Area		0.6264	0.7915		
	Transect		0.8013	0.8951		
	Month		0.177	0.4207		
Nyctalus sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		0.6407	1.4832	0.432	0.66576
	Distance to light		-1.0983	0.4511	-2.435	0.014912 *
	Vegetation	Herbaceous	-1.9492	0.5057	-3.855	0.000116 ***
		Unoccupied soil	-0.2766	0.3623	-0.763	0.445235
	Canopy		-0.4356	0.1386	-3.143	0.001672 **
	Canopy height		1.1416	0.5861	1.948	0.051432 .
	Random effects		***V***	***SD***		
	Transect		0.6876	0.8292		
	Month		1.4952	1.2228		
P. kuhlii	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		1.51823	1.0045	1.511	0.130678
	Distance to light		0.57617	0.46177	1.248	0.212123
	Habitat	*Montado*	1.34493	0.65863	2.042	0.041150 *
		Eucalyptus	-4.42079	0.90816	-4.868	1.13e-06 ***
		Mixed forest	0.21599	0.40447	0.534	0.593338
		Pine forest	-1.92173	0.55882	-3.439	0.000584 ***
		Riparian	-2.32357	0.77235	-3.008	0.002626 **
	Canopy height		0.13727	0.06016	2.282	0.022490 *
	Random effects		***V***	***SD***		
	Area		1.4778	1.2156		
	Transect		0.6748	0.8215		
	Month		0.3185	0.5643		

Species	Effect	Level				
P. pipistrellus	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		3.8472	0.6733	5.714	1.1e-08 ***
	Distance to light		-0.9773	0.3177	-3.076	0.0021 **
	Vegetation	Herbaceous	0.6297	0.4337	1.452	0.1465
		Unoccupied soil	0.6058	0.2771	2.186	0.0288 *
	Random effects		***V***	***SD***		
	Area		0.832	0.9122		
	Transect		0.1637	0.4046		
	Month		0.1068	0.3267		
P. pygmaeus	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		2.36695	0.46903	5.046	4.50e-07 ***
	Distance to light		1.63562	0.46101	3.548	0.000388 ***
	Habitat	*Montado*	-0.08041	0.53076	-0.151	0.879586
		Eucalyptus	-2.8519	0.6477	-4.403	1.07e-05 ***
		Mixed forest	-0.21465	0.36678	-0.585	0.55839
		Pine forest	-3.47983	0.45742	-7.608	2.79e-14 ***
		Riparian	-0.20645	0.66732	-0.309	0.757037
	Canopy		-1.28993	0.53199	-2.425	0.015320 *
	Canopy height		0.08663	0.04464	1.941	0.052296 .
	Random effects		***V***	***SD***		
	Transect		0.06189	0.2488		
	Month		0.08331	0.2886		
Pipistrellus sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		3.15556	0.60386	5.226	1.74e-07 ***
	Distance to light		-0.32019	0.35381	-0.905	0.3655
	Habitat	*Montado*	-0.20089	0.575	-0.349	0.7268
		Eucalyptus	-5.18007	0.89259	-5.803	6.50e-09 ***
		Mixed forest	0.30552	0.41352	0.739	0.46
		Pine forest	-0.88077	0.44116	-1.996	0.0459 *
		Riparian	-0.1146	0.66368	-0.173	0.8629
	Vegetation	Herbaceous	-1.03903	0.5836	-1.78	0.0750 .
		Unoccupied soil	-0.02907	0.25345	-0.115	0.9087
	Canopy height		0.14233	0.05547	2.566	0.0103 *
	Random effects		***V***	***SD***		
	Area		0.370135	0.60839		
	Transect		0.007888	0.08882		
Plecotus sp.	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		-1.21926	1.06038	-1.15	0.2502
	Distance to light		-0.39584	0.42751	-0.926	0.3545
	Vegetation	Herbaceous	-1.38627	0.6393	-2.168	0.0301 *
		Unoccupied soil	-0.74122	0.29178	-2.54	0.0111 *
	Canopy height		0.14198	0.06054	2.345	0.0190 *
	Random effects		***V***	***SD***		
	Area		1.7284	1.3147		
	Transect		0.3334	0.5774		
T. teniotis	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		-1.9972	2.6726	-0.747	0.4549
	Distance to light		0.802	0.8113	0.989	0.3229
	Habitat	*Montado*	-1.8497	1.0436	-1.772	0.0763 .
		Eucalyptus	-9.6734	106.7658	-0.091	0.9278
		Mixed forest	-1.2867	0.7679	-1.675	0.0938 .
		Pine forest	-1.14	0.9866	-1.156	0.2479
		Riparian	-1.0399	1.0958	-0.949	0.3427
	Random effects		***V***	***SD***		
	Area		11.528	3.395		
	Month		5.144	2.268		

			B	SE	z	p
Bat passes	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		5.6838	0.4889	11.626	< 2e-16 ***
	Distance to light		-0.9761	0.3165	-3.084	0.00204 **
	Habitat	*Montado*	0.362	0.4528	0.799	0.42409
		Eucalyptus	-1.7148	0.4312	-3.977	6.97e-05 ***
		Mixed forest	0.1921	0.271	0.709	0.47832
		Pine forest	-0.4575	0.3457	-1.323	0.18567
		Riparian	-0.6988	0.4991	-1.4	0.16148
	Random effects		***V***	***SD***		
	Area		0.4334	0.6583		
	Transect		0.15071	0.3882		
	Month		0.05603	0.2367		
Species richness	***Fixed effects***		***B***	***SE***	***z***	***p***
	Intercept		1.976737	0.091294	21.652	< 2e-16 ***
	Distance to light		-0.130285	0.128203	-1.016	0.31
	Habitat	*Montado*	0.020031	0.154536	0.13	0.897
		Eucalyptus	-1.268175	0.253247	-5.008	5.51e-07 ***
		Mixed forest	-0.037882	0.102144	-0.371	0.711
		Pine forest	-0.043753	0.133598	-0.327	0.743
		Riparian	-0.005789	0.194856	-0.03	0.976
	Random effects		***V***	***SD***		
	Area		0.01329	0.01329		



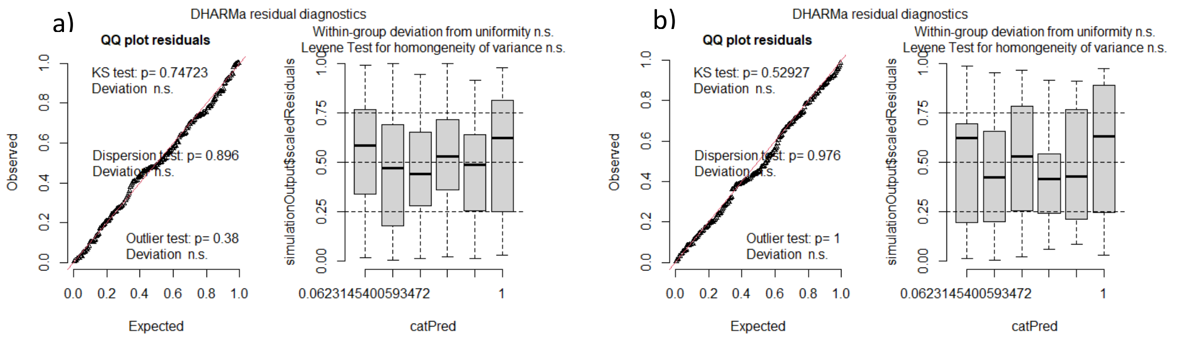
*Annexe 6 - **Bat assemblage composition dissimilarity** - Dissimilarity of bat assemblage composition based on a negative exponential (black) and power-law function (grey) in a gradient of distance to light per transect for all study areas.*

*Annexe 7 - **National GLMs results** - Multivariate GLMs with all significant variables for each species/group with estimate (B), standard error (SE), z-value (z) and p-value (p) with variable significance (*** < 0,001; ** < 0,01; * < 0,05 ; . < 0,1). For the soil occupation variable, the reference class is urban areas.*

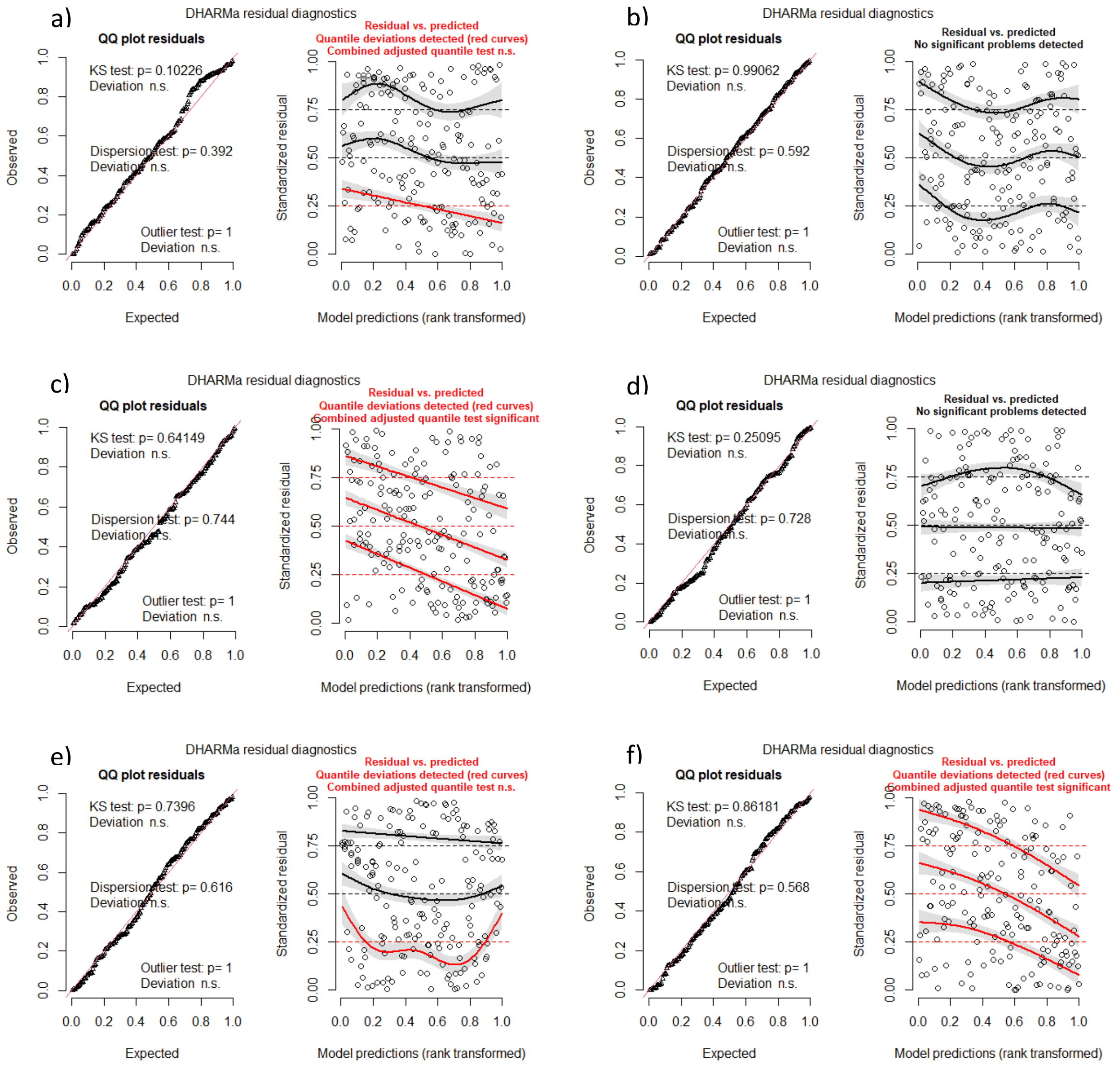
	Explanatory variables		***B***	***SE***	***z***	***p***
B. barbastellus	Intercept		1.02E+00	9.20E+00	0.11	0.912
	Radiance		-9.11E-03	8.81E-03	-1.034	0.30117
	Latitude		3.65E-06	1.04E-06	3.515	0.00044 ***
	Slope		-8.43E-02	2.99E-02	-2.821	0.00479 **
	NDVI		2.57E-02	5.50E-03	4.679	2.88E-06 ***
E. serotinus	Intercept		22.1659019	10.404458	2.13	0.033137 *
	Radiance		0.0099673	0.0182046	0.548	0.584026
	Elevation		0.0053168	0.0009945	5.346	8.97E-08 ***
	Slope		-0.1012313	0.0415491	-2.436	0.014833 *
	NDVI		0.0316818	0.0110685	2.862	0.004205 **
	Soil occupation	Agricultural and agro-forestry areas	-5.2301486	1.4185195	-3.687	0.000227 ***
		Forests	-4.768093	1.4541517	-3.279	0.001042 **
		Open forests, shrub and herbaceous vegetation	-5.6479303	1.5111218	-3.738	0.000186 ***
		Naked soil or sparsely vegetated	-4.3391277	1.7224327	-2.519	0.011763 *
H. savii	Intercept		23.15361	3.90355	5.931	3E-09 ***
	Radiance		-0.06486	0.01854	-3.498	0.000469 ***
	Average temperature		-1.08158	0.18498	-5.847	5E-09 ***
M. schreibersii	Intercept		-1.8305097	0.793413	-2.307	0.021 *
	Radiance		-0.0004458	0.0104506	-0.043	0.966
	NDVI		0.0139617	0.0061869	2.257	0.024 *
M. bechsteinii	Intercept		-4.69099	2.36521	-1.983	0.0473 *
	Radiance		-0.04592	0.03332	-1.378	0.1681
	NDVI		0.04059	0.01805	2.25	0.0245 *
M. blythii	Intercept		4.10E+01	1.21E+01	3.391	0.000697 ***
	Radiance		-6.00E-02	2.95E-02	-2.032	0.042126 *
	Latitude		-9.61E-06	2.85E-06	-3.379	0.000729 ***
	Distance to water		3.41E-04	1.19E-04	2.87	0.004110 **
	Distance to urban areas		-6.37E-04	3.14E-04	-2.028	0.042573 *
	Elevation		3.63E-03	1.52E-03	2.393	0.016700 *
M. daubentonii	Intercept		-2.47E+01	5.24E+00	-4.717	2.40E-06 ***
	Radiance		-1.46E-02	9.03E-03	-1.618	0.1056
	Latitude		5.68E-06	1.20E-06	4.743	2.11E-06 ***
	Distance to water		-1.62E-04	6.12E-05	-2.648	0.0081 **
M. emarginatus	Intercept		31.6659181	13.257521	2.389	0.01692 *
	Radiance		0.0211498	0.0153106	1.381	0.16716
	Distance to water		0.0002215	0.0001025	2.162	0.03064 *
	Slope		-0.1459428	0.0532554	-2.74	0.00614 **
	NDVI		0.0240713	0.0099678	2.415	0.01574 *
M. escalerai	Intercept		13.571959	9.845408	1.379	0.16805
	Radiance		-0.008636	0.016695	-0.517	0.60496
	Slope		-0.068984	0.038982	-1.77	0.07678 .
	NDVI		0.025325	0.007497	3.378	0.00073 ***
M. myotis	Intercept		-1.28E+01	6.36E+00	-2.017	0.0437 *
	Radiance		-2.06E-02	1.41E-02	-1.46	0.1442
	Latitude		3.12E-06	1.43E-06	2.181	0.0292 *
	Distance to urban areas		-3.93E-04	1.83E-04	-2.146	0.0319 *
N. lasiopterus / noctula	Intercept		19.1840259	6.8807129	2.788	0.00530 **
	Radiance		-0.0283746	0.0133364	-2.128	0.03337 *
	Distance to urban areas		-0.000383	0.0001467	-2.611	0.00902 **
	Slope		-0.0751097	0.0281404	-2.669	0.00761 **

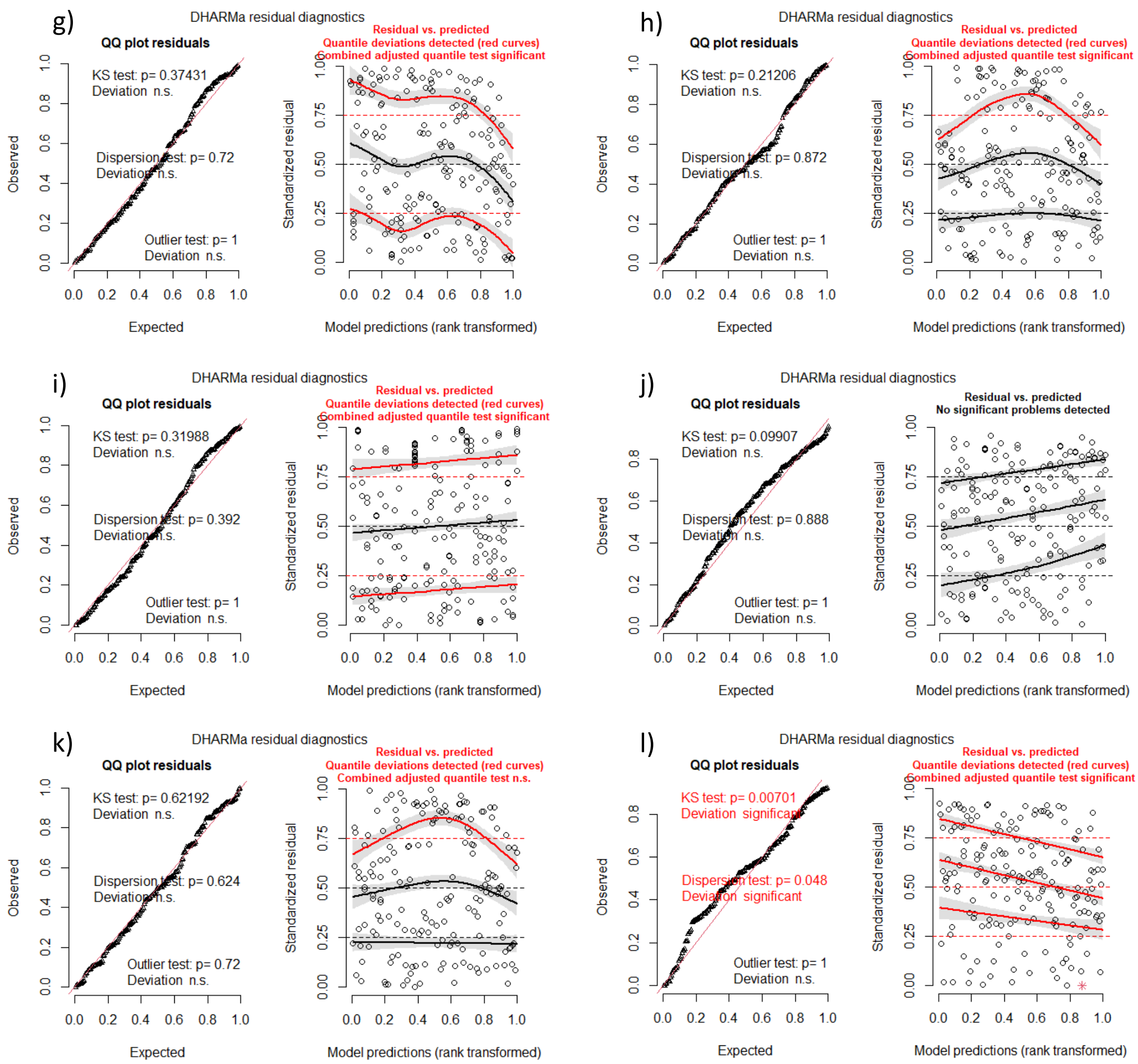
N. leisleri	Intercept		8.9680091	4.0430532	2.218	0.02655 *
	Radiance		0.0125767	0.0065157	1.93	0.05358 .
	Elevation		0.0017544	0.0003609	4.861	1.17E-06 ***
	Slope		-0.0457109	0.0158388	-2.886	0.00390 **
	NDVI		0.0197392	0.0037866	5.213	1.86E-07 ***
	Precipitation		-0.0484938	0.0155269	-3.123	0.00179 **
	Soil occupation	Agricultural and agro-forestry areas	-0.8354495	0.4160873	-2.008	0.04466 *
		Permanent pastures	-0.5601475	0.6380045	-0.878	0.37996
		Forests	-0.8126353	0.4200311	-1.935	0.05303 .
		Open forests, shrub and herbaceous vegetation	-0.5763754	0.4243489	-1.358	0.17438
		Naked soil or sparsely vegetated	-0.0440344	0.6469635	-0.068	0.94574
		Wetlands	-0.3282978	0.7048657	-0.466	0.64139
P. kuhlii	Intercept		7.50E+00	3.06E+00	2.454	0.01413 *
	Radiance		-2.84E-02	5.22E-03	-5.44	5.33E-08 ***
	Distance to urban areas		-1.22E-04	4.85E-05	-2.518	0.01181 *
	Slope		-2.97E-02	1.19E-02	-2.491	0.01275 *
	NDVI		9.85E-03	2.44E-03	4.041	5.33E-05 ***
	Soil occupation	Mining, construction and waste disposal sites	-7.49E-01	9.44E-01	-0.794	0.42743
		Agricultural and agro-forestry areas	-8.40E-01	3.35E-01	-2.509	0.01210 *
		Permanent pastures	-1.19E+00	4.34E-01	-2.745	0.00606 **
		Forests	-1.05E+00	3.41E-01	-3.069	0.00215 **
		Open forests, shrub and herbaceous vegetation	-1.11E+00	3.45E-01	-3.201	0.00137 **
		Naked soil or sparsely vegetated	-9.42E-01	5.52E-01	-1.708	0.08769 .
		Wetlands	-5.51E-01	5.09E-01	-1.082	0.2792
P. pipistrellus	Intercept		-1.67E+00	4.21E-01	-3.972	7.11E-05 ***
	Radiance		3.96E-03	4.95E-03	0.799	0.42451
	Distance to urban areas		-1.73E-04	5.46E-05	-3.159	0.00158 **
	Elevation		1.27E-03	2.27E-04	5.583	2.36E-08 ***
	NDVI		1.38E-02	2.38E-03	5.804	6.47E-09 ***
	Soil occupation	Agricultural and agro-forestry areas	-6.70E-01	2.74E-01	-2.445	0.01450 *
		Permanent pastures	-1.42E-01	4.08E-01	-0.347	0.72846
		Forests	-5.83E-01	2.83E-01	-2.064	0.03901 *
		Open forests, shrub and herbaceous vegetation	-6.27E-01	2.93E-01	-2.136	0.03266 *
		Naked soil or sparsely vegetated	-9.20E-02	4.91E-01	-0.187	0.8514
		Wetlands	5.61E-01	4.65E-01	1.205	0.22828

P. pygmaeus	Intercept		-1.520529	0.461911	-3.292	0.000995 ***
	Radiance		0.006038	0.005124	1.178	0.238631
	NDVI		0.016883	0.003414	4.945	7.62E-07 ***
	Precipitation		-0.044747	0.012621	-3.546	0.000392 ***
	Soil occupation	Agricultural and agro-forestry areas	-0.171355	0.310837	-0.551	0.581447
		Permanent pastures	-0.343999	0.486396	-0.707	0.479417
		Forests	-0.66579	0.335382	-1.985	0.047123 *
		Open forests, shrub and herbaceous vegetation	-0.39843	0.341756	-1.166	0.243683
		Naked soil or sparsely vegetated	0.452108	0.726955	0.622	0.533995
		Wetlands	0.914113	0.570452	1.602	0.109059
P. auritus	Intercept		13.160655	3.401807	3.869	0.000109 ***
	Radiance		-0.008061	0.019449	-0.414	0.678551
	Average temperature		-0.633778	0.164249	-3.859	0.000114 ***
P. austriacus	Intercept		11.989316	4.447281	2.696	0.00702 **
	Radiance		-0.004064	0.014239	-0.285	0.77531
	Average temperature		-0.564689	0.207786	-2.718	0.00657 **
R. euryale	Intercept		-2.917487	0.91251	-3.197	0.001388 **
	Radiance		0.032929	0.023273	1.415	0.157092
	Elevation		0.006043	0.001657	3.648	0.000265 ***
R. ferrumequinum	Intercept		-3.33E+00	6.86E+00	-0.485	0.62748
	Radiance		-1.41E-02	8.09E-03	-1.746	0.08084 .
	Latitude		3.67E-06	8.96E-07	4.092	4.28E-05 ***
	Slope		-5.70E-02	1.91E-02	-2.98	0.00288 **
	NDVI		8.47E-03	4.25E-03	1.992	0.04633 *
R. hipposideros	Intercept		2.44E+01	4.76E+00	5.131	2.89E-07 ***
	Radiance		-2.23E-02	8.31E-03	-2.679	0.00739 **
	Distance to urban areas		-2.91E-04	9.28E-05	-3.135	0.00172 **
	Slope		-9.28E-02	1.92E-02	-4.822	1.42E-06 ***
	Soil occupation	Mining, construction and waste disposal sites	-8.88E-01	1.32E+00	-0.672	0.50173
		Agricultural and agro-forestry areas	-1.24E+00	5.26E-01	-2.36	0.01829 *
		Permanent pastures	-1.94E+00	9.51E-01	-2.038	0.04154 *
		Forests	-9.95E-01	5.32E-01	-1.869	0.06160 .
		Open forests, shrub and herbaceous vegetation	-7.52E-01	5.35E-01	-1.407	0.15948
		Naked soil or sparsely vegetated	-2.86E+00	9.88E-01	-2.897	0.00377 **
R. mehelyi	Intercept		2.1781644	0.7534204	2.891	0.00384 **
	Radiance		0.0095811	0.018276	0.524	0.60011
	Distance to urban areas		-0.0005372	0.0002142	-2.508	0.01215 *
	Elevation		0.0048417	0.0016844	2.874	0.00405 **
	Precipitation		-0.3495568	0.0795779	-4.393	1.12E-05 ***
T. teniotis	Intercept		30.9642176	5.1267484	6.04	1.54E-09 ***
	Radiance		0.0146584	0.0092479	1.585	0.113
	Elevation		0.0011859	0.0004883	2.428	0.0152 *
	Slope		-0.0893607	0.0188405	-4.743	2.11E-06 ***
	Average temperature		-0.4788466	0.1006396	-4.758	1.95E-06 ***

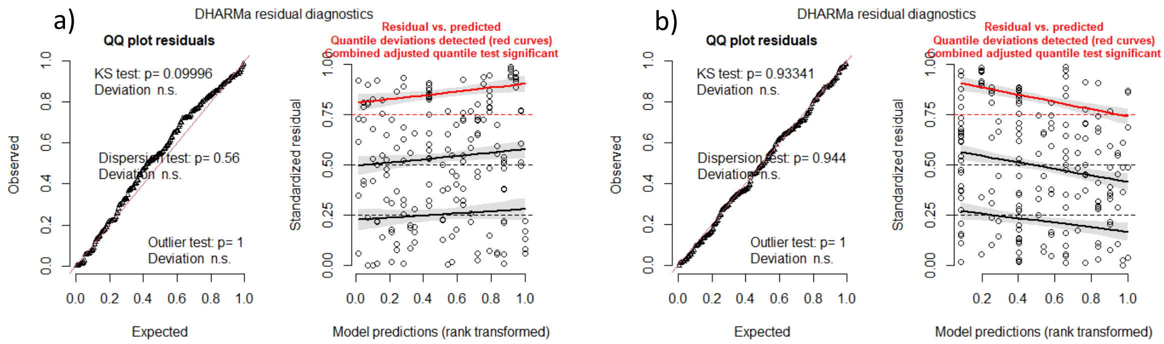


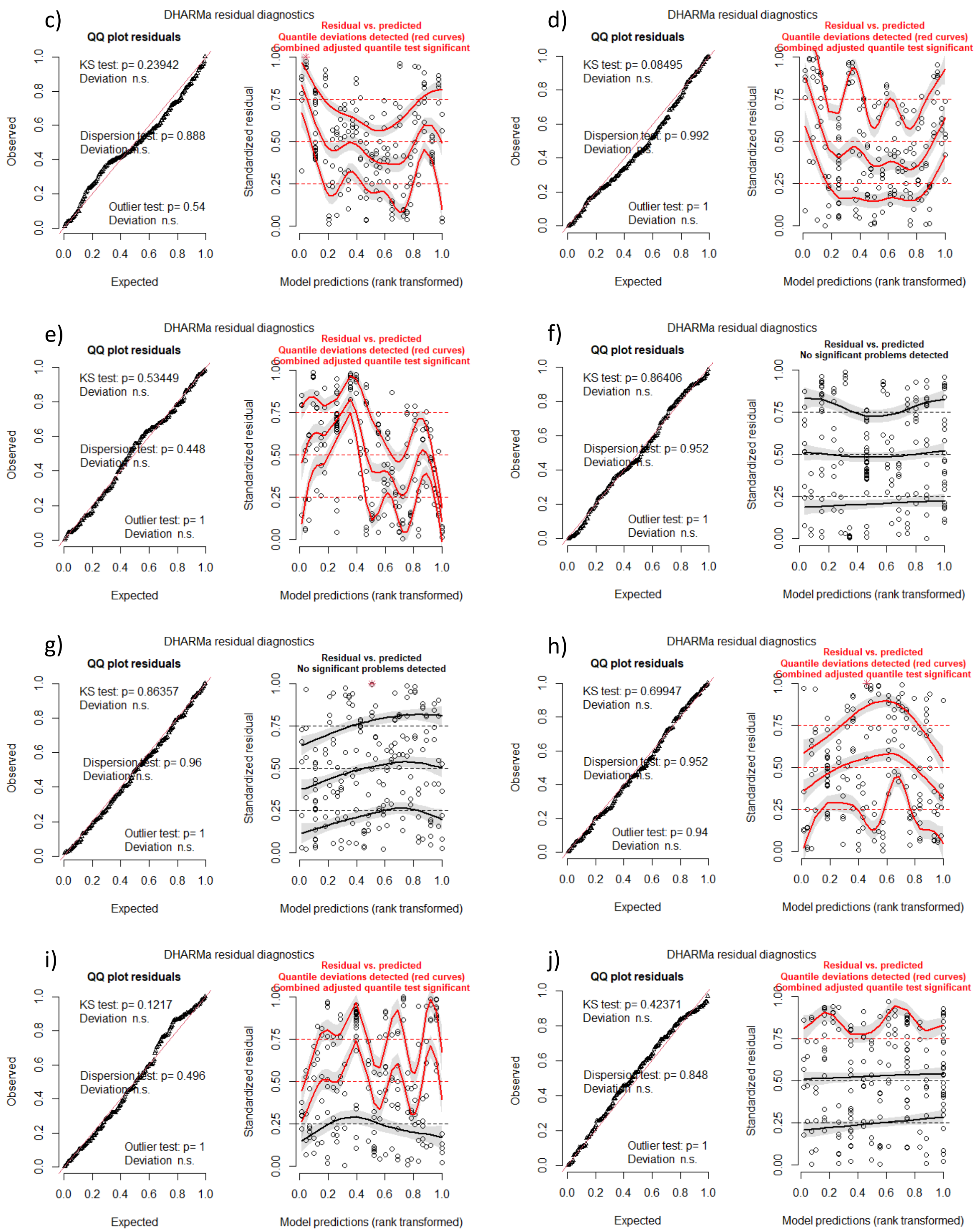
Annexe 8 – ***Distance to light residual diagnostics*** *- QQ plot residuals with KS test, dispersion test and outlier test, within-group deviation from uniformity and test for homogeneity of variance: (a) H. savii / P. kuhlii and (b) N. lasiopterus / N. noctule*

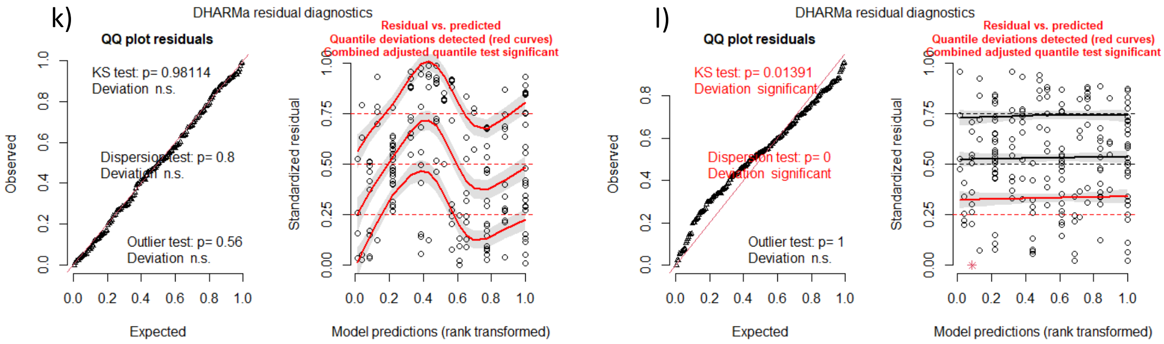




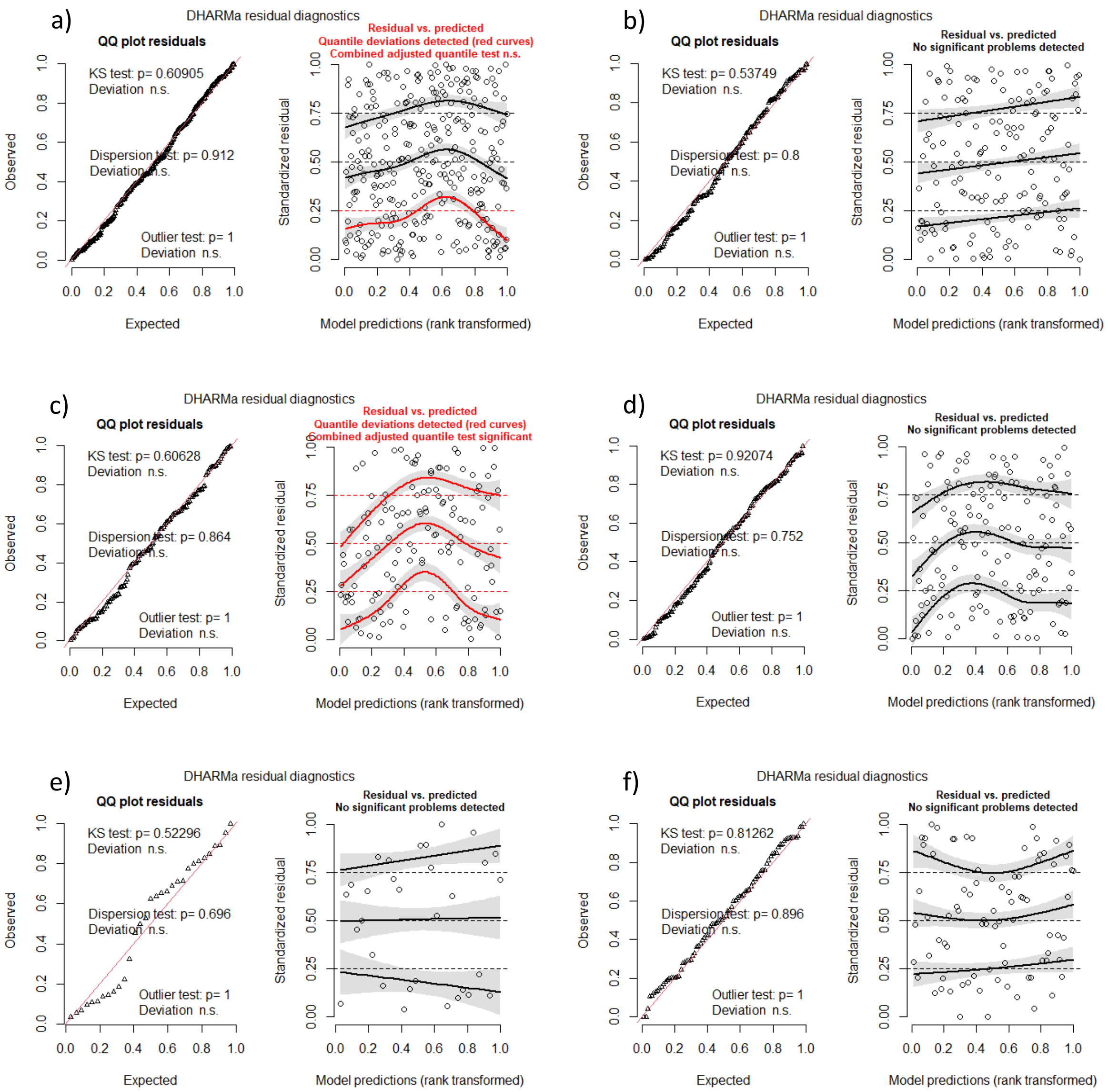
*Annexe 9 – **Environmental models residual diagnostics** - QQ plot residuals with KS test, dispersion test and outlier test, model predictions with residual vs. predicted: (a) Eptesicus sp., (b) Myotis sp., (c) N. leisleri / Eptesicus sp., (d) Nyctalus sp., (e) P. kuhlii, (f) P. pipistrellus, (g) P. pygmaeus, (h) Pipistrellus sp., (i) Plecotus sp., (j) T. teniotis, (k) total bat activity and (l) species richness.*



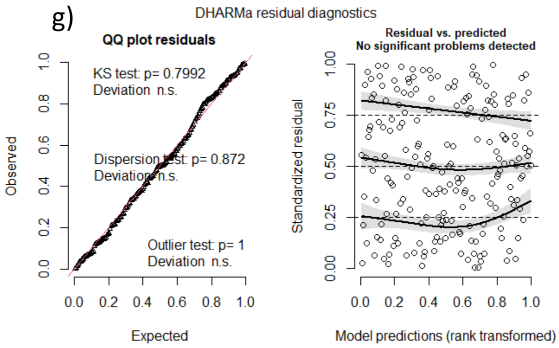

c)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.23942
Deviation n.s.
Dispersion test: p= 0.888
Deviation n.s.
Outlier test: p= 0.54
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)
d)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.08495
Deviation n.s.
Dispersion test: p= 0.992
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)
e)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.53449
Deviation n.s.
Dispersion test: p= 0.448
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)
f)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.86406
Deviation n.s.
Dispersion test: p= 0.952
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)
g)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.86357
Deviation n.s.
Dispersion test: p= 0.96
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)
h)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.69947
Deviation n.s.
Dispersion test: p= 0.952
Deviation n.s.
Outlier test: p= 0.94
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)
i)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.1217
Deviation n.s.
Dispersion test: p= 0.496
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)
j)
DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.42371
Deviation n.s.
Dispersion test: p= 0.848
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test significant
Standardized residual
Model predictions (rank transformed)



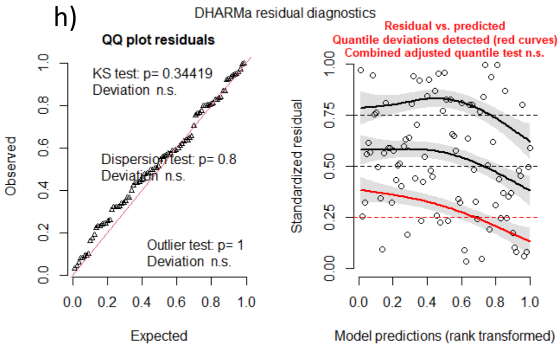
*Annexe 10 - **Vegetation models residual diagnostics** - QQ plot residuals with KS test, dispersion test and outlier test, model predictions with residual vs. predicted: (a) Eptesicus sp., (b) Myotis sp., (c) N. leisleri / Eptesicus sp., (d) Nyctalus sp., (e) P. kuhlii, (f) P. pipistrellus, (g) P. pygmaeus, (h) Pipistrellus sp., (i) Plecotus sp., (j) T. teniotis, (k) total bat activity and (l) species richness.*



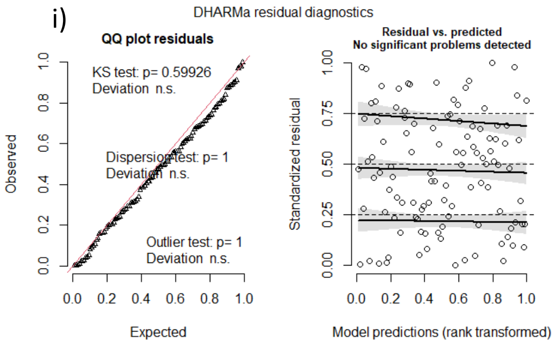
g)


DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.7992
Deviation n.s.
Dispersion test: p= 0.872
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

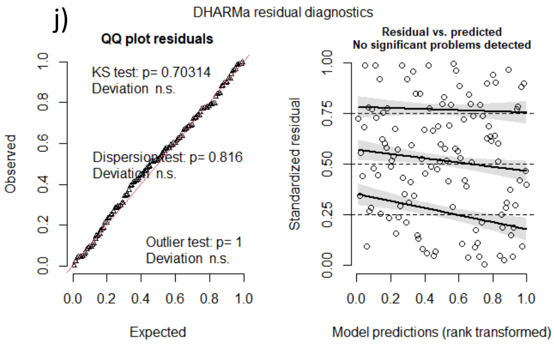
h)


DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.34419
Deviation n.s.
Dispersion test: p= 0.8
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
Quantile deviations detected (red curves)
Combined adjusted quantile test n.s.
Standardized residual
Model predictions (rank transformed)

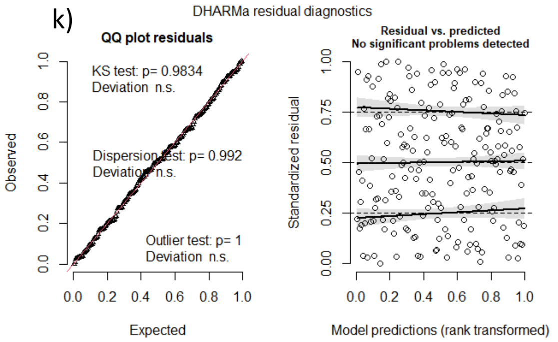
i)


DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.59926
Deviation n.s.
Dispersion test: p= 1
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

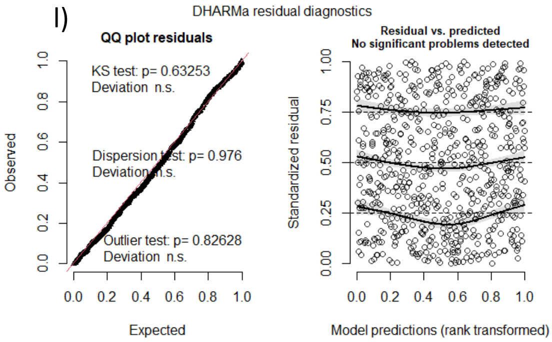
j)


DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.70314
Deviation n.s.
Dispersion test: p= 0.816
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

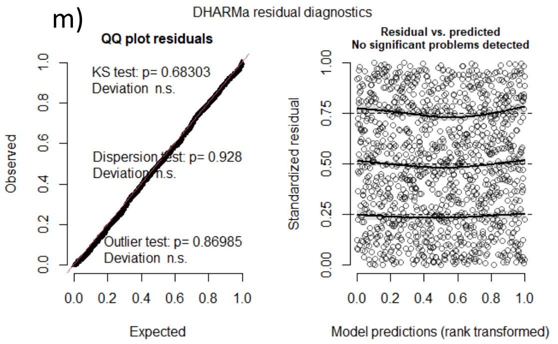
k)


DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.9834
Deviation n.s.
Dispersion test: p= 0.992
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

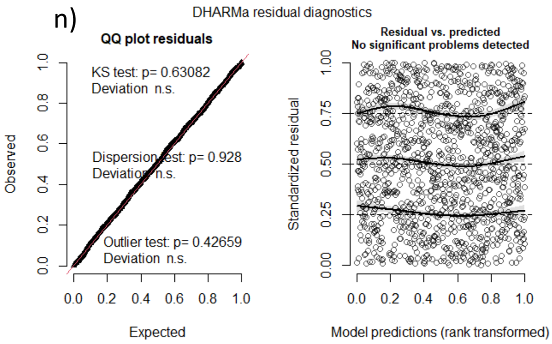
l)

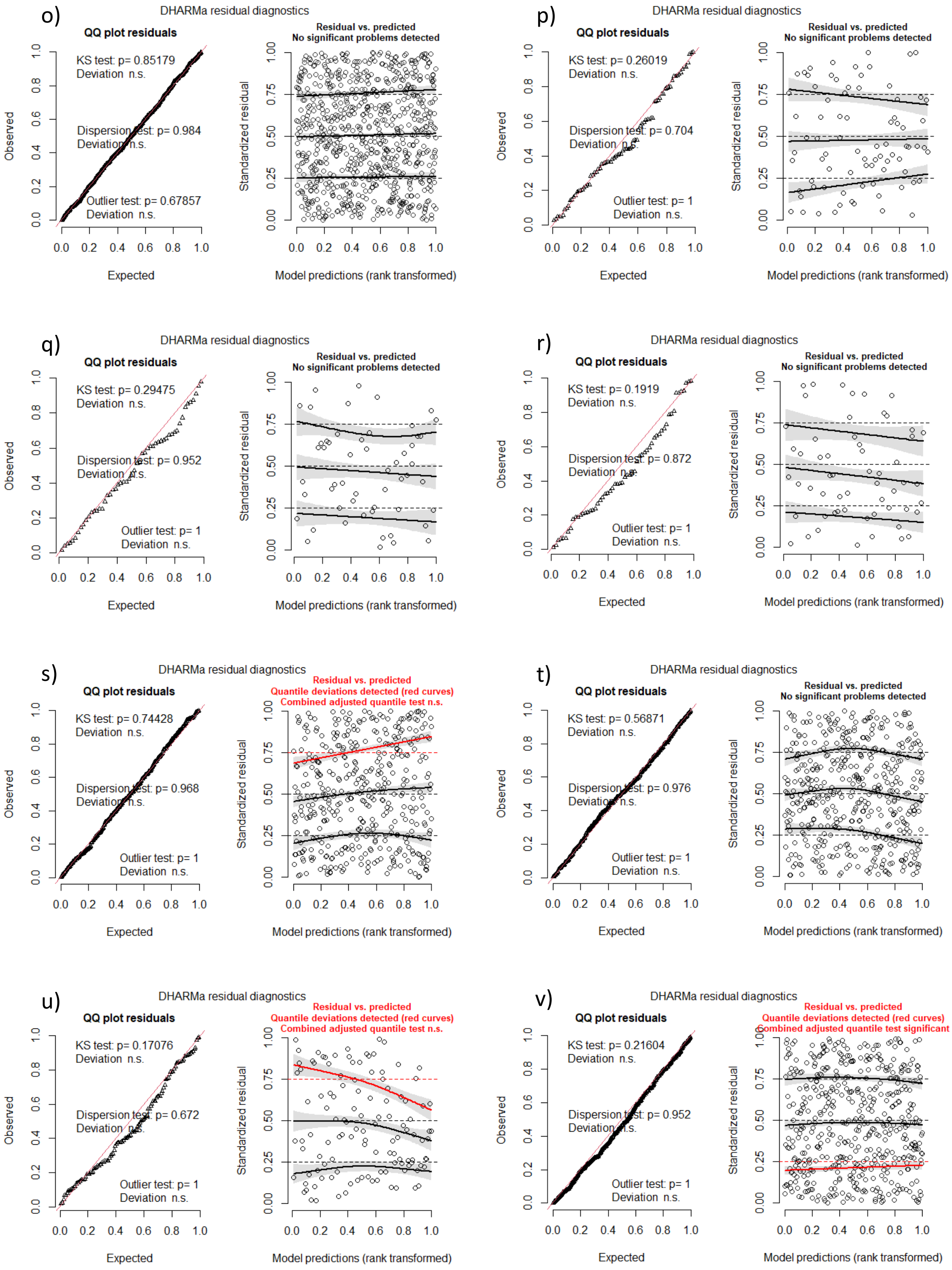

DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.63253
Deviation n.s.
Dispersion test: p= 0.976
Deviation n.s.
Outlier test: p= 0.82628
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

m)

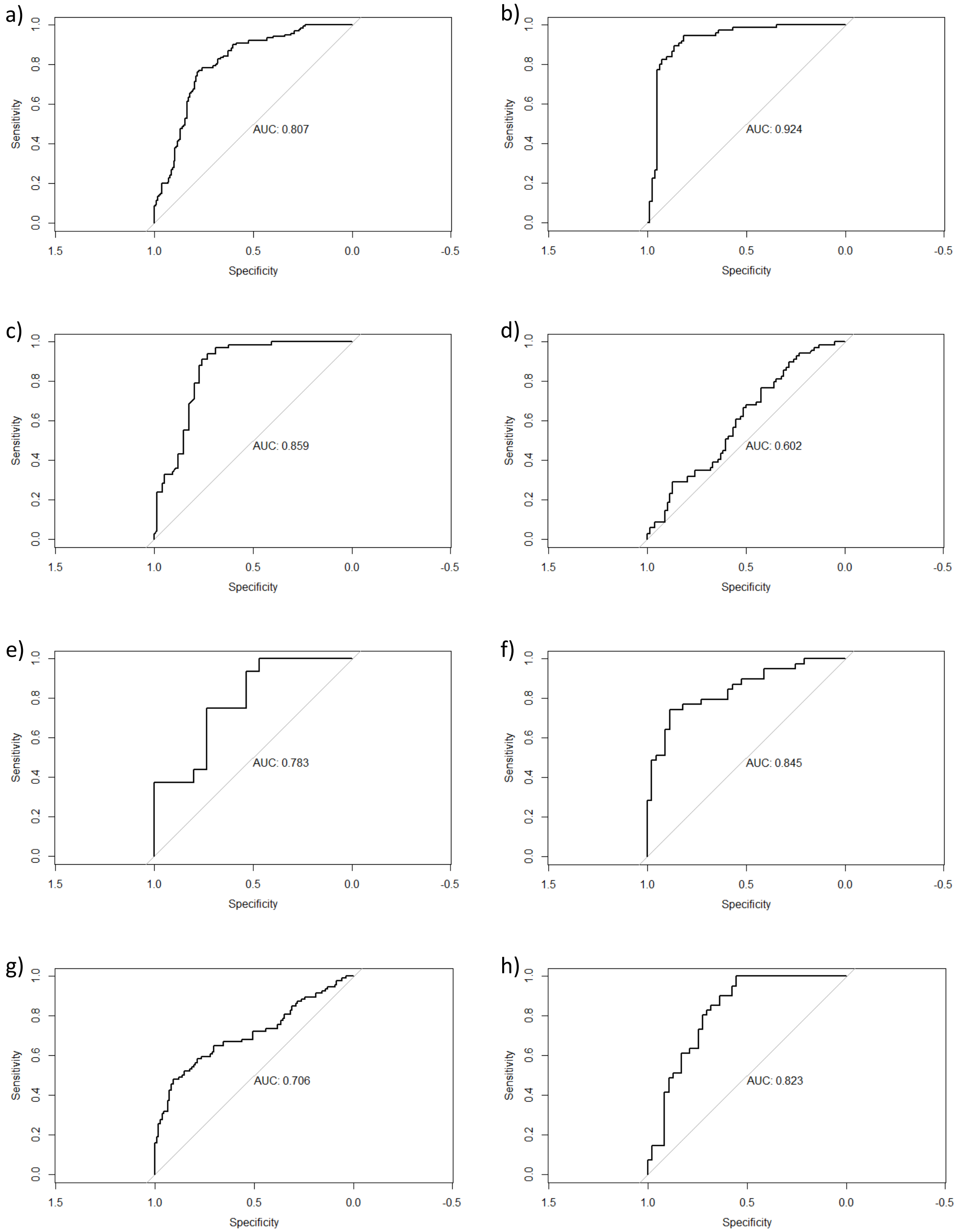

DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.68303
Deviation n.s.
Dispersion test: p= 0.928
Deviation n.s.
Outlier test: p= 0.86985
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)

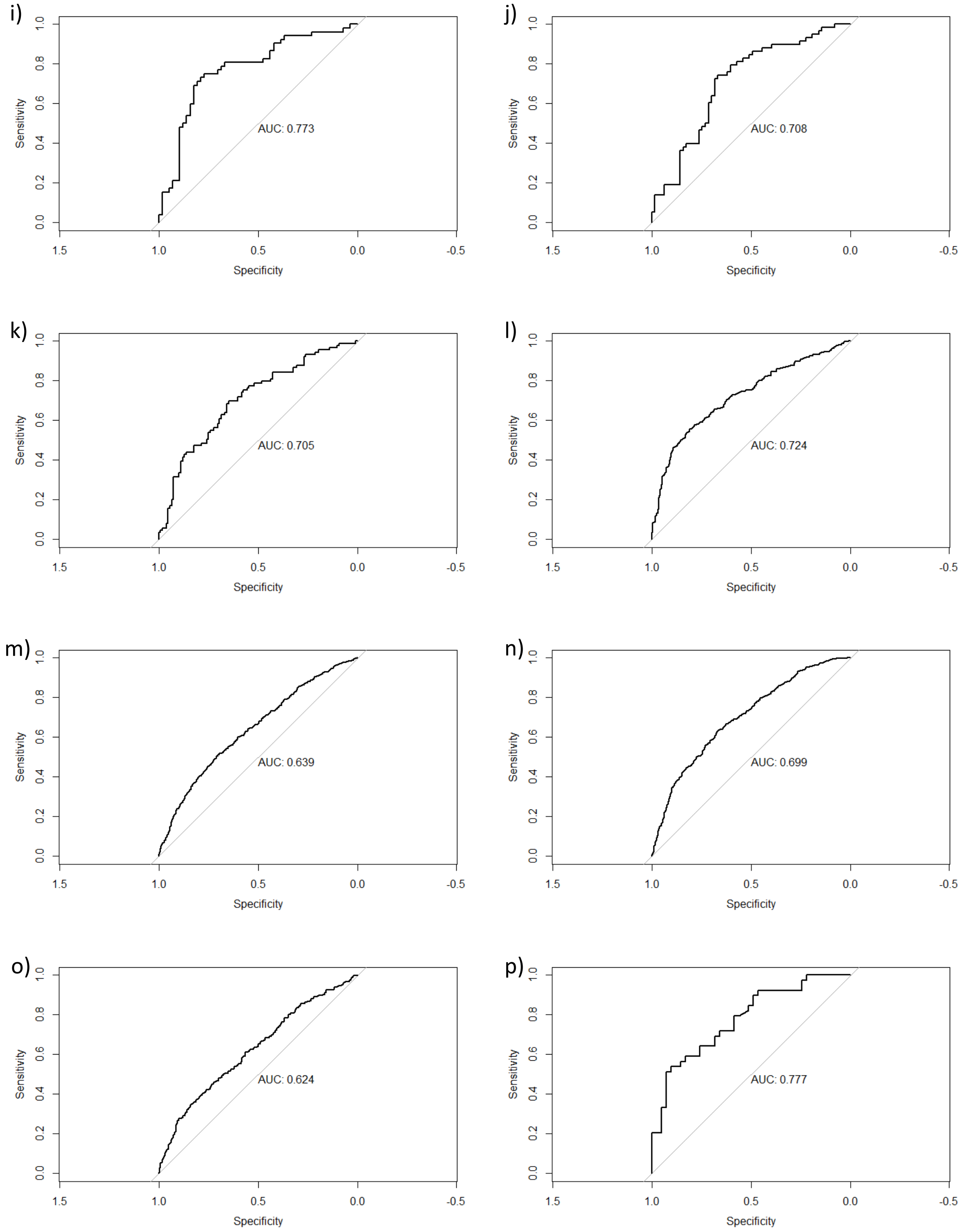
n)

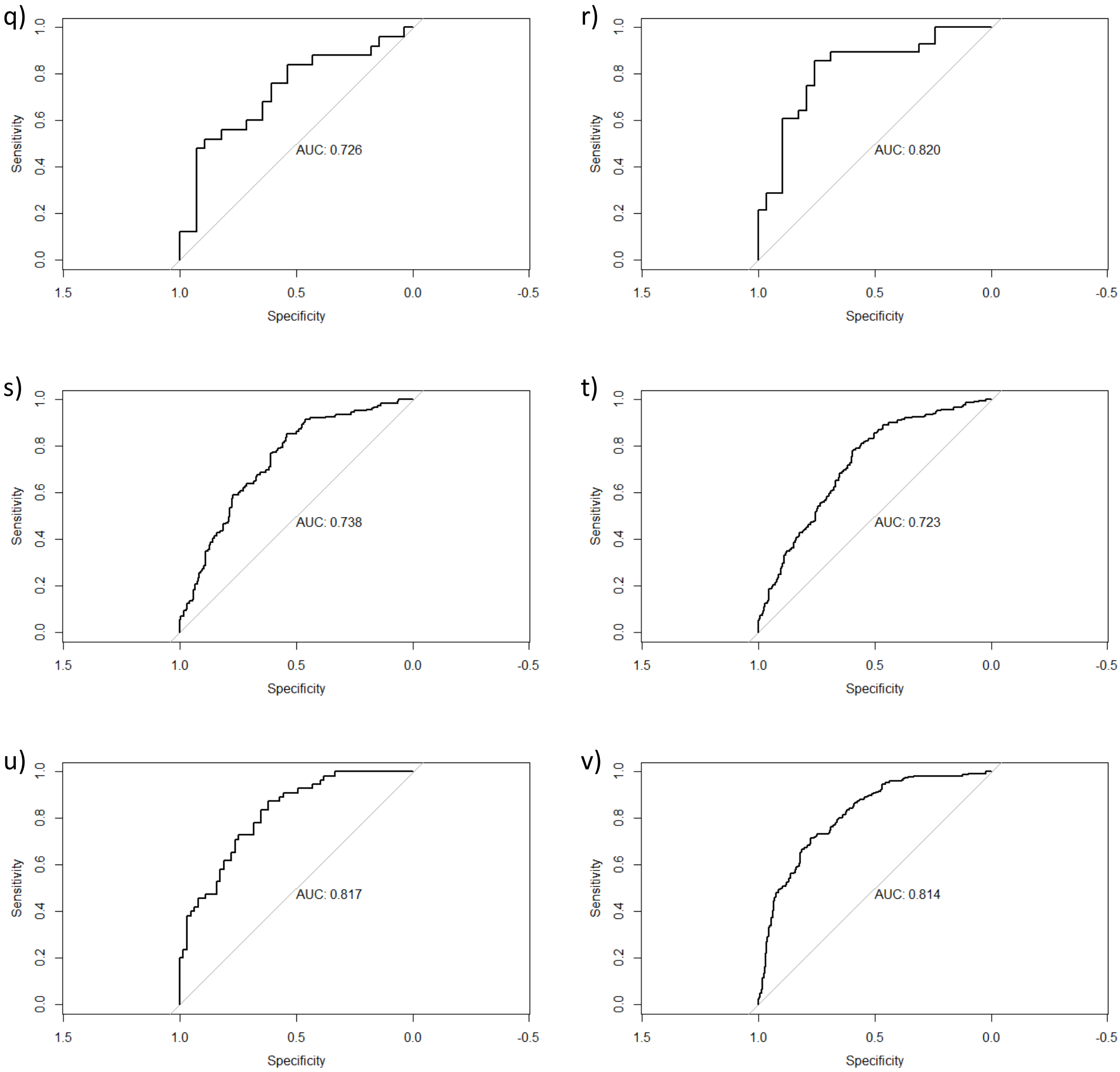

DHARMa residual diagnostics
QQ plot residuals
KS test: p= 0.63082
Deviation n.s.
Dispersion test: p= 0.928
Deviation n.s.
Outlier test: p= 0.42659
Deviation n.s.
Observed
Expected
Residual vs. predicted
No significant problems detected
Standardized residual
Model predictions (rank transformed)



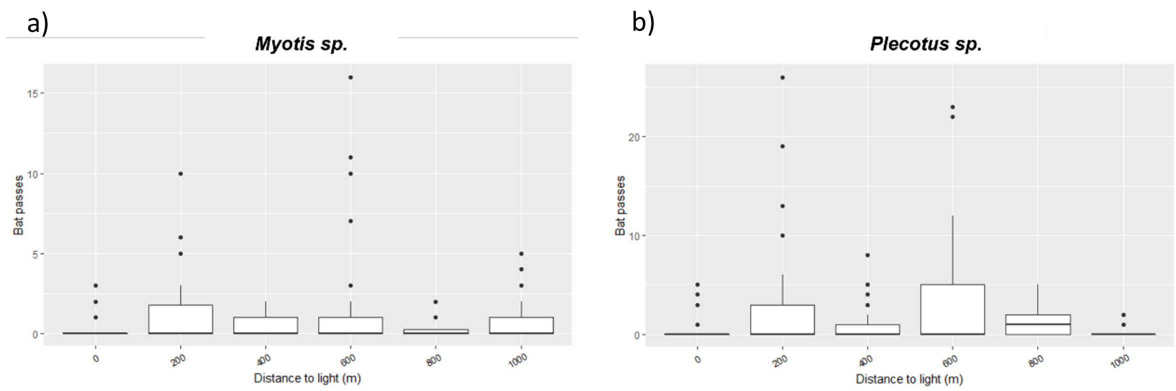
Annexe 11 - ***National models residual diagnostics*** *- QQ plot residuals with KS test, dispersion test and outlier test, model predictions with residual vs. predicted: (a) B. barbastellus, (b) E. serotinus, (c) H. savii, (d) M. schreibersii, (e) M. bechsteinii, (f) M. blythii, (g) M. daubentonii, (h) M. emarginatus, (i) M. escalerai, (j) M. myotis, (k) N. lasiopterus / N. noctule, (l) N. leisleri, (m) P. kuhlii, (n) P. pipistrellus, (o) P. pygmaeus, (p) P. auratus, (q) P. austriacus, (r) R. Euryale, (s) R. ferrumequinum, (t) R. hipposideros, (u) R. mehelyi and (v) T. teniotis.*


a)
b)
c)
d)
e)
f)
g)
h)
Sensitivity
Specificity
0.0
0.2
0.4
0.6
0.8
1.0
1.5
1.0
0.5
0.0
-0.5
AUC: 0.807
AUC: 0.924
AUC: 0.859
AUC: 0.602
AUC: 0.783
AUC: 0.845
AUC: 0.706
AUC: 0.823


i)
AUC: 0.773
j)
AUC: 0.708
k)
AUC: 0.705
l)
AUC: 0.724
m)
AUC: 0.639
n)
AUC: 0.699
o)
AUC: 0.624
p)
AUC: 0.777
Sensitivity
Specificity
0.0
0.2
0.4
0.6
0.8
1.0
1.5
1.0
0.5
0.0
-0.5



Annexe 12 - ***National models AUC*** *- Area Under the Receiver Operator Characteristic (AUC) Curve establishing model explanatory capacity: (a) B. barbastellus, (b) E. serotinus, (c) H. savii, (d) M. schreibersii, (e) M. bechsteinii, (f) M. blythii, (g) M. daubentonii, (h) M. emarginatus, (i) M. escalerai, (j) M. myotis, (k) N. lasiopterus / N. noctule, (l) N. leisleri, (m) P. kuhlii, (n) P. pipistrellus, (o) P. pygmaeus, (p) P. auratus, (q) P. austriacus, (r) R. Euryale, (s) R. ferrumequinum, (t) R. hipposideros, (u) R. mehelyi and (v) T. teniotis.*



Annexe 13 - ***Bat passes per sampling point*** *– Raw number of bat passes per sampling point, with an increasing distance to light for: Myotis sp. (a) and Plecotus sp. (b).*