

Response of bats and nocturnal insects to urban green areas in Europe



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Abstract

Animal biodiversity in cities is generally expected to be uniformly reduced, but recent studies show that this is modulated by the composition and configuration of Urban Green Areas (UGAs). UGAs represent a heterogeneous network of vegetated spaces in urban settings that have repeatedly shown to support a significant part of native diurnal animal biodiversity. However, nocturnal taxa have so far been understudied, constraining our understanding of the role of UGAs on maintaining ecological connectivity and enhancing overall biodiversity. We present a well-replicated multi-city study on the factors driving bat and nocturnal insect biodiversity in three European cities. To achieve this, we sampled bats with ultrasound recorders and flying insects with light traps during the summer of 2018. Results showed a greater abundance and diversity of bats and nocturnal insects in the city of Zurich, followed by Antwerp and Paris. We identified artificial lighting in the UGA to lower bat diversity by probably filtering out light-sensitive species. We also found a negative correlation between both bat activity and diversity and insect abundance, suggesting a top-down control. An in-depth analysis of the Zurich data revealed divergent responses of the nocturnal fauna to landscape variables, while pointing out a bottom-up control of insect diversity on bats. Thus, to effectively preserve biodiversity in urban environments, UGAs management decisions should take into account the combined ecological needs of bats and nocturnal insects and consider the specific spatial topology of UGAs in each city.

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Introduction

Urbanisation is a heterogeneous, worldwide phenomenon imposing important challenges to wildlife conservation. Rapid urbanisation in the last decades negatively impacts biodiversity in complex ways (e.g. Parris, 2016; Rivkin et al., 2019). However, the specific effects of urbanisation are neither linear nor constant, but vary amongst and within cities (Beninde, Veith & Hochkirch, 2015). In Europe, most cities have developed in former agricultural lands sharing similar environmental histories. Nonetheless, they are still heterogeneous in their cityscape. Although this heterogeneity has been noticed previously (Ramalho & Hobbs, 2012), most urban ecology studies still follow a single-city approach hampering the extrapolation of the results to other cities (Beninde et al., 2015). Finally, despite urbanisation reducing the amount of available habitat, cities also contain a network of urban green areas (UGAs) that have been shown to be a key factor enhancing biodiversity (McIntyre, Rango, Fagan & Faeth, 2001; Sattler, Duelli, Obrist, Arlettaz & Moretti, 2010).

In most European cities, densely built-up districts with little or no green areas represent a small fraction of the whole urban areas. The majority of the urban districts have intermediate levels of urbanisation and contain a variable and sometimes dominant proportion of UGA. UGAs represent a network of highly heterogeneous patches usually distributed forming mosaics, such as parks, green roofs or tree pits (Lepczyk et al., 2017). Locally, UGAs strongly vary in many features such as size, structure, vegetation composition, water availability, ownership or management. For instance, UGAs may range from large sites with a complex, multi-layered vegetation structure to linear, highly managed lawn stripes. At the landscape scale, the contribution of UGAs to the habitat amount is mediated by their composition and configuration as well as by the permeability of the surrounding matrix (Lepczyk et al., 2017). Altogether, this hampers disentangling the factors shaping biodiversity and ultimately making conservation assessments. Finding tools to successfully measure and synthesise these complex relationships is a key step towards a more holistic urban biodiversity management.

A long-lasting problem in urban ecology is how to reliably infer the effects of urban intensification (e.g. modifications on habitat amount, heterogeneity, disturbances, stressors or isolation) on biodiversity. Remote sensing tools such as LiDAR (i.e. Light Detection and Ranging) or artificial light at night (ALAN) maps are becoming more accessible, and have been proven to be good proxies of habitat amount and disturbance, respectively (Sánchez De Miguel et al., 2019). Still, the potential of remote sensing tools remains underutilised as few studies to date have included this type of metrics (but see Hale, Fairbrass, Matthews, Davies & Sadler, 2015; Zellweger et al., 2016), probably because their potential is not yet fully understood. Habitat, land-cover and land-use maps are generally

available for most cities in Europe and used as proxies of habitat amount, heterogeneity and connectivity (e.g. Munzi et al., 2014). However, they significantly vary in grain and most importantly, in the ecological information used to define the different mapping categories. Finally, ALAN maps have been used to show the responses of a wide variety of organisms to light pollution (Hale et al., 2015; Knop et al., 2017). Nevertheless, there is limited understanding of the effects of artificial lightning on biotic communities (Sanders & Gaston, 2018).

Bats and nocturnal insects represent an understudied assemblage showing ecological features that make them a striking group to monitor the effects of urbanisation. First, they represent a prey-predator system as European bats feed on nocturnal insects. Prey-predator systems might exhibit two types of responses towards modifications of the habitat amount or disturbances: bottom-up, such as greater feeding bat activity with increasing insect biomass (Threlfall, Law & Banks, 2012a) or top-down, for instance insect pest control by bats (Puig-Montserrat et al., 2020). Second, nocturnal animals, such as bats and nocturnal insects, might have a different susceptibility towards anthropogenic disturbances (e.g. light pollution) than diurnal ones. Further, they strongly differ from diurnal organisms in terms of the orientation system they use to move and forage. These two traits regulate the scale at which the organisms perceive the environment and thus the modifications and disturbances that occur (Concepción, Moretti, Altermatt, Nobis & Obrist, 2015). Finally, bats can be classified in three general guilds (i.e. long-, mid- and short-range echolocators) with differences in their foraging strategies (see Frey-Ehrenbold, Bontadina, Arlettaz & Obrist, 2013; Froidevaux, Zellweger, Bollmann & Obrist, 2014). Therefore, bats can be considered a potential bioindicator of land-use changes, particularly urbanisation, but studies on these groups are still scarce (but see Jones, Jacobs, Kunz, Wilig & Racey, 2009).

Prior research testing the effects of urbanisation on bats and nocturnal insects has yielded mixed results. Generally, urbanisation has been reported to simplify bat communities by filtering out sensitive species and keeping those with generalistic traits leading to a certain degree of biotic homogenisation (Russo & Ancillotto, 2015), a process documented also for other taxa (Chong et al., 2014; but see Fournier, Frey & Moretti, 2020). For instance, earlier research has revealed a decrease in bat diversity following reductions of the amount of available habitat due to urban intensification (e.g. Kurta & Teramino, 1992). Nonetheless, other urban intensification drivers have unclear effects. Light pollution has been shown to negatively impact many groups, particularly nocturnal animals (Stone, Harris & Jones, 2015). Still, some studies propose that this disturbance might not have a significant effect on bats, as they could move to more suitable patches (Krauel & LeBuhn, 2016); or even be advantageous for them. For instance, streetlights on linear paths attract large amounts of nocturnal insects facilitating foraging of light-opportunistic bats

(Russo & Ancillotto, 2015). Conversely, bat species with low tolerance to light pollution (i.e. light-averse) are filtered out (Stone et al., 2015). On the other hand, the effects of urbanisation on nocturnal insects have been little investigated but some patterns have been reported. Similarly to bats, a negative relationship appears between building density and nocturnal insect diversity (Krauel & LeBuhn, 2016; Russo & Ancillotto, 2015). Threlfall et al. (2012a) suggest that the negative effects on nocturnal insects' biomass could be explained by the increase in impervious surfaces, leading to loss and fragmentation of available habitat and, thus, to low primary productivity. On the contrary, urban native vegetation has been proposed to sustain nocturnal insect populations (Russo & Ancillotto, 2015). Thus, it is expected that insect abundance and its drivers greatly influence bat distribution in urban areas (Krauel & LeBuhn, 2016).

In this paper, we studied the influence of biotic and abiotic factors in shaping the diversity, activity and abundance of bats and nocturnal insects in urban green areas using two contrasting designs in terms of the number of cities included and the type of the urban intensification proxies used. First, we investigated the responses across three European cities (Antwerp, Paris and Zurich) to test whether the effects of urbanisation on the response variables were consistent. We used a standardised set of urbanisation proxies across all cities including land use and light pollution maps. Second, we additionally studied the same set of responses of bats and nocturnal insects but adding high-resolution predictors available for the city of Zurich to further infer the amount of available habitat and the role of vegetation structure.

Materials and methods

Study region and selection of sampling sites

The study region is Western and Central Europe, in particular Paris, France (48°51'23"N, 2°20'58"E), Zurich, Switzerland (47°22'40"N, 8°32'23"E) and Antwerp, Belgium (51°12'48"N, 4°24'55"E). These cities vary in terms of population density, size and percentage of green areas (United Nations, 2019).

We focused on the UGAs mapped and defined in the European Urban Atlas (see EEA, 2012) to select patches. We used an orthogonal gradient of patch size (area in m²) and connectivity. Connectivity was calculated using the Proximity Index (PI) which considers the area and the distance to all nearby patches with a favourable habitat, within a given search radius. Thus, the PI measures the degree of patch isolation, with highest values given to less isolated patches (McGarigal, Cushman & Ene, 2012). We considered as favourable habitat all patches with high probability of having trees (that is, UGAs, urban forest and grey urban land-cover with less than 30% impervious surface, see EEA, 2012). The search radius was set to 5 km from each focal patch, in order to accommodate all possible animal

mobility ranges. Lower buffer values (from 500 m onwards) did not greatly change the PI values, because the distance is squared, thus greatly limiting the impact of patches beyond a certain distance. To select patches using the orthogonal design, all possible patches were classified in six size classes and six classes of PI (36 possible combinations). Within these combinations patches were selected randomly (random stratified sampling design). Due to resource limitations we only used $\frac{1}{3}$ of the possible combinations in Paris and Antwerp (maximizing the gradient) and the full range of combinations in Zurich (32 combinations, the other combinations were not available). This resulted in the final selection of 56 sites: 12 in Paris, 12 in Antwerp and 32 in Zurich. Sites were selected keeping a minimum distance of 500 m (except for two sites in Zurich selected by their position in the urban gradient, separated by 360 m). Median distance to the nearest site was 1050 m and 85% of the sites were separated by at least 800 m.

Field data collection

Cities were visited twice from mid-May to mid-July 2018. Bat recordings and nocturnal insect collections were conducted simultaneously at the 12 selected UGAs of each city, except the 32 sites in Zurich, which were split in two sampling periods due to limited equipment. Samplings were scheduled for 5 consecutive nights per site for each of the two sampling periods, in order to avoid insufficient data sizes and reliably sample the species community. Samplings were carried out under favourable weather conditions, that is, without rain and temperatures above 12 °C (Hutson, Mickleburgh & Racey, 2001).

Acoustic bat survey

Echolocation sampling was conducted with acoustic data loggers installed on the trunk of a suitable tree with open canopy (1 m² with no branches in front of the device), between 3–4 m above ground. Bat foraging activity was measured with the autonomous ultrasound recorders Batlogger M (Elekon AG, 2018). The recording systems were sensitive from 10 to 150 kHz (± 5 dB) and were set up to record from 15 min before sunset to 15 min after sunrise – adapted to each city and date – during 5 consecutive nights. Bat echolocation calls were identified using Batscope 3 (<http://www.batscope.ch>; Obrist & Boesch, 2018). This software automatically processes the sequences and assigns each single call to a suitable species with a mean rate of correct classifications of 95.7% (Obrist & Boesch, 2018). Not all calls could be identified to species level for some cryptic calls. In such cases, classification was done manually to the best possible taxonomic level (see Appendix A), thereby avoiding errors that can occur in automated species identification (Russo & Voigt, 2016; Rydell, Nyman, Eklöf, Jones & Russo, 2017). Subsequently, taxa were classified into

three ecologically meaningful guilds, according to their clutter resistance and echolocation range: short-range echolocators (SRE), mid-range echolocators (MRE) and long-range echolocators (LRE) (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2014).

Bat foraging activity was calculated on a daily basis, computing the activity of the three considered guilds in windows of 5 min, to balance for possible extended foraging bouts of a single bat around a site. Counts were then weighted by the number of possible observational 5-minute periods per night, resulting in a relative activity. Bat diversity was estimated per night with the Shannon Index in two ways: using the best possible taxonomic level (i.e. bat group diversity) and only reliably identified species (i.e. bat species diversity).

Nocturnal insect collection

We collected nocturnal flying insects (hereafter referred to as insects) in parallel to bats. Based on the assumption that nocturnal insects possess positive phototaxis (Price & Baker, 2016; van Grunsven et al., 2014), we designed an intercept LED light-trap to sample insects (for details see Appendix A). To minimize interferences, the faint (5 lx) light-traps were installed in a suitable tree 10–20 m distant from the Batlogger, hung from an open foliage branch at least 4.5 m above ground. Traps were emptied daily after each sampling night. In the laboratory, insects were classified to the order level using an Olympus SZ40 stereo microscope, entomological guidebooks (e.g. Chinery, 1988) and expert advice. Insect diversity was estimated per night with the Shannon Index and insect abundance as the counts of each sample. As organism type or size may influence its quality as bat food (Hutson et al., 2001), each order was assigned a relative factor according to its body length and a wet biomass index calculated per sample. We assumed insect shapes to be ellipsoids for the calculations. Some orders were additionally divided into size classes (e.g. Lepidoptera: <5 mm, 5–20 mm, >20 mm; see Appendix A: Table 2). Note that insect variables could not be estimated for all the sites, as several of the initial light-traps were vandalised in the course of the sampling. From the initial 56 sampling patches, we obtained unbalanced data for 12 sites in Paris, 11 in Antwerp and 26 in Zurich.

Biotic variables

We attempted to study the bottom-up and top-down controls, as our groups represent a prey-predator system. To infer the bottom-up control, we used insect diversity and abundance, while top-down control was measured with bat group and species diversity and both total bat and guild relative activity (Table 1).

Environmental and landscape variables

We used environmental and landscape variables of ecological relevance for the studied organisms (Cusimano, Massa & Morganti, 2016; Threlfall, Law & Banks, 2012b). We obtained climatic predictors including night temperature, precipitation levels and wind speed for Zurich (Meteo Schweiz database), Antwerp and Paris (Weather Underground, 2018). Landscape variables were calculated with different buffer radii from the focal sampling point: 50, 100, 350 and 500 m, in order to suit the dispersal abilities of insects (Ropars, Dajoz, Fontaine, Muratet & Geslin, 2019) and bats (Hutson et al., 2001). For each sampling site, we used the European Urban Atlas (EEA, 2012) for calculating the size (area of each patch), the Proximity Index, the edge-to-edge distance to the nearest UGA and the proportion of impervious surfaces (e.g. urban fabric, roads). We estimated the distance to the nearest water body following Krauel and LeBuhn (2016) and Price and Baker (2016). The land-use heterogeneity (Matthies, Rüter, Schaarschmidt & Prasse, 2017; McIntyre et al., 2001) was calculated as the Shannon Index of habitats per site, using the European Urban Atlas for the three cities and in Zurich also using a high-resolution land-cover map (Gruen Stadt Zuerich, 2010) (see Table 1). All the connectivity and landscape measurements were calculated in ESRI ArcMap 10.4.1.

Moreover, for the city of Zurich we used Airborne Laser Scanning (ALS) metrics of woody vegetation (>1 m). These types of remote sensing data are surrogates of habitat amount and vertical heterogeneity of vegetation structure and have been shown to be good predictors of biodiversity in urban ecosystems (Frey et al., 2018; Zellweger et al., 2016). The habitat amount was estimated as the woody vegetation cover and the heterogeneity of structures as the standard deviation of woody vegetation heights at 50, 100, 350 and 500 m radii (Table 1; for details see Frey et al., 2018).

Increasing ALAN has been shown to disturb bat and insect biodiversity (Knop et al., 2017; Lewanzik & Voigt, 2017). We estimated ALAN by measuring illuminance levels in a set of randomly selected points in each city (Paris = 50, Zurich = 40, Antwerp = 43) using a lux metre Testo 540 (<https://www.testo.com>). We intended to cover the radiance range of every city to calibrate a night image from the International Space Station (Earth Science & Remote Sensing Unit NASA, 2018). Once the raster was calibrated, light emission in lux at each sampling site was extrapolated. However, the correlation of the lux metre readings with the calibration data was low in Paris ($R^2 = 0.1189$), thus the raw RGB colour values (of the night image) of the raster were calculated at each focal sampling point (pixel size of 40×40 m) and used as surrogate of ALAN (Table 1).

Statistical analysis

All the analyses and statistical figures were done with the statistical computing software R v.3.5.1 (R Core Team, 2018) and

Table 1. Classification of predictors into categories. The table depicts the seven categories (i.e. City, Connectivity, Landscape, Remote sensing, Prey and Predator estimates and Statistical interactions) used to aggregate the 44 predictors included in the models in order to facilitate reporting of the results (see Figs. 1–3). Each category is described and the number and type of predictors included and their availability in each city for analysis is reported (A=Antwerp, P=Paris, Z=Zurich).

Category	Description	Number of predictors	Predictors	Availability
City	Contains a single variable, the city identity	1	City	–
Connectivity	Metrics of habitat connectivity used as proxy of the amount of available habitat based on the European Urban Atlas	6	Distance near patch Distance water Area Isolation Proximity Index (500 and 5000 m)	A, P, Z A, P, Z A, P, Z A, P, Z A, P, Z
Landscape	Landscape metrics measuring the diversity of land-uses (land-use heterogeneity) and the amount of impervious surfaces (impervious cover) used as proxy of the amount of available habitat and based on the European Urban Atlas and the Zurich Habitat Map	12	Land-use heterogeneity (50, 100, 350, 500 m) of European Urban Atlas Land-use heterogeneity (50, 100, 350, 500 m) of Zurich Habitat Map Impervious cover (50, 100, 350, 500 m)	A, P, Z Z A, P, Z
Remote sensing	High-resolution remote sensing predictors used to assess light pollution (ALAN and ALAN RGB) and vegetation structure (vegetation cover, heterogeneity and foliage height diversity)	14	ALAN ALAN RGB Vegetation cover (50, 100, 350, 500 m) Vegetation heterogeneity (50, 100, 350, 500 m) Foliage height diversity (50, 100, 350, 500 m)	A, P, Z A, P, Z Z Z Z
Prey estimates	Insect biodiversity metrics	2	Insect diversity Insect abundance	A, P, Z A, P, Z
Predator estimates	Bat biodiversity metrics	9	Bat group diversity Bat species diversity Bat relative activity Long-/Mid-/Short-Range Echolocators relative activity Long-/Mid-/Short-Range Echolocators relative activity quadratic	A, P, Z A, P, Z A, P, Z A, P, Z A, P, Z
Statistical interactions	Interaction between pairs of predictors	4	City x Distance water City x Impervious cover (100, 500 m) City x Proximity Index 5000 m	A, P, Z A, P, Z A, P, Z

packages *lme4* v.1.1-20, *glmmLasso* v.1.5.1, *car* 3.0-3, *npar-comp* v.3.0 and *multcomp* v.1.4.14.

Variable selection

Due to the high number of predictors, we first selected the relevant ones using an L1-Penalised Estimation via the *glmmLasso* function (Groll & Tutz, 2014). In addition, we also included possible interactions (identified by exploratory analysis) and ecologically meaningful variables. Finally, we

checked the correlation amongst predictors (see Appendix A) and discarded those highly correlated ($\rho > 0.7$) to avoid collinearity (Zuur, Ieno & Elphick, 2010).

Effects of predictors on bat and insect response variables in the three cities and in Zurich

We performed Generalised Linear Mixed-Effects Models (GLMMs) on insect abundance and relative bat activity (i.e. total, LRE, MRE and SRE), with a negative binomial error

structure and log link for the former, and a binomial error structure and logit link for the latter (Zuur, Ieno, Walker, Saveliev & Smith, 2009). We ran the function *glmmTMB* and *glmer*, respectively. In each model, the sampling site was included as a random factor to allow for repeated measures of the same UGA on different nights. Meteorological values were also included as random factors to avoid them masking the effects of other predictors. Once the models were fitted, the Variance Inflation Factor (VIF) was used to identify multicollinearity via the function *vif*. When $VIF > 3$, we sequentially dropped the predictor with the highest VIF and recalculated the VIFs (Zuur et al., 2010). We also checked that the selected model was the one with the lowest corrected AIC value (AICc). The goodness-of-fit was investigated by calculating the conditional coefficient of determination for Generalised Mixed-Effects Models (R^2_C) (Nakagawa & Schielzeth, 2013). Finally, the model assumptions were validated by plotting the residuals against fitted values and the Q-Q plots of the random effects (Zuur & Ieno, 2016). We ran Linear Mixed-Effects Models (LMMs) on bat and insect diversity, with a normal error (Crawley, 2007), using the function *lmer*. The model that best explained the data variability was the one with no multicollinearity ($VIF < 3$), the lowest AICc value and a plot of residuals versus fitted values without pattern.

Models were run separately for each response variable: first for the 36 sites in Paris, Zurich and Antwerp (12 each) including the city as a fixed factor in order to identify biodiversity differences between the cities, and secondly for the 32 sites in Zurich. Overall, the graphics of the residuals versus the fitted values of the GLMMs and LMMs pointed out to a good fit of the model, as the point clouds did not exhibit any particular trend and were well dispersed over the axis (see Appendix A). We also computed the Moran's I test on the model residuals to check for spatial autocorrelation and no autocorrelation was found (data not shown).

Pairwise comparisons between the three cities

To investigate the possible differences between the three cities on each response variable, we made the respective multiple pairwise comparisons via the functions *mctp* (count data) and *glht* (continuous and binary data).

Results

We sampled a total of 12,714 insects and recorded 283,126 bat passes containing 5 million echolocation calls. Small Diptera and Trichoptera represented 56% of the sampled individuals, while medium-sized Lepidoptera and small-sized Coleoptera together represented 20%. The remaining groups accounted for less than 10% of total

abundance each. Around 91% of the bat calls belonged to *Pipistrellus pipistrellus*, while LREs and SREs accounted for 5% and 4% of the bat calls, respectively. Thus, MREs were significantly more present than the remaining guilds.

Nocturnal insect diversity showed a significant negative effect with increasing isolation. Conversely, insect abundance was reduced with increasing quadratic MRE relative activity and bat group diversity, but increased with bat species diversity (Fig. 1). We found artificial light (i.e. ALAN RGB) to have a city-specific effect on bat group diversity. Moreover, the range of ALAN RGB and the response of bat diversity differed amongst cities (Fig. 2). In Antwerp and Paris bat diversity was strongly reduced with increasing values of ALAN RGB, despite having a different range of illumination. Conversely, Zurich had the shortest range of illuminance values, which translated into a small increase of bat diversity (Fig. 2). In addition, Zurich harboured a more diverse bat community than Antwerp and Paris (see Appendix B). The total bat relative activity in Antwerp was significantly higher than in the other cities (see Appendix B). Moreover, we found the relative activity of the guild of LRE to be significantly decreased with increasing ALAN RGB in all cities, but not with any other category of predictors. Similarly, no significant effects were found for the connectivity, landscape or remote sensing predictors on MRE. The model only selected an increase of the MRE relative activity with insect diversity gain. Finally, SRE activity was negatively affected by the proportion of impervious cover in the 100 m radius (Fig. 1). The pairwise comparison between cities revealed that Paris and Antwerp were different in terms of total bat, LRE and MRE relative activity; while Paris and Zurich differed in insect abundance, bat group and species diversity and LRE and SRE relative activity. Likewise, Antwerp and Zurich showed differences in insect abundance and bat group and species diversity (see Appendix B).

The analyses of bat and insect responses in an extended set of sampling sites in Zurich unveiled the influence of new predictors (Fig. 3). Insect responses were enhanced by the size of the UGA and by the activity and diversity of bats. Strikingly, we found a scale-dependant response with increasing vegetation heterogeneity, which was positive at 100 m and negative at 350 m radius. Bat diversity and activity responses depended on a combination of predictors including connectivity (distance to water), bottom-up (insect diversity) and landscape (impervious surfaces at different radii) variables. Overall, bat diversity and activity increased together with insect diversity gain but was constrained by increasing distance to water and the amount of impervious surfaces at 100 m. The land-use heterogeneity predictors, both from the Urban Atlas and from the ecologically-based land-cover map of Zurich, only showed significant effects for small landscape scales (i.e. 50 and 100 m).

Detailed model results (e.g. fitted models, *p*-values) can be found in Appendix B: Tables 2 and 3.

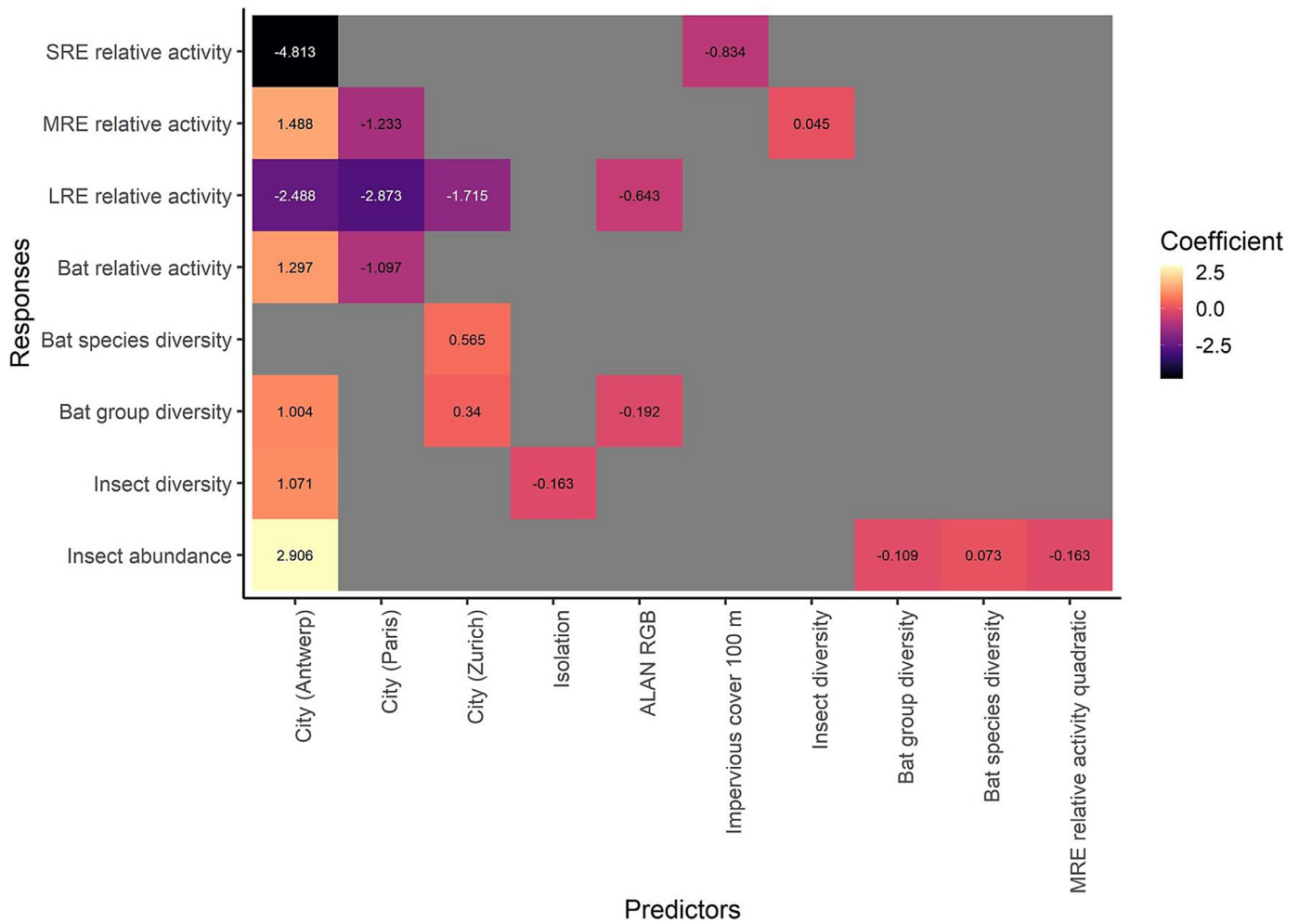


Fig. 1. Heatmap of the significant results of Generalised Linear Mixed-Effects Models for the three cities. Significance threshold is defined at a 0.05 level. The colour gradient reflects the magnitude of a predictor’s estimate for individual response variables. Grey colour indicates lack of statistical significance. SRE: short-range echolocators, MRE: mid-range echolocators, LRE: long-range echolocators (Frey-Ehrenbold et al., 2013).

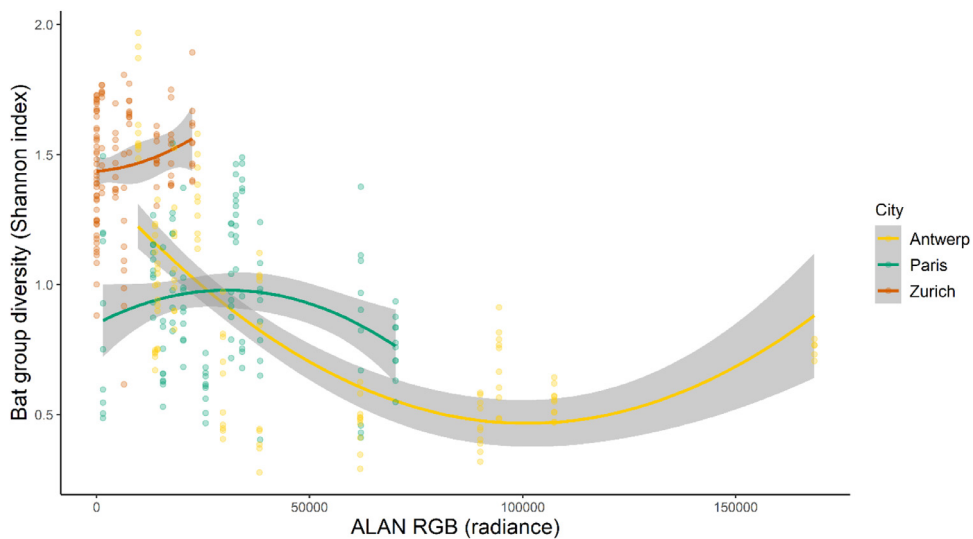


Fig. 2. Relationship between the RGB values of nocturnal rasters of the cities (ALAN RGB) and bat group diversity for Antwerp, Paris and Zurich. Each city shows a specific range in radiance and a response of the bat diversity. Lines represent second order polynomial GLM models and bands the 95% confidence level interval for model predictions. Dots represent individual bat group diversity measurements.

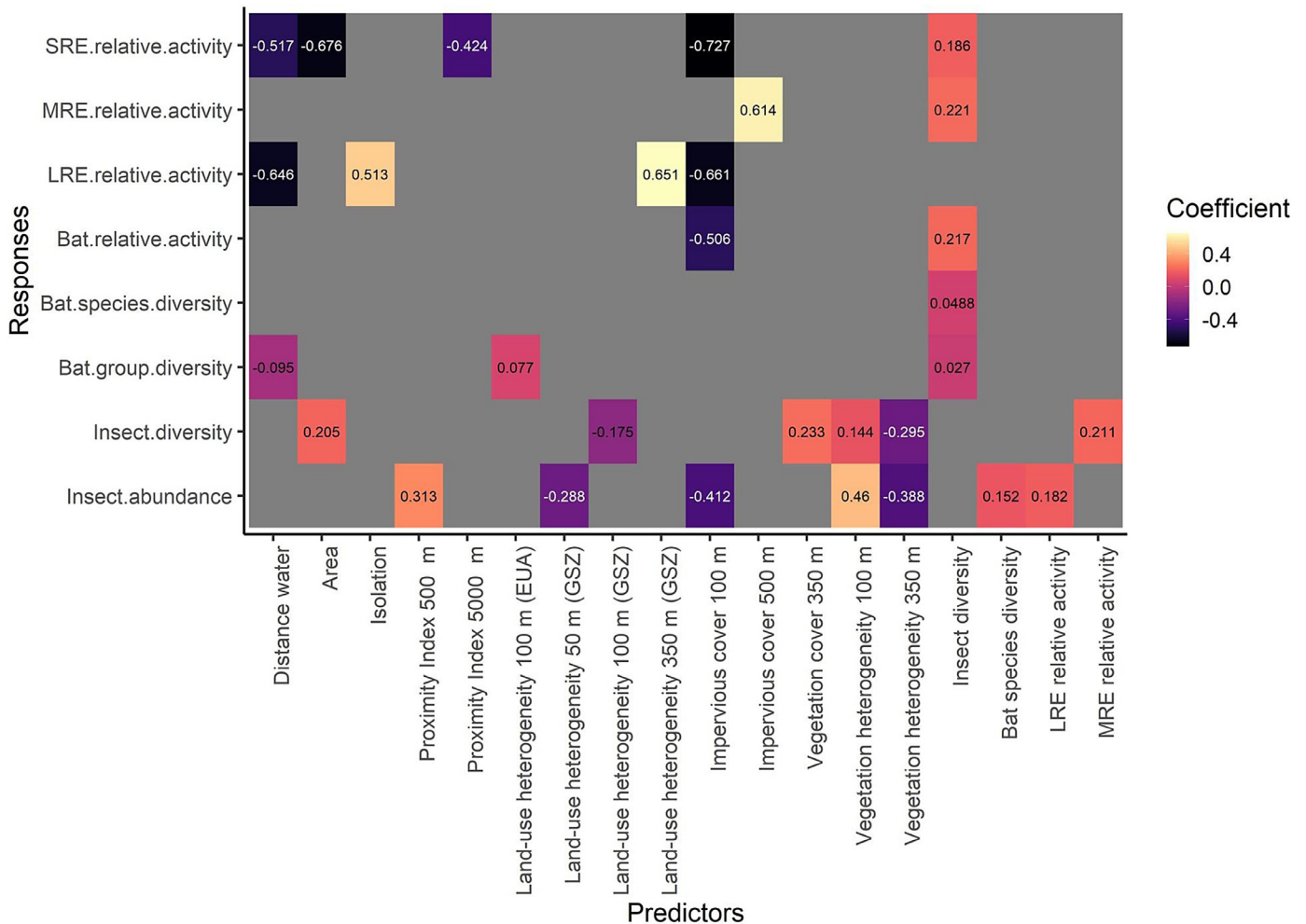


Fig. 3. Heatmap of the significant results of Generalised Linear Mixed-Effects Models in the city of Zurich. Significance threshold is defined at a 0.05 level. The colour gradient reflects the magnitude of a predictor's estimate for individual response variables. Grey colour indicates lack of statistical significance. SRE: short-range echolocators, MRE: mid-range echolocators, LRE: long-range echolocators (Frey-Ehrenbold et al., 2013). GSZ: habitat map of the city of Zurich, EUA: European Urban Atlas.

Discussion

The multi-city approach revealed some consistent responses of nocturnal biodiversity to urbanisation across cities. Isolation had a negative influence on nocturnal insect diversity, which might be related to the limited mobility of insects and their dependence on vegetation for reaching new patches (Concepción et al., 2015). Contrastingly, Turini and Knop (2015) found that patch isolation plays a limited role in urban ecosystems and arthropods can be diverse when sufficient vegetated space is provided. Except for distance to water, connectivity metrics did not show significant effects on bats, likely because they are highly mobile organisms and can reach distant patches (Krauel & LeBuhn, 2016). However, our connectivity metrics were mainly at landscape scale, which might have underrepresented the role of small-sized connecting elements (hedges, tree lines, etc.) seen in previous studies (Frey-Ehrenbold et al., 2013). Unlike SRE and LRE bats that are

respectively clutter- or open-adapted species, MRE bats include a wide range of intermediate echolocation strategies that could explain their tolerance to fragmentation and might make the most common guild in our study prone to cross less suitable areas (Frey-Ehrenbold et al., 2013).

We identified ALAN to be a prominent factor lowering bat group diversity. Particularly, Paris and Antwerp showed high radiance levels and low bat diversity, suggesting for the filtering out of light-averse species. ALAN can modify the foraging behaviour of bat communities (Russo & Ancillotto, 2015), enhancing a subset of light-opportunistic species (e.g. *Pipistrellus pipistrellus*, the most common bat in our study) that can take advantage of insect resources at the expense of light-averse ones. However, nocturnal biodiversity responses are species- and context-dependant (Mathews et al., 2015) as shown by the pairwise comparisons between cities (see Appendix B). This might indicate an ongoing behavioural change of the urban bat community, possibly caused by adaptation or plasticity towards light

pollution as noted in moths (Altermatt & Ebert, 2016), yet evidence is lacking. Future studies delving into the eco-evolutionary dynamics of urban fauna could provide important insights to better inform nocturnal biodiversity management (Lambert & Donihue, 2020). Further, recent trends to replace traditional street lighting with LED might help to rebalance this filtering effect, as LEDs can reduce the phototaxis of insects and their availability (Wakefield, Broyles, Stone, Jones & Harris, 2016), especially when combined with appropriate choice of longer-wave emission spectra (i. e. >500 nm, see Bennie, Davies, Cruse, Inger & Gaston, 2018; Bolliger et al., 2020). Moreover, the negative effect of bat group diversity and relative activity on insect abundance seems to indicate a top-down control. Still, our results have to be taken cautiously due to opposite effect of bat species diversity. In any case, our results point out the importance of considering such urban trophic dynamics (Shochat, Warren, Faeth, McIntyre & Hope, 2006).

Our single-city approach revealed that insect diversity increased both bat relative activity and diversity in Zurich, similarly as shown by Lewanzik and Voigt (2017). These results emphasise a bottom-up regulation in the nocturnal insect-bat trophic system in Zurich. In addition, vegetation heterogeneity appeared to have a scale-dependant effect on nocturnal insects, positive at 100 m and negative at 350 m radius. Thus, our results are consistent with previous works on arthropods (Turrini & Knop, 2015) and other little mobile organisms, which more likely rely on local patch characteristics (i.e. 100 m radius) (Concepción et al., 2015; Threlfall et al., 2012a). On the other hand, we were not able to assess an effect of vegetation structure metrics on bats although their significance has been proven on prior studies in urban environments (Suarez-Rubio, Ille & Bruckner, 2018). Furthermore, Threlfall et al. (2017) have pointed out that native plant species in UGAs increase bat diversity, likely because bats feed on insects that depend on plants. Similarly, land use heterogeneity derived from the detailed land-cover map of Zurich did not show significant effects for most responses. In this regard, high-resolution predictors did not contribute substantially to our data understanding. Interestingly, no model selected ALAN or ALAN RGB, likely because of the low radiance values within the city (Fig. 2). Studying European cities with intermediate radiance levels might help finding the tipping point at which ALAN starts decreasing nocturnal biodiversity.

In summary, our study provides evidence of the role of UGAs sustaining nocturnal biodiversity in European cities and sheds light on the importance of proxies used to infer the effects of urban intensification. Nocturnal habitats are main ecological niches in cities responsible for several ecosystem services such as insect regulation and pollination, but have been so far neglected in urban management (Pinho et al., 2021 in this issue). We developed a standardized multi-city design to consistently compare responses of bats and nocturnal insects to urban intensification. Our results may set a starting point for planning and managing

nocturnal biodiversity in UGAs of Western and Central Europe. Overall, our findings showed an urgent need of regulating and reducing ALAN, but accounting also for the existing trophic controls. The specific responses of our study groups to urbanisation highlight the need for manifold management strategies in UGAs that reflect the different traits of the nocturnal species. Currently, European cities face a scenario of urban densification to avoid the sprawl to other ecosystems, leading to increasing levels of stressors and thus threatening biodiversity within cities. In this context, UGAs are key elements to preserve and enhance present and future urban biodiversity.

Declaration of Competing Interest

None.

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CRedit authorship contribution statement

LVV: Validation, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Project administration. JCA: Methodology, Investigation, Writing - Original Draft, Writing - Review & Editing, Project administration. MM: Conceptualization, Methodology, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. PP: Conceptualization, Methodology, Formal analysis, Resources, Writing - Review & Editing, Funding acquisition. RS: Conceptualization, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. AVM: Investigation, Writing - Review & Editing. FC:

Conceptualization, Writing - Review & Editing. FZ: Formal analysis, Resources, Writing - Review & Editing. MKO: Conceptualization, Methodology, Validation, Investigation, Resources, Data Curation, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Data accessibility

Data is available at the EnviDat data portal ([10.16904/envidat.185](https://doi.org/10.16904/envidat.185)).

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2021.01.006](https://doi.org/10.1016/j.baae.2021.01.006).

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