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Research Article

Winners and losers in an urban bat community: a case study from southeastern Europe

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Abstract

Increasing urbanisation is reported to have significant effects on bat communities, due to habitat modifications, light and noise pollution and reduced prey availability. Recent studies have indicated that species show varying responses to urbanisation, with a few able to exploit man-made structures and adjust to the new environmental conditions. This study aimed to identify how landscape composition influences bat diversity and community structure along the urbanisation gradient in a coastal Mediterranean city (Patras, Greece) and whether particular species benefit from the novel conditions. We conducted acoustic surveys along 45 transects during the post-breeding season for two years. The effect of land cover, the number of streetlamps (a proxy of artificial illumination), the presence of water bodies and weather conditions on bat activity, and community structure were investigated using Generalized Linear Mixed Models, and multivariate statistics respectively. Eight bat species and five species groups were identified. Bat communities were affected by urbanisation in general and diversity was low in the entire study area. The community was dominated by the synurbic species *Pipistrellus kuhlii*, which comprised more than 70% of the total bat activity recorded. A positive relationship between built-up areas and bat activity was found, probably because *P. kuhlii* usually forages around streetlamps in urban areas. In contrast, vegetation cover did not affect bat activity, even in the less urbanised areas. The remainder of the bat species were not frequently recorded and were mostly detected close to water bodies, highlighting their value for foraging bats and the need for their conservation.

Introduction

Urbanisation is a major cause of land use change, habitat degradation and fragmentation, as urban areas expand rapidly at the expense of natural ecosystems. The novel ecosystems that arise are very heterogeneous (Pickett et al., 2011), containing a mosaic of artificial structures such as buildings and roads, green spaces with ornamental vegetation, bare ground, agricultural land, natural and artificial ponds, as well as patches of remnant natural or semi-natural vegetation (Cadenasso et al., 2007). In addition, they are characterized by new environmental conditions, such as increased temperatures (Urban Heat Island), pollution, anthropogenic noise and artificial lighting (Grimm et al., 2008) All these features render urban areas a challenging ecosystem for wildlife.

To date, numerous studies have shown the detrimental effects of urbanisation on biodiversity. At a global scale, urban wildlife communities have been found to become rather homogeneous along latitudinal gradients within specific continents (Clergeau et al., 2006; McKinney, 2006) or even among different continents indicating biodiversity loss (La Sorte et al., 2007). At a local scale, biological communities may show varying responses to urbanisation intensity, yet, a general pattern has been observed among animal communities: species richness tends to decrease towards more urbanised areas (McKinney, 2008). A few generalist species manage to exploit the urban habitat by adjusting their behaviour and ecology and are usually found in high abundances ("urban exploiters" or "synurbic"); other species can successfully occur in both urbanised and natural areas ("urban adapters"), while moderate generalists and specialists tend to become scarcer ("urban avoiders") (McKinney, 2006; Devictor et al., 2007; McKinney, 2008; Francis and Chadwick, 2012; Sullivan et al., 2016).

This pattern has also been observed in bat communities, as only a few species manage to adjust to the urban environment, while other more sensitive species avoid it (Avila-Flores and Fenton, 2005; Jung and Kalko, 2011; Russo and Ancillotto, 2015; Jung and Threlfall, 2018). Urban life may be harsh for many bat species due to high levels of light and noise pollution (Schaub et al., 2008; Stone et al., 2015), increased risk of collisions (Medinas et al., 2013) and spread of diseases (Mühldorfer et al., 2011), increased exposure to predators (Ancillotto et al., 2013; Threlfall et al., 2013), reduced prey availability and higher inter- and intraspecific competition (Russo and Ancillotto, 2015). Furthermore, artificial nighttime illumination may affect bat commuting, breeding, roosting, foraging behaviour and hibernation (Stone et al., 2015; Azam et al., 2016). Anthropogenic noise may also affect bat feeding success, as noise frequencies often overlap with the frequencies of sounds emitted by bat prey (Schaub et al., 2008). Similarly, noise might affect communication with conspecifics by masking bat social calls (Russo and Jones, 1999).

In general, urbanisation has negative effects on bat activity and diversity, though these effects are highly species-specific (Jung and Threlfall, 2018). Despite the generally adverse conditions in urban environments, new opportunities may arise for the more tolerant species (Francis and Chadwick, 2012; Threlfall et al., 2012; Ancillotto et al., 2015, 2019). Streetlamps attract large numbers of insects, offering an easily accessible prey for some species (Rydell, 1992; Ancillotto et al., 2015; Schoeman, 2016 but see Arlettaz et al., 2000; Stone et al., 2015). In addition, man-made structures such as buildings, roofs and tunnels

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may be used as roosts especially due to natural roost loss (Russo and Ancillotto, 2015). Warmer microclimatic conditions prevailing in artificial roosts may benefit reproductive females and the growth of their young (Lausen and Barclay, 2006; Ancillotto et al., 2015). Hence, generalists may be more widespread and abundant in the urban environment than specialists by exploiting man-made structures. However, urban areas may also act as ecological traps for bats (Russo and Ancillotto, 2015). Gaining an insight into bat responses to urbanisation is important for the generation of effective management actions and their contribution to biodiversity conservation.

In recent years, there has been a growing interest in the study of bat foraging and roosting ecology and behaviour in urban areas, particularly in Europe (e.g. Lintott et al., 2015; Border et al., 2017; Suarez-Rubio et al., 2018; Ancillotto et al., 2019), Australia (Threlfall et al., 2012; Caryl et al., 2016), North America (Dixon, 2012; Krauel and LeBuhn, 2016; Schimpp and Kalcounis-Rueppell, 2018), Central America (Jung and Kalko, 2011; Rodríguez-Aguilar et al., 2017), South America (Oprea et al., 2009) and South Africa (Schoeman, 2016). However, studies on bat responses to urbanisation in south-eastern Europe are lacking, despite its high bat diversity (Dietz et al., 2009). In this study, we aimed to fill this knowledge gap and identify (a) how bat activity varies along the urbanisation gradient, (b) the environmental factors that affect bat activity and (c) whether urbanisation favours particular species in a densely-built Mediterranean coastal city (Patras, Greece).

Materials and methods

Study area and site selection

The study area covered the city of Patras and its surroundings (total area $110\,\text{km}^2$), located in SW Greece ($38^{\circ}14'$ N, $21^{\circ}44'$ E). Patras is the third largest city in Greece with approximately 200000 inhabitants (ELSTAT, 2011). The city has an elongated expansion along the coast of Patraikos Gulf and is delimited by Mount Panachaikon (1926 m a.s.l., Natura 2000 site GR2320007) to the east-southeast (Fig. 1). Due to various historical reasons and inadequate spatial planning, the town has a very dense urban core with severely reduced green space (Papadatou-Giannopoulou, 1991; Tzortzakaki et al., 2019). The surrounding peri-urban and rural areas consist of agricultural land, orchards (mostly olive groves), Mediterranean shrublands, and a few scattered small remnant patches of coniferous or deciduous forests and riparian vegetation. Due to complex geological processes (i.e. the tectonic uplift caused by the rifting of the Corinth and Patraikos Gulfs), a number of gorges and gullies containing streams were formed on Mount Panachaikon, which flow through the study area into the Patraikos Gulf (Fig. 1). The climate is typical Mediterranean with a long dry period and mild winter (average annual temperature 17.9 °C), and relatively high precipitation levels (average annual rainfall: 607 mm; HNMS, 2017).

The study area was stratified into three zones of decreasing built cover (b.c.): the "urban zone" (b.c.>50%), the "suburban zone" (30%<b.c.<50%), and the “peri-urban zone” (b.c.<30%), after overlaying a grid of 500×500 m cells and calculating the proportion of built cover in each cell using the Urban Atlas (EEA, 2010; Tzortzakaki et al., 2019). In each zone, 15 grid cells were randomly selected, on the basis that they were situated at least 500 m from their nearest neighbouring cell (Tzortzakaki et al., 2019). Each gird cell encompassed one bat sampling site (45 sites in total; Fig. 1).

Bat surveys and sound analysis

Bat surveys were conducted during the post-breeding period from the end of August to the beginning of October in two consecutive years (2015–2016). In each of the 45 grid cells, a 300 m line transect was established, which was walked in one direction once in each year (90 transects in total). Surveys started half an hour after sunset (Vaughan et al., 1997) and were completed within three hours. On average, three sites were sampled on each survey night, in random order (Dixon, 2012) and regardless of their location along the urbanisation gradient to reduce possible temporal or spatial sampling bias. Sampling was conducted by the same individual and under good weather conditions, i.e., without rain or strong winds and minimum nightly temperature >19 °C.

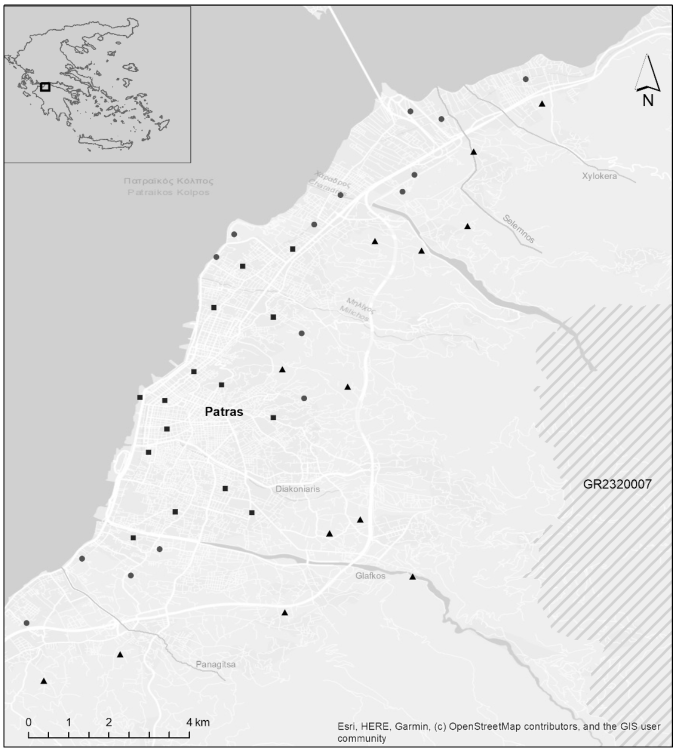

Figure 1 – Map of the study area, showing the distribution of the sampling sites in the urban (squares), suburban (circles) and peri-urban zone (triangles). Urbanisation zones were delineated based on land use data from the Urban Atlas (EEA, 2010). Grey diagonal lines represent the Natura 2000 site of Mount Panachaikon (GR2320007).

Bat vocalizations were recorded using a Pettersson M500 USB ultrasound microphone (Pettersson Electronik AB, Uppsala, Sweden), set at approximately 1.8 m above the ground and connected to a tablet computer. Recordings were performed with the Pettersson Bat Sound Touch Lite software at a 500 kHz sampling rate, set in the automatic mode with a sound power level of -10 dB and a bandwidth ranging from 19 to 120 kHz, which was defined after testing microphone sensitivity in the field to avoid recording low-frequency noise. The bat detector was automatically triggered by sounds above the lower threshold and was set to record for 6 seconds each time (5 seconds from the trigger point + 1 second before). Social calls and echolocation calls of *Tadarida teniotis* were recorded while recording other species’ echolocation calls.

Bat ultrasound analysis was performed using SonoBat 3.0 (SonoBat Bat Call Analysis Software); echolocation call parameters were automatically measured, after applying manual filters to minimize masking by noise where necessary. Batsound 4.2 (Pettersson Electronik AB, Uppsala, Sweden) was additionally used to explore the possible presence of more than one individual or species or social calls within sound files. Spectrograms were visualized in Batsound with a 512 samples Hanning FFT window.

Bat species identification was conducted with the open source automated software for the identification of European bats “iBatsID” (Walters et al., 2012). iBatsID uses the parameters measured by Sonobat and assigns each call sequence to one or more species based on a classification probability. We considered identification at the species level as trustworthy, when classification probability was $\geq$90%. When probability was <90%, call sequences were initially assigned to the species group with the highest classification probability. They were subsequently evaluated manually and identified to species level where possible using BatSound. Where frequency of echolocation call and time parameters fell into the overlap zone of at least two species (Dietz and Kiefer, 2014), identification remained at the species group level, unless social calls were present (Russo and Jones, 1999; Pfalzer et al., 2003; Russo and Papadatou, 2014; Nardone et al., 2017). Call sequences that could not be assigned to species or species groups were recorded as unknown and were only included in total bat activity estimates.

Calls of *Myotis* species were grouped, as their identification is often ambiguous (Lintott et al., 2015). Call sequences classified as *P. nathusii* by iBatsID were considered as *P. kuhlii* in the analysis, because *P. nathusii* is rare in southern Greece (Georgiakakis and Papadatou, unpubl. data) and none of the social calls recorded belonged to the latter species.

The number of bat passes of each species or species group within each recording, i.e., within 6 seconds, was used as an index of bat activity. A bat pass is defined as a sequence of two or more echolocation pulses emitted by a bat (Thomas, 1988).

Environmental variables

In each sampling site, mean hourly temperature (MHT) and relative humidity (MHRH) were extracted from the meteorological data that were provided by the Laboratory of Atmospheric Physics of the University of Patras, given the known influence of weather conditions on bat activity (O'Donnell and Sedgeley, 2001). Second, the percent cover of the predominant land-cover types (buildings, impervious surfaces, woody vegetation, open green spaces and water bodies) was assessed within a 200 m radius circular buffer zone around each transect centroid (Tzortzakaki et al., 2019), so that the buffer zones fit within the respective grid cells (500×500 m) and do not overlap with nearest neighbouring buffers. Proximity of sampling sites to the closest natural (i.e., streams and marshes) or artificial water body (hereafter all referred as water bodies), and to motorway (Fig. 1) was measured using ArcGIS 10.1 (ESRI). Finally, the number of streetlamps along each transect was recorded as a proxy of the intensity of illumination in the sampling sites.

Data analysis

First, pairwise comparisons of mean daily temperature (° C), mean daily relative humidity (%) and total daily rainfall (mm) were performed for each month between the two sampling years with Analysis of Variance (ANOVA), in order to test for possible differences in the meteorological conditions between the two years.

To examine bat activity patterns along the urbanisation gradient, bat activity was compared among the urbanisation zones for each year separately, using Kruskal-Wallis tests, because the data were not normally distributed. A Wilcoxon signed-rank test was used to compare bat activity at each sampling site between the two years.

To investigate the effect of the environmental parameters on bat activity, Generalized Linear Mixed Models (GLMMs) were used. Prior to model building, the relationships among the response and explanatory variables were investigated (Zuur et al., 2010). Land-cover types were highly correlated, therefore Principal Components Analysis (PCA) was used to reduce their number and only the first two axes were retained: PC1 represented a gradient of decreasing vegetation cover to increasing built cover, while PC2 characterised a gradient of decreasing open spaces to increasing water cover (Tzortzakaki et al., 2019). The distance to motorway and the number of streetlamps were excluded from the analyses, because they were both collinear with PC1 (Pearson r=0.63 and r=0.78, respectively), as well as MHRH, because it was correlated with MHT (r=-0.66). No evidence for spatial and temporal autocorrelation was found after plotting bat activity vs. spatial coordinates and Julian date, respectively (Zuur et al., 2010).

GLMMs were carried out using negative binomial error distribution with a log link function. Since two visits per site were conducted, sampling site was considered as a random factor, while PC1, PC2, MHT, distance to water bodies (DistW) and year of study (Year) were included as fixed terms. Continuous explanatory variables were standardised (Schielzeth, 2010).

Model selection was performed with backward stepwise deletion: the global model was constructed, and then non-significant covariates were sequentially removed until the best model with the smallest Akaike's Information Criterion (AIC) was achieved. Tests of homogeneity of variance, normality of residuals, independence of observations and model overdispersion were carried out for model validation (Zuur et al., 2010). Analyses were carried out with `lme4` package (Bates et al., 2015) in R v.3.3.1 (R Core Team, 2016).

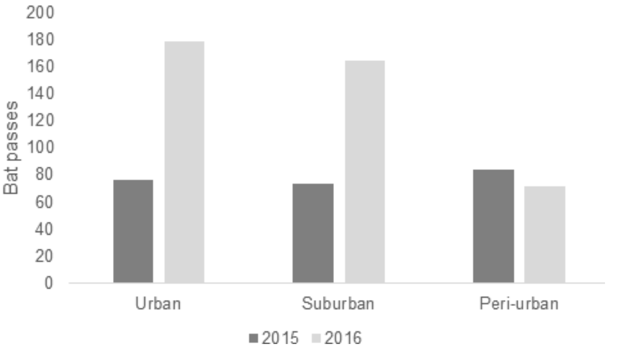

Figure 2 – Total bat activity (number of bat passes) per urbanisation zone and year of study. Bat activity was significantly higher in 2016, but no statistically significant differences were found among the urbanisation zones in either year.

To examine the relationship between community composition and environmental variables, Redundancy Discriminant Analysis (RDA) was performed separately for each year using the `vegan` package (Oksanen et al., 2016) in R. Permutation tests with 999 permutations were used to assess the significance of the relationships between species composition and the explanatory variables. For this analysis, calls at the frequency overlap zone that could not be identified to species level were excluded, as well as species with less than two bat passes. Prior to the analysis, bat activity data were Hellinger-transformed (Oksanen et al., 2016), while environmental data were standardised (Leps and Smilauer, 2003).

To assess the relationship between species composition and the urbanisation gradient, Permutational Multivariate Analysis of Variance (PERMANOVA) was carried out separately for each year (Anderson, 2001). PERMANOVA allowed for pairwise comparisons of the community composition among the urbanisation zones. The analysis was performed on the community data matrix (same as RDA) using the Bray-Curtis dissimilarity index with 999 permutations with the "adonis" function of the `vegan` package (Oksanen et al., 2016), after applying a Hellinger transformation. Pairwise comparisons among the urbanisation zones were conducted with the `pairwise.Adonis` package (Martinez Arbizu, 2017). Multivariate homogeneity of group dispersions (PERMDISP), performed with the "betadisper" function (Oksanen et al., 2016), did not indicate violation of the homogeneity of variances assumption (p>0.05 for both years).

Results

A total of 653 bat passes were analysed, 67% of which were identified to species level. Eight bat species and five species groups were identified (Tab. 1). *P. kuhlii* was the most common species in the study area, comprising more than 70% of the bat passes in both years and occurring at approximately 80% of the sites (Tab. 1). Excepting *P. pygmaeus* and *T. teniotis*, other species were recorded very infrequently (<10% of the sites in both years). The occurrence of *H. savii* could not be assessed precisely, as respective calls were mostly in the overlap zone of *H. savii* and *P. kuhlii* (Tab. 1).

Bat activity did not vary considerably along the urbanisation gradient in 2015. In contrast, it was remarkably higher in the urban and suburban zones than in the peri-urban zone in 2016 (Fig. 2). However, statistical comparisons of bat activity among the urbanisation zones did not show any significant differences in either year (2015: Kruskal-Wallis H=1.281, p=0.527; 2016: H=2.893, p=0.235). Bat activity was significantly higher in the second year (Wilcoxon test: V=229, p=0.015), noting that significantly higher temperatures occurred in the study area during the winter and spring of 2016 (Tab. S1). However, summer and autumn temperatures were similar across the two years and no differences were found in most cases for relative humidity (Tab. S1).

Table 1 – Proportion of bat passes assigned to bat species or species group in each urbanisation zone per year of study (calculated as the proportion of the total annual bat passes). Occupancy indicates the proportion of sampling sites (out of 45) where a given species or species group was recorded.

	2015					**2016**				
	Bat passes (%)				**Occ. (%)**	**Bat passes (%)**				**Occ. (%)**
Species / Group	**Urban**	**Suburban**	**Peri-urban**	**Total**		**Urban**	**Suburban**	**Peri-urban**	**Total**	
Eptesicus serotinus / Nyctalus leisleri	0	0	2.14	2.14	2.22	0	0	0	0	0
Nyctalus noctula	0	0	0	0	0	0	0	0.24	0.24	2.22
Hypsugo savii	0.43	0	0	0.43	2.22	0.48	0.72	0	1.2	4.44
Pipistrellus kuhlii	24.79	22.65	24.36	71.79	80	33.17	23.56	14.9	71.64	82.22
P. kuhlii / H. savii	1.71	3.42	2.99	8.12	31.11	4.09	1.68	1.2	6.97	37.78
Pipistrellus pipistrellus	0.43	0.85	0.85	2.14	8.89	0	3.85	0	3.85	4.44
P. pipistrellus / P. kuhlii	0.43	0	0.43	0.85	4.44	0.48	0.72	0	1.2	8.89
Pipistrellus pygmaeus	0.43	3.85	2.14	6.41	13.33	0	6.97	0.48	7.45	13.33
Miniopterus schreibersii	0	0	0	0	0	0	0.48	0	0.48	2.22
M. schreibersii / P. pygmaeus	0	0	0	0	0	0	1.44	0	1.44	2.22
Myotis spp.	0.43	0.43	2.99	3.85	6.67	0.24	0	0	0.24	2.22
Tadarida teniotis	3.85	0.43	0	4.27	8.89	4.57	0.24	0.48	5.29	13.33
Total	32.48	31.62	35.9	100		43.03	39.66	17.31	100	

The GLMMs indicated a positive effect of built cover (PC1), water cover (PC2) and the year of study on bat activity (Tab. 2). Temperature and distance to water bodies were non-significant and not included in the final statistical model. Bat activity increased with increasing building and water cover, but it was strongly correlated with *P. kuhlii* activity (r = 0.92). Therefore, a positive relationship between these variables and *P. kuhlii* activity can be inferred.

RDA performed on the 2015 data did not show any significant relationships between the environmental variables and bat community composition (total variance explained=15.8%; model: F=1.888, p=0.064; Fig. 3 a). In contrast, in 2016 a significant relationship was found between PC2 (presence of water) and community composition (PC2: F=3.539, p=0.034; Fig. 3). The environmental variables accounted for only 14.4% of the total variance (model: F=1.675, p=0.127).

PERMANOVA showed a significant relationship between community composition and the urbanisation gradient, but only for 2016 (2015: F=0.359, p=0.912; 2016: F=2.329, p=0.037). Pairwise comparisons indicated a statistically significant difference between the suburban and the urban zone in 2016 (F=3.319, p=0.026), while no differences were found between the urban and the peri-urban zone (F=0.345, p=0.721) and between the suburban and the peri-urban zone (F=2.266, p=0.093).

Discussion

This current study provides the first insights into bat activity and diversity patterns in an urban area in southeastern Europe (Patras, Greece), demonstrating the sensitivity of bat communities to urbanisation and the differential responses among species. Bat diversity was generally low in the city of Patras and its surroundings, although the area lies within a biodiversity hotspot containing a high number of species (Dietz et al., 2009, Papadatou and Georgiakakis, unpubl. data). The bat community was dominated by *P. kuhlii*, which together with the group *P. kuhlii* / *H. savii* comprised approximately 80% of the total bat activity in the study area in both years. The rest of the species were much less abundant, likely implying decreased tolerance to the urban environment in the study area.

Table 2 – Parameter estimates (± standard error) of fixed effects of the best GLMM.

Fixed effects	**Estimate (±S.E.)**	**Z**	***p***
Intercept	1.257 (± 0.191)	6.604	<0.001
PC1	0.323 (±0.151)	2.142	0.032
PC2	0.384 (±0.155)	2.479	0.013
Year	0.477 (±0.202)	2.365	0.018

Bat activity and species richness did not differ along the urbanisation gradient, contradicting the generally observed pattern of bat activity declining with increasing urbanisation intensity (Walsh and Harris, 1996; Hale et al., 2012; Russo and Ancillotto, 2015; Jung and Threlfall, 2016) or studies showing higher diversity in suburban areas (Hourigan et al., 2010; Threlfall et al., 2011). Contrary to our expectations, the peri-urban area did not hold greater bat activity or more species than the urban and suburban areas, despite the fact that it includes less disturbed landscapes with high vegetation cover (Tzortzakaki et al., 2019). Bat activity was highest in the urban zone in the second sampling year. As indicated by several studies, species richness may be generally low in urban areas, but total abundance and biomass is often increased due to the occurrence of a few synurbic species (Avila-Flores and Fenton, 2005; Francis and Chadwick, 2012; Krauel and LeBuhn, 2016).

A positive relationship between built cover and bat activity was indicated by the GLMMs. These results may reflect the ability of *P. kuhlii* to exploit the urban landscape and forage around sources of artificial illumination (Tomassini et al., 2014; Russo and Ancillotto, 2015; Ancillotto et al., 2019), as the number of streetlamps was highly correlated with built cover in the study area. Streetlamps seem to play an important role in *P. kuhlii* foraging, as they prey upon insects that are attracted by the light (Rydell, 1992; Tomassini et al., 2014).

Surprisingly, vegetation cover did not have any positive effect on bat activity, although it is considered a key landscape element for foraging bats in urban environments, as it is associated with increased insect prey abundances (Avila-Flores and Fenton, 2005 and references therein). Furthermore, urban green spaces such as parks (Glendell and Vaughan, 2002; Gehrt and Chelsvig, 2003; Russo and Ancillotto, 2015), gardens (Hale et al., 2012; Lintott et al., 2016) or even small green areas (Avila-Flores and Fenton, 2005) can enhance insect abundances, while tree networks in green spaces can facilitate bat commuting and foraging (Dixon, 2012; Hale et al., 2012).

The lack of a positive relationship between vegetation cover and urban green spaces, and bat activity in this study may in part be explained by the dominance of *P. kuhlii*. However, green spaces in the study area may be too small or generally inadequate (e.g. due to inadequate vegetation structure) for most bat species, even in the peri-urban zone. The latter is an agricultural area covered mainly by agricultural mosaics and olive groves, which have been found to support relatively high bat diversity in other Mediterranean areas (Russo and Jones, 2003). A negative relationship between rural areas and bat activity was reported in Illinois, USA, where, unlike Patras, intensive crop agriculture prevails (Gehrt and Chelsvig, 2003). More natural areas in

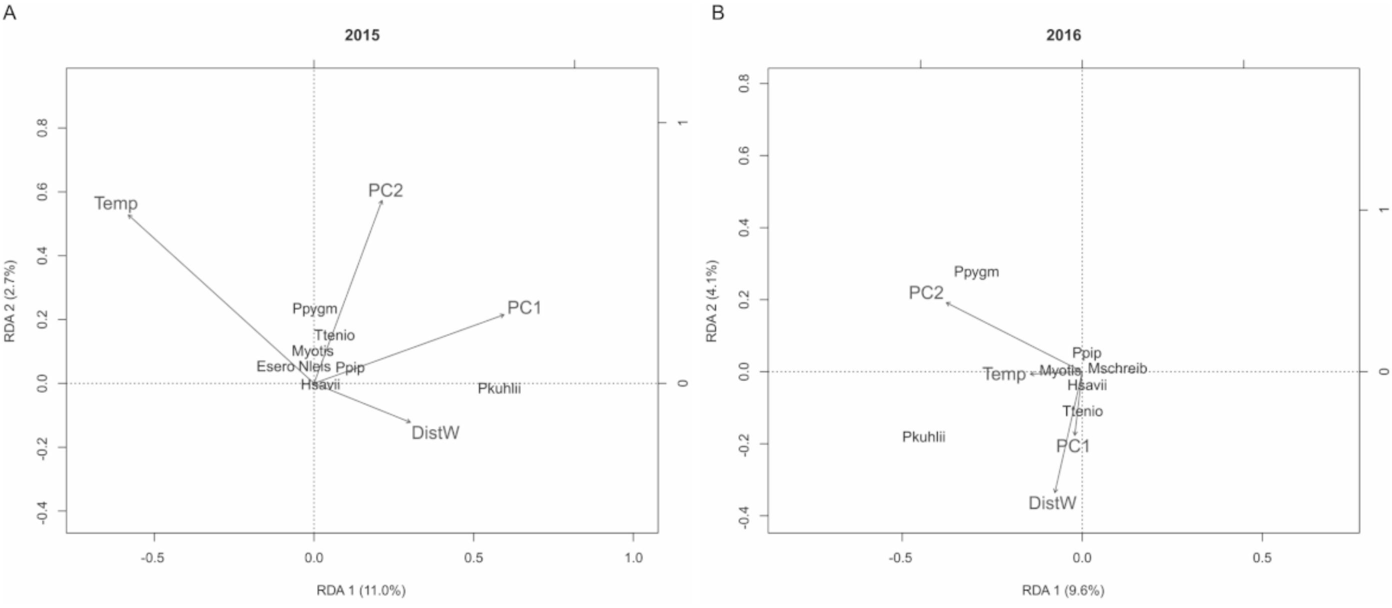

Figure 3 – RDA ordination plots showing the relationship between the environmental variables (PC1: built cover, PC2: water cover, Temp: mean hourly temperature, DistW: distance to water) and bat community composition in (a) 2015 and (b) 2016. No significant relationships were found, except for a significant relationship between water cover (PC2) and community composition in 2016.

the surroundings of the study area (e.g. within the adjacent Natura 2000 site) may provide higher prey availability and, thus, be more attractive to foraging bats.

Similar to other studies (e.g. Li and Wilkins, 2014), the highest bat activity was in most cases recorded in specific sites with presence of water, i.e. along the banks of water bodies. However, these sites varied between the study years. In general, the highest total bat activity was recorded at the main wastewater treatment plant of the city, while the upstream section of Glafkos river (Fig. 1) and a remnant natural mire also provide important foraging grounds. In the rest of the sites where water is present such as streams, bat activity was lower than expected. In contrast, one of the few remaining seaside open green spaces was also important for foraging bats. Despite the positive effect of water cover for foraging bats, site proximity to water did not have any effect on bat activity contrary to the findings of previous studies (Dixon, 2012; Ancillotto et al., 2015; Krauel and LeBuhn, 2016). These findings imply that the main factors influencing bat activity are possibly associated with water cover and/or particular characteristics of the water bodies (e.g. shape or structure) and not with the site proximity to water per se.

Water bodies in Patras have generally undergone degradation due to modification of riverbeds, residential and industrial development, draining and dumping of refuse, and, consequently, degradation of their riparian character. Lintott et al. (2015) showed that even if waterways are accessible to bats, their use may largely depend on the riparian vegetation cover, while it may also be negatively affected by the proportion of the adjacent sealed surfaces.

Nevertheless, the value of the remaining water bodies for the local bat community should be emphasised, as the highest bat activity was recorded at some of these sites. In particular, *P. pygmaeus* was found to have a positive (although not statistically significant) relationship with water cover (Fig. 3b), which supports the findings of Nicholls and Racey (2006) and Lintott et al. (2016) who found a strong association with freshwater (but see Hale et al., 2012). Water bodies such as rivers and lakes are highly important for insectivorous bats, because they provide high insect prey availability and drinking water (Vaughan et al., 1997; Russo and Jones, 2003; Li and Wilkins, 2014). Linear water bodies (waterways) may also function as corridors facilitating bat movements between the urban core and peri-urban natural habitats (Rouquette et al., 2013; Lintott et al., 2016). Hence, their maintenance and management are important for bat conservation in large urban settlements (Russo and Ancillotto, 2015).

The year of the study affected bat activity and this was more evident in sites located along water bodies (Tab. S2). In the second year, bat activity was significantly higher, underlying that changes in spatio-temporal patterns of bat activity may be due to either stochastic or specific factors related to bat biology. Differences between years may reflect changes in environmental conditions or bat behaviour (O'Donnell and Sedgeley, 2001). In this study, differences in bat activity observed between the two years may be attributed to the prevailing weather conditions preceding the sampling, as the winter and spring of the second year were significantly warmer. Higher temperatures may increase insect abundance (Scanlon and Petit, 2008), but may also influence bat reproductive success (Ancillotto et al., 2015). They may lead to advanced parturition, which in turn may result in increased juvenile survival (Frick et al., 2010) or more females reaching sexual maturity during the first autumn (Dietz et al., 2009). The scenario of increased prey availability is considered more plausible, since winters in the study area are generally mild and do not show strong fluctuations among years, while the influence of other stochastic undetermined factors cannot be excluded.

Our findings are in agreement with the conclusion of other studies that the response of bats to urbanisation is highly species-specific (e.g. Avila-Flores and Fenton, 2005; Threlfall et al., 2012; Russo and Ancillotto, 2015). The bat community was mainly represented by *P. kuhlii*, particularly in the urban zone in the second year of the study. Pipistrelle bats such as *P. kuhlii*, *P. pipistrellus* and *H. savii* have been reported to successfully inhabit urban areas and expand their range across Europe (Russo and Ancillotto, 2015; Ancillotto et al., 2019). Specifically in southern Europe, *P. kuhlii* has shown notable behavioural and ecological flexibility and has adjusted to artificial structures such as buildings and streetlamps for roosting and foraging, respectively (Russo and Jones, 2003; Ancillotto et al., 2015), while *P. pipistrellus* occupies a similar niche in Northern Europe (Vaughan et al., 1997).

Similarly, *T. teniotis* was mainly recorded in the urban zone, demonstrating its ability to exploit human-modified landscapes and man-made structures (Avila-Flores and Fenton, 2005; Threlfall et al., 2012; Krauel and LeBuhn, 2016). *Tadarida* species have been documented flying over cluttered environments and large areas such as the dense city core (Russo and Jones, 2003; Avila-Flores and Fenton, 2005; Krauel and LeBuhn, 2016), foraging on passing insect swarms (Marques et al., 2004). It should be noted that in this study, its occurrence may have been underestimated, as it usually flies high above the ground and produces low frequency sounds (Zbinden and Zingg, 1986).

Pipistrellus pygmaeus and *P. pipistrellus* were rarely detected in the urban zone but were in general not common in the study area (<10% of the total bat activity). These two pipistrelle species together with *M. schreibersii* were principally recorded in the suburban zone and they showed higher activity in sites near water bodies especially in the second year (Tab. S2). As mentioned above, *P. pygmaeus* is associated with freshwater and avoids densely built areas (Nicholls and Racey, 2006; Lintott et al., 2016), whereas *P. pipistrellus* is considered a generalist and more tolerant of intermediate urbanisation levels ("urban adapter", Hale et al., 2012), and thus, occurs in a broader spectrum of habitats (Lintott et al., 2016). The latter species appears to avoid habitats with high freshwater coverage, in order to avoid competition with *P. pygmaeus* (Nicholls and Racey, 2006; Lintott et al., 2016). In this study, *P. pipistrellus* was principally found in the wastewater treatment plant foraging together with *P. pygmaeus* and other species, but it was rare in any other habitats. *Miniopterus schreibersii* was only found at the wastewater treatment plant.

Larger species such as *Nyctalus* sp./*E. serotinus* were only detected in one site in the peri-urban zone. *Nyctalus* species have been reported to roost in buildings and forage in parks and city edges, if high vegetation and insect densities are provided (Dietz and Kiefer, 2014), and in urban waterways (Lintott et al., 2015), while *E. serotinus* often forages in settlements and big cities (Dietz and Kiefer, 2014). Both *N. leisleri* and *E. serotinus* have been recorded to forage at streetlights (Azam et al., 2015). However, in this study these species were rarely recorded, thus, no conclusions on their occurrence can be drawn. Similarly, *Myotis* spp. were mostly found in sites out of the urban zone and close to water bodies, in accordance with other studies (Vaughan et al., 1997; Russo and Jones, 2003; Avila-Flores and Fenton, 2005; Dixon, 2012; Lintott et al., 2015).

The negative impact of urbanisation on many bat species due to habitat fragmentation and patch isolation (Hale et al., 2012; Threlfall et al., 2012), reduced vegetation cover (Lintott et al., 2016), and artificial lighting (Azam et al., 2016) possibly explains the low number of species recorded in the urban and the suburban zones. However, it is unclear why bat diversity was low in the peri-urban zone, despite retaining significant natural and semi-natural characteristics (Tzortzakaki et al., 2019). The effects of some landscape aspects such as land-cover were investigated at a relatively small scale (200 m), considering that bats are highly mobile organisms and that species responses may vary depending on their different foraging and roosting requirements (Dixon, 2012; Hale et al., 2012; Lintott et al., 2016). Previous studies have underlined the importance of local habitat features such as vegetation structure, water bodies and streetlamps on urban bat communities, but also of the surrounding landscape (Walsh and Harris, 1996; Gehrt and Chelsvig, 2003; Threlfall et al., 2012; Lintott et al., 2015). Hence, further investigation of the local habitat characteristics (e.g. vegetation structure and the existence of buildings providing bat roosts) and the landscape structure (e.g. habitat heterogeneity and connectivity) at a larger scale may provide insight into the factors affecting bat community response to urbanization, especially in the peri-urban zone. Bat surveys in the adjacent natural areas would be useful as it would allow the magnitude of the effect of urbanisation on bat communities to be assessed.

Finally, we need to acknowledge that the low bat diversity and the rare occurrence of most species may have resulted from the sampling methodology (i.e., short acoustic transect surveys), which was designed to be consistent with two companion studies of birds (Tzortzakaki et al., 2018) and butterflies (Tzortzakaki et al., 2019). Additionally, surveys were not conducted during the breeding season (late spring – mid summer) and this would likely provide a better assessment of bat activity patterns in the urban environment.

Despite its limitations, our study provides an insight into the effects of urbanisation on the local urban bat community and may be used as a baseline for a more thorough investigation of urban habitat use by bats in the Eastern Mediterranean. It also emphasises the need for preserving and upgrading natural freshwater resources for bats within an urban environment.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Monthly mean temperature (T), relative humidity (RH) and total monthly rainfall recorded for each sampling year.

Table S2 Total number of sampling sites with species occurrences, number of sites near water bodies (<100 m) with species records, and proportion of bat passes of each species recorded in sites near water bodies for each survey year.