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# Response of bats to landscape structure surrounding urban green areas

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## Abstract

Urbanization is a major process of land-use change that results in transformation of natural habitats and landscape structure due to increasing sealed areas, higher density of buildings, and reduced green areas. Urbanization has been associated with the loss of biodiversity due to habitat loss and fragmentation; therefore, conserving biodiversity in urban areas is a pressing challenge. Although different taxonomic groups are negatively affected by urbanization, little is known about the effects of urbanization on insectivorous bats. In addition, the influence of different urban green areas on bat activity and species richness has not been explored. The aim of this study was to assess whether landscape structure surrounding urban green areas influenced bat activity and species richness in total, as well as to assess differences in the response between functional groups. During summer 2014, I acoustically surveyed bats at 180 points distributed in nine types of green areas in Vienna and quantified landscape structure at 0.5 km and 1 km radius-buffer areas. My results showed that bats responded to landscape structure in diverse ways depending on the scale of analysis. Therefore, response assessments of a high mobile order like bats on land-use changes has to be done at least at two scales, because the influence of landscape characteristics changes with the scale of analysis. Although my study clearly showed differences in the response of bats based on morphological and behavioral traits of bat species, certain landscape characteristics seem to be important for most groups and management efforts need to take these findings into consideration. Bat activity of most functional groups was favored by size and shape of green areas, the latter also increased species richness of most functional groups. Also, heterogeneous landscape with high diversity and high intermixture of land-use strongly influenced species richness and bat activity of many analyzed bat groups. And, industrial areas had negative effects on most bat groups and even on the occurrence of the urban adapted *Pipistrellus pipistrellus*. Thus, large and simply shaped green areas as well as a diverse and intermixed landscape are important to mitigate the impact of urbanization on bats. Also, the negative effects of industrial areas on most bat groups need to be considered especially when authorizing new industrial areas in the outer districts of Vienna. Additionally, my assessment of the influence of building heights on the bat assemblage gave first indications that building heights affected bat activity and species richness. In this context, it is important for bats to ensure the possibility to exploit the urban landscape with low energy costs by maintaining intermixed building heights within highly urbanized areas.

## Zusammenfassung

Urbanisierung ist ein Prozess der Landnutzungsänderung und beeinflusst sowohl natürliche Habitate als auch die gesamte Landschaftsstruktur, etwa durch die Erhöhung des Versiegelungsgrades und der Gebäudedichten und die Reduktion von Grünflächen. Urbanisierung wird aufgrund des resultierenden Habitatverlustes und der Fragmentierung verbleibender Habitate als einer der Gründe für den fortschreitenden Verlust der Biodiversität gehandelt. Der Schutz der Biodiversität ist vor allem in urbanen Gebieten daher weltweit eine Herausforderung. Die negative Wirkung der Urbanisierung auf verschiedene taxonomische Gruppen ist zwar bekannt, doch besteht ein Informationsdefizit betreffend den Auswirkungen der Urbanisierung auf Fledermäuse. Das Ziel dieser Arbeit war es herauszufinden, inwieweit Fledermausaktivität und die Anzahl der dort vorkommenden Arten von der umgebende Landschaftsstruktur urbaner Grünräumen beeinflusst wird. Zusätzlich untersuchte ich die möglichen Unterschiede des Einflusses der Landschaftsstruktur auf funktionelle Gruppen der Fledermäuse. Im Sommer 2014 nahm ich daher die Ultraschalllaute von Fledermäusen an 180 verschiedenen Standorten, ausgewählt basierend auf neuen verschiedenen Grünraumtypen, in Wien auf. Die Landschaftsstruktur wurde in einem 0.5 km und 1 km Radius um den Aufnahmeort analysiert. Die Fledermausaktivität reagierte in anderer Weise als die Anzahl der gefundenen Arten auf die umgebende Landschaftsstruktur urbaner Grünräume. Auch zeigten sich Unterschiede im Einfluss der Landschaftsstruktur zwischen dem Auftreten der urbanen Fledermaus *Pipistrellus pipistrellus* und seltenen Fledermausarten im urbanen Gebiet. Einfach geformte Grünräume begünstigen sowohl die Aktivität als auch die Anzahl der meisten untersuchten Fledermausgruppen, während die Größe des Grünraums die Aktivität aller analysierten Gruppen steigert. Außerdem wurden Fledermäuse durch eine vielfältige Landschaftsstruktur und die räumliche Verteilung der Landnutzungstypen begünstigt. Auch die relative Gebäudehöhe hat Einfluss auf die Fledermausaktivität und Anzahl an Arten und sollte in Studien zum Einfluss der Urbanisierung berücksichtigt werden. Außerdem zeigte sich deutlich, dass manche Landschaftsvariablen ihren Einfluss entsprechend der Analyseradien (0.5 km, 1 km) ändern. Zusammenfassend lässt sich sagen, dass sich die Reaktion der Fledermäuse auf die Landschaftsstruktur je nach räumlicher Skala und entsprechend der Ökologie der Fledermausarten ändert. Daher sollten mehrere räumliche und ökologische Ebenen bei der Analyse der Auswirkung der Urbanisierung auf Fledermäuse berücksichtigt werde.

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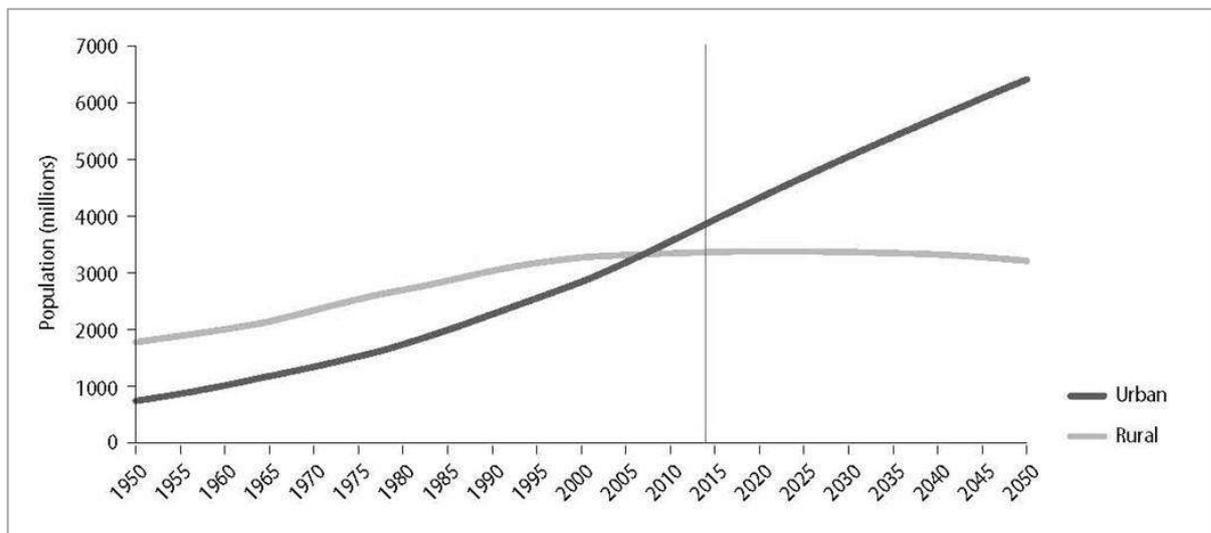
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## 1. Introduction

Urbanization is a worldwide and dominant trend which is influenced by human population increase and the influx of people into cities. About 50 % of the world population lives in towns and cities and it is expected that by 2050 almost 66 % of humans will live in urban areas, whereas the population in rural sites is prospected to stay stable or to decrease slightly (United Nations 2012) (Figure 1). In addition, human population is expected to increase worldwide from 7.0 billion to around 9.3 billion people by 2050 (United Nations 2012). Indeed, the size of the cities is prospected to grow. By 2030, 41 mega cities (10 million and more inhabitants), 63 large cities (5 to 10 million inhabitants) and 558 medium-sized cities (1 to 5 million inhabitants) are expected to exist worldwide (United Nations 2014). But the development of urban areas differs between regions. In 2011, North and South America were already above 80 % urban, whereas in Europe about 70 % of the population lived in cities (United Nations 2014), although the percentage of urban inhabitants is prospected to increase to 80 % by 2050 (United Nations 2014).



**Figure 1: Prospected growth of rural (light grey) and urban (dark grey) population worldwide, from 1950 to 2050 (United Nations 2014)**

Urbanization alters the landscape by reducing and degrading natural habitats, changing utilization of landscape, increasing sealed areas and reducing and fragmenting green areas. Urbanization modifies both the natural landscape composition (i.e., amount of resources available within a certain landscape) and configuration (i.e., spatial distribution of resources within the landscape) and therefore changes their availability for animals and plants (Parrish and Hepinstall-Cymerman 2012). Moreover, urbanization has been associated with the loss of biodiversity (IUCN 2013). The impacts of urbanization on species richness are

well studied for certain taxa, whereas others are still unrepresented. Most research focuses on birds (e.g. Blair and Johnson 2008; McKinney 2008; McIntyre 2011) and show evidence that species richness, diversity and evenness decreases from natural to urban areas, with a slight increase in suburban areas (Blair and Johnson 2008). For other taxa (e.g. invertebrates, reptiles and amphibians) a high level of urbanization leads to a decrease of species richness (Gilbert 1989; McKinney 2008). For example, number of butterflies is reported to decrease with increasing urbanization level (Bergerot et al. 2011).

Another threat of urbanization is the so-called process of biotic homogenization which has been described for bird and butterfly communities in urban areas (e.g. Blair 2001; McKinney 2008). The concept of biotic homogenization describes the replacement of urban avoider species by few urban adapters and urban exploiter species (Blair 2001; Lockwood and McKinney 2001; Blair 2004). Thus, urban species assemblages are often dominated by few generalist urban adapted species. Specialized mostly endangered species disappear in urbanized landscapes due to their low ecological amplitude and their inability to adapt to the fast changing environmental conditions (Gilbert 1989; Blair and Johnson 2008; Bergerot et al. 2011; Meffert and Dziocck 2013). Although biotic homogenization differs between taxa (e.g. birds are stronger influenced than butterflies due to their higher flexibility as invaders), this process is happening in all urban areas around the world (e.g. Blair 2001, 2004). Thus, it is a pressing challenge for land managers and urban planners to assess the impacts of urbanization on organisms in an effort to mitigate the negative impacts, to promote species richness in cities and to set efficient management efforts for conserving biodiversity.

Bats (Chiroptera) are the second largest order among mammals worldwide (> 1200 species; e.g. Dietz et al. 2007) and the most abundant mammalian order in urban areas (Avila-Flores and Fenton 2005). Although bat species play an important role in ecosystems (e.g. pest control; Maas et al. 2013), they are highly unrepresented in urban studies (McIntyre 2011). This un-consideration is worrisome (Racey and Entwistle 2003; Oprea et al. 2009; Jung and Kalko 2011; Threlfall et al. 2012) because bats are a group of global (IUCN 2013) and local (European Union 1992; Hüttmeir et al. 2010) conservation concern and protected by different laws (e.g., Flora-Fauna-Habitat Directive; European Union 1992). The few existing studies often show that most species of insectivorous bats are negatively affected by a high level of urbanization (Avila-Flores and Fenton 2005; Luck et al. 2013) or that species diversity decreases along a rural-urban gradient (e.g., Gaisler et al. 1998; Threlfall et al. 2012). In addition, urbanization is reported to decrease bat abundance and

activity (Geggie and Fenton 1985). However, little is known about the effects of the urban landscape structure and the importance of diverse urban green area types on both bat activity and bat species richness.

Limitation factors for bats in urban areas are prey abundance and roost availability due to the highly transformed landscape (Avila-Flores and Fenton 2005; Russo and Ancillotto 2014). The availability of these essential resources is likely to be influenced by the diverse array of buildings' heights and the flying behavior of bats. Barrier and fragmentation effects could occur if bats are not able to overcome the present buildings. However, some bat species are well adapted to urban areas and use buildings as roost sites (e.g. *Pipistrellus pipistrellus*, *P. kuhlii*; Kunz and Fenton 2003; Dietz et al. 2014). But bat species differ in their requirements and use habitats in diverse ways depending on the ecology, morphology and echolocation abilities (Schnitzler and Kalko 2001; Kunz and Fenton 2003; Dietz et al. 2007; Denzinger and Schnitzler 2013) which influence the ability to adapt to urbanized landscapes (Jung and Kalko 2011; Russo and Ancillotto 2014). However, no research about the impacts of diverse building heights in an urban area on bat species and activity exists so far.

Also, species' response to urbanization may be dependent on the spatial scale considered. Highly mobile species with the ability to fly like bats may exploit large areas and response to urbanization in other ways than non-flying species (Gilbert 1989). However, the scale at which urbanization influences bats have been critically discussed in the last decades (e.g. Gorresen et al. 2005; McKinney 2008). Many studies have investigated the influence of urban landscape at a single scale (e.g. Gehrt and Chelsvig 2003; Threlfall et al. 2012), but also some studies using multiple scales exist (Johnson et al. 2008; Lookingbill et al. 2010; Fabianek et al. 2011; Hale et al. 2012; Gorresen et al. 2005). It is likely that the scale of analysis influence the response of species and therefore a multi-scale or at least two-scale approach is crucial especially when focusing on a high mobile taxa like bats (e.g. Gorresen et al. 2005; Razgour et al. 2011).

Despite an increasing interest in bats as bioindicators for land-use changes (Russo and Jones 2015) and the influence of urban areas on this group, few studies have assessed the influence of urbanization on bats in Europe (e.g. Gaisler et al. 1998; Guest et al. 2002; Razgour et al. 2011; Ducci et al. 2015). Most publications on the interactions of bats and urban landscape were done in Australia, North and South America (e.g. Kurta and Teramino 1992; Gehrt and Chelsvig 2003; Avila-Flores and Fenton 2005; Gorresen et al. 2005; Johnson et al. 2008; Fabianek et al. 2011; Threlfall et al. 2012). It is uncertain whether the patterns in

non-European cities also occurred in Europe given the differences in the landscape structure between regions.

The aim of this study was to assess whether landscape structure surrounding urban green areas had an influence on bat activity and species richness. I used two different spatial scales (0.5 km and 1 km radius) to account for species using smaller ranges as well as highly mobile species (e.g. *Vespertilio murinus*; Dietz et al. 2014). Because the response of bats to landscape structure might be dependent on the species' ecology, I also assessed the influences of the urban landscape structure on functional groups using the classification of Denzinger and Schnitzler (2013). Additionally, I compared the influence of the landscape structure on an urban adapted (*Pipistrellus pipistrellus*) and on urban avoider (i.e., rare) species.

I hypothesize that bat activity and species richness in urban green areas will be affected by landscape composition and configuration of the surroundings. Green areas surrounded with high percentage of vegetation cover will have higher species richness than areas surrounded with high percentage of built-up areas. Contrary, I expect higher bat activity in green areas surrounded with higher percentage of built-up areas because urban adapted species (e.g. *Pipistrellus kuhlii*) will highly contribute to total activity. In addition, I expect higher species richness and higher bat activity in green areas with different land-use classes in its surroundings, because here species can find adequate habitats (roosting and foraging) and bats are known to use diverse forage grounds during one night (Dietz et.al. 2007). Regarding landscape configuration, I expect that green areas surrounded with a highly intermixed landscape will have higher bat activity and species richness because bats will have lower energy costs in obtaining essential resources (e.g. roost, prey; Dietz et.al. 2007). I also expect higher species richness and higher bat activity in large green areas than in small ones because insect abundance is reported to increase with increasing size of green area (Avila-Flores et.al. 2005). I also expect that green areas with simple shape might favor bats because of less disturbance from the surrounding (Forman 1995).

I also hypothesize that the proximity to certain landscape elements (i.e. urban green area, water bodies, and city center) may influence bat activity and species richness. I expect higher bat activity and species richness close to green areas and water sites because both are reported to be good foraging grounds (e.g. Dietz et al. 2007; Denzinger and Schnitzler 2013) and the proximity to green areas may be an indication for diverse foraging grounds (Dietz et.al. 2007). Contrary, I expect lower species richness close to city centre because only

few bat species will be well adapted to urbanization. But I expect bat activity to increase with decreasing distance to city centre because the few urban adapted species will highly influence the total activity based on the biotic homogenization (e.g. Blair 2001).

Although the influence of building heights on urban bat assemblage has not been considered so far, I hypothesize that building heights in the surrounding of urban green areas influence bat activity and species richness. I expect low species richness in areas with high mean building heights and in areas with low intermixed building heights because both might have barrier-effects for certain bat species (e.g. energy effort to adapt flying altitude). Also, the building heights might be an indication for high urbanization which certain bat species might avoid. Contrary, I expect higher bat activity in areas with high mean building heights and no effect of the spatial arrangement of building heights because urban adapted species use buildings as roost and foraging sites and are well adapted to urbanized areas.

Lastly, I hypothesize that the influence of the landscape structure surrounding urban green areas varies between functional groups and between urban adapted (*P. pipistrellus*) and urban avoider (i.e, rare) species because it will correspond with group's ecological requirements, morphology and behavior of included bat species. I expect that urban adapted species (e.g. *P. pipistrellus*) occur frequently throughout the city because of their plasticity of resource use (e.g. Dietz et al. 2014; Ducci et al. 2015). Contrary, urban avoiders which occur less frequently in highly urbanized areas will be dependent on resources that are limited in urban areas (e.g. large woodlands) and negatively influenced by highly urbanized areas.

## 2. Methods

### 2.1. Study area

The study was conducted in Vienna (16°22'23" E and 48° 12' 31" N), the capital of Austria. Vienna has a total area of 414.65 km<sup>2</sup> and about 1 741 246 inhabitants (Statistik Austria 2014). The landscape of Vienna is characterized by a high percentage of green areas with diverse land-use and spatial arrangement within the city. About 50 % of the total area of the city are defined as green area (Hoffert et al. 2008) with utilization ranging from small parks to large woodlots (e.g. Wienerwald) (MA 18 2008). Urban green areas vary also in size (<0.05 ha – 1922.61 ha; MA 18 2008) and distribution among the 23 districts (Figure 2). For example, Vienna's first district has fewer green areas than its surrounding districts. Large parks and protected areas such as the Wienerwald, the Prater, the Bisamberg and the Donau-Auen National Park are included in the overall percentage of Vienna's green areas (Figure 2).

The diversity of habitats offered in the various urban green areas of Vienna is influenced by the geographic location of the city, the climate and elevation differences which results in a high diversity of vegetation types. Vienna is located in a depression within the transition zone between the Alps and the Carpathian Mountains and the climate is influenced by oceanic and continental climate and by the Danube river (Mrkvicka 2011). Additionally, elevation differences (elevation 150 – 543 m) between the higher Wienerwald and the lower city centre (Mrkvicka 2011) generate differences in the annual precipitation (Wienerwald: 800-1500 mm, city center: 550 – 600 mm) and in the temperature (Niklfeld and Rabitsch 2011). These factors influence the vegetation of green areas which ranges from typical woodland vegetation of the more oceanic areas (e.g. *Quercus robur*) to Sub-Mediterranean (e.g. *Quercus pubescens*) and Mid-European areas (e.g. *Fagus sylvatica*) (Niklfeld and Rabitsch 2011).

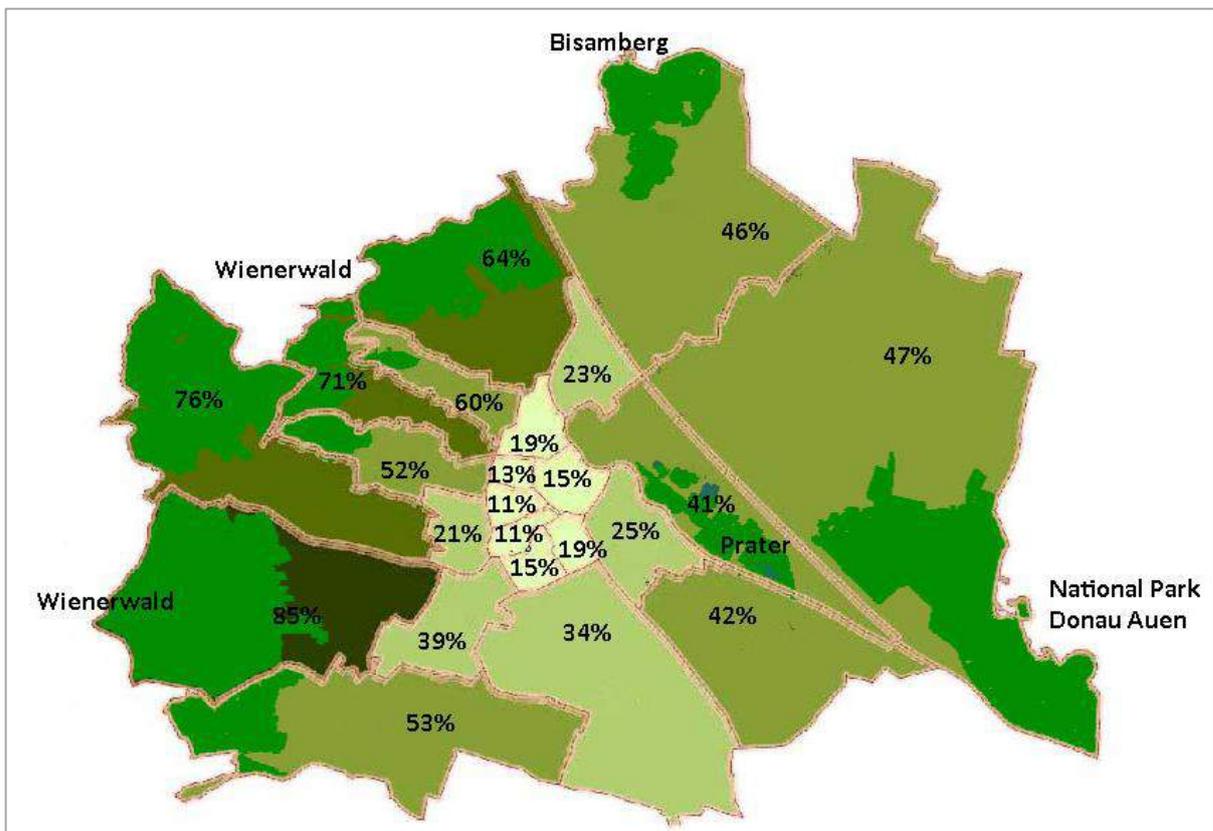


Figure 2: Percentage of Vienna's green areas summarized by district based on "Grünraummonitoring Wien 2005" (Hoffert et al. 2008). Bright green patches illustrate the distribution of the large green areas Bisamberg, parts of Wienerwald, Prater and parts of National Park Donau Auen.

## 2.2. Selection of survey points

I selected 180 survey points distributed in nine different types of urban green areas classified in the Realnutzungskartierung 2009 (RNK 2009) of Vienna (MA 18 2008) (Figure 3). Survey points were located at least 250 m apart in cemeteries (FR), areas with health purpose (GE), housing units (HU), parks (PK), sport areas (SP), tree lines (TL), woods (WD), vineyards (WG) and pastures (WI). Because urban green areas differ in size, I randomly selected green areas greater than 0.25 ha and divided their area into four quartiles to equally represent the size classes in the selection. I randomly selected five survey points within each quartile for a total of 20 points per green area type. Therefore, each survey point was selected based on its size and land-use category. These survey points were marked in a map of Vienna using ArcMap v.10.2 (Esri 2011) and exported to GPS-devices (Garmin 62st) for precise batcorder placing.

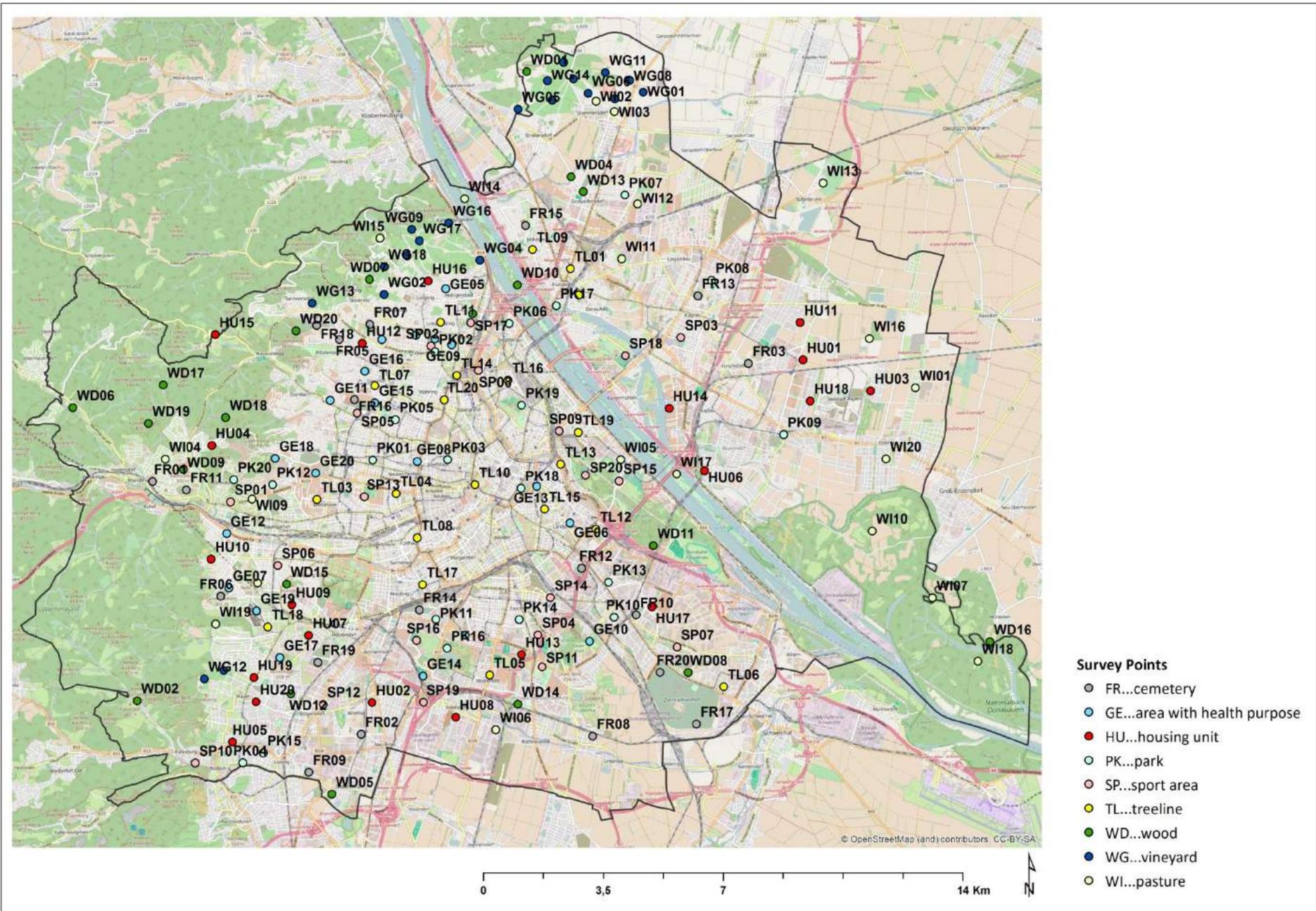


Figure 3: Survey point locations for the acoustic bat survey in Vienna overlay on Open Street Map.

### 2.3. Acoustic bat survey

Between end of April and end of September 2014, the peak of bat activity (Razgour et al. 2011), batcorders from ecoObs were placed at the selected survey points. The batcorders were placed on a stick 2 m high with minimum two meters distance to any tree, bush or other obstacles (Figure 4). Each survey point was sampled three times in a randomized sequence with a different batcorder to minimize recording differences due to season and batcorder (Greis 2012). Batcorders recorded from one hour before sunset to one hour after sunrise (Jung and Kalko 2011; Razgour et al. 2011; Threlfall et al. 2012). Batcorders were only placed during good weather conditions (no rain, no unusually strong winds, temperature >12°C) and the default settings recommended by the manufacturers were used (quality: 20; threshold level: -27 dB; post trigger: 400 ms; critical frequency: 16kHz; ecoObs 2015).



Figure 4: Batcorder placed on a 2 m stick with minimum 2 m distance to any obstacle

## 2.4. Bat call validation

The recorded bat calls were imported to the software bcAdmin from ecoObs for organizing the records, and identified using the program BatIdent from ecoObs. BatIdent automatically identifies the ultrasonic sounds using random forest algorithms which allow identification of large datasets (Marckmann and Runkel 2010). These bat identifications had to be validated manually because confusion between species, especially false-positive identifications appeared depending on the call quality and the echolocation behavior of the bat species. For the call validation, I used functionalities of bcAdmin (e.g. decision tree of identified bats, nightly activity bars) and the software bcAnalyze from ecoObs which provides sonograms of the bat calls. Using bcAnalyze, it was possible to take distinct measurements of sonograms and to play bat sounds about tenfold slower than in nature.

The validation of the bat species was done by three operators, thus to reduce operator bias (Fritsch and Bruckner 2014), validation criteria for each identified species were set. The guidelines of Hammer and Zahn (2009) were used and extended based on information of Dietz et al. (2014), Skiba (2003) and personal communication with experienced bat-researcher (e.g. Claudia Kubista and Ulrich Hüttmeier, 2015) (Table 1). Species with a high identification error rate in the confusion table in Marckmann and Runkel (2010) (false-positive rate >3; false-negative rate >3) were validated with stricter criteria (Table 1). Because of the adherence to these criteria and frequent discussions of all validation results by the operators, the bat species validations did not differ much between operators thus indicating a low operator bias. Additionally, background noises like cricket calls or subway brakes were deleted manually, because they were wrongly identified as bats by BatIdent.

Species like *Myotis bechsteinii*, *Eptesicus serotinus*, *E. nilsonii*, *Nyctalus leiserii* and *Vespertilio murinus* were hard to identify because the range of their call frequencies and the call structure overlapped with other species such as *Myotis* species or *Hypsugo savii*. The operator bias was potentially higher for these species and occurrence of these species was possibly underestimated. Certain difficulties appeared when the program suggested *Miniopterus schreibersii* and *M. dasycneme* because these species show a high degree of overlap of echolocation features (Russo and Papadatou 2014) and are easily confused other bat species. Additionally, these species have not yet been reported in Vienna (Hüttmeier et al. 2010). Thus, records of these species were especially critically appraised. To identify *M. schreibersii* we measured the length of each call because it has to be longer than 18 ms to

discriminate it from *P. pipistrellus* and *P. pygmaeus* (personal communication Ulrich Hüttmeier, 2015). For *M. dasycneme* we looked for the characteristic quail-like call as described in Skiba (2003). It was not possible to distinguish between *P. kuhlii* and *P. nathusii* as well as between *Plecotus auritus* and *P. austriacus*, therefore the species complexes Pmid (*P. kuhlii* and *P. nathusii*) and *Plecotus* (*P. auritus* and *P. austriacus*) were used. Likewise batIdent does not distinguish between *M. mystacinus* and *M. brandtii*, and the species complex Mbart was therefore used.

Further analyses were done using the validated data of total bat activity and species richness. Bat activity can be measured as number of calls, number of call sequences and sequence length. I used sequence length as measure for bat activity because number of calls and sequence length were highly correlated ( $r^2 = 0.90$ ) and sequence length had higher data quality (interval scale). To minimize the influence of outliers, I summed up the length of the sequences per point and survey night and took the median of these sums as measure for total bat activity. So the measurement for total bat activity was more robust against outliers than i.e. the arithmetic mean of the sums. Species richness was defined as total number of recorded species during all three surveys.

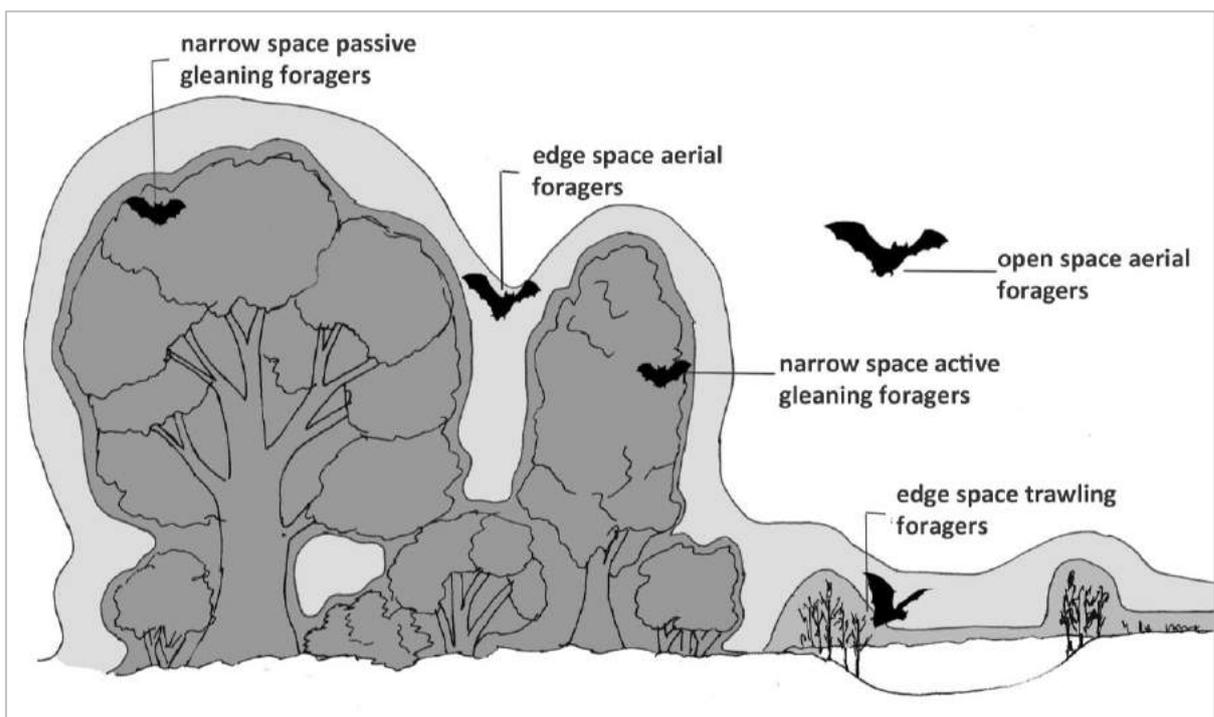
**Table 1: Criteria for bat species validation. Enlarged Criteria = criteria according to <sup>1</sup> Hammer and Zahn (2009), <sup>2</sup> Dietz et al. (2014), <sup>3</sup> Skiba (2003); Confusing Species according to Marckmann and Runkel (2010) and Hammer and Zahn (2009). CF= constant frequently call, QCF = quasi-constant frequently call, FM= frequency modulated call, LH = lower harmonic, UH = upper harmonic**

Species	Acronym	Min. Calls	Enlarged Criteria	Confusion Species
<i>Pipistrellus pipistrellus</i>	Ppip	2 calls	Best frequency: 43-51 kHz (up to 53 kHz) <sup>1</sup> Mind. 1 call > 46 kHz	Ppyg at 51-53 kHz Pmid at 36 – 41 kHz
<i>Pipistrellus pygmaeus</i>	Ppyg	2 calls	Best frequency: 53 - >60 kHz <sup>1</sup>	-
<i>Pipistrellus kuhlii</i> / <i>Pipistrellus nathusii</i>	Pmid	3 calls	Best frequency: 36-41 (43) kHz <sup>1</sup> Mind. 1 call between 38 -41 kHz > 70% probability;	Hsav
<i>Minopterus schreibersi</i>	Misch	25 calls	BF: 49-53 kHz, short calls 50 – 58 kHz; alternating loud and soft calls <sup>2</sup> Discrimination between Misch and Ppip or Ppyg using call length call length: Misch up to 18 ms, Ppip up to 10 ms, Ppyg up to 12 ms <sup>2</sup> Best frequency: 32 – 36 (38) kHz	Ppyg, Ppip
<i>Hypsugo savii</i>	Hsav	2 calls	32-33 kHz flatter than Enil ca. 36 kHz more abrupt than Pnat <sup>1</sup> 1 call < 36 kHz (than no confusion with Pmid) Harmonics visible	Pmid at 36 – 41 kHz Enil (short calls) > 30 kHz
<i>Plecotus auritus</i> / <i>Plecotus austriacus</i>	Plecotus	3 calls	<i>Pl.auritus</i> : LH begins 48-55 kHz ends at 27-17 kHz; UH >80 kHz ends at 35-40 kHz <i>Pl.austriacus</i> : LH begins at 40-44 kHz ends 19-25 kHz; UH at 70-80 kHz ends 38-40 kHz <sup>2</sup>	Bbar, Eser, Vmur
<i>Barbastella barbastellus</i>	Bbar	1 call	Both call types visible BF: Deep call 28-35 kHz; high call 32-45 kHz <sup>1</sup>	-
<i>Nyctalus noctula</i>	Nnoc	1 call	QCF: <= 21 kHz <sup>1</sup> FM-QCF: <=13 ms length; begin at 30-60 kHz ends at 22-28 kHz <sup>2</sup> Best frequency: short calls: 24-26 kHz; long calls: 21-24 kHz (plip-plop);	Nlei, Vmur, Eser
<i>Nyctalus leiseri</i>	Nlei	> 15 calls	highly variable <sup>1</sup> > 5 sequences with > 15 calls; probability 70% Best frequency: 24-27 kHz, often pauses <sup>1</sup>	Nnoc, Vmur, Eser, Enil
<i>Eptesicus serotinus</i>	Eser	> 30 calls	> 5 sequences, > 30 calls; probability > 90% <sup>1</sup> FM <=23ms CL;QCF end 23-27 kHz <sup>2</sup> Distance between calls < 200 ms;	Nnoc, Vmur, Enil
<i>Eptesicus nilsonii</i>	Enil	10 calls	Short calls > 30 kHz; Long calls <= 29 kHz (26 kHz), calls frequently <sup>1</sup>	Hsav, Eser, Vmur

<i>Vespertilio murinus</i>	Vmur	30 calls	QCF: 22-24 kHz, Calls not frequently, differences in frequency and call length <sup>1</sup> > 10 sequences, > 30 calls, probability = 70% <sup>1</sup> Best frequency: begins 65-85 kHz, ends 25-35 kHz, often < 30 kHz; Characteristic QCF: call length 15-25 ms, end frequency 32-37 kHz <sup>2</sup>	Nnoc, Eser
<i>Myotis dasycneme</i>	Mdas	10 calls	Occasional “call of a quail” between normal calls! “Call of a quail”: Frequency around 32 kHz, CL around 20ms, scattered calls between normal ones <sup>3</sup>	Not defined
<i>Myotis daubentonii</i>	Mdau	3 calls	Begin < 100kHz, end often < 30 kHz Myotis kink = soft, often at < 40kHz <sup>1</sup>	Mbart, Malc, Mbec, Mnat
<i>Myotis mystacinus/ Myotis brandtii</i>	Mbart	3 calls	Begin 100 – 125 kHz, MK = sharp at 40 kHz (max. 45 kHz), calls bend, not linear <sup>1</sup>	Mdau, Mbec, Malc, Nlei, Pnat, Mmyo, Mema
<i>Myotis bechsteinii</i>	Mbec	30 calls	Highly variable Frequency: begin often 120 kHz (seldom > 130 kHz → discrimination to Mema); Myotis kink soft most often at > 30kHz but highly variable! often calls without Myotis kink > sequences, 30 calls, probability > 70% highly variable calls <sup>1</sup>	Mbart, Mdau, Mnat, Malc, Nlei, Mema, Mymo, Mdau
<i>Myotis natterii</i>	Mnat	3 calls	Begin often > 135 kHz, end < 20 kHz (often 17 kHz, minimum 7 kHz) linear calls <sup>1</sup>	Mbart, Mbec, Mdau, Mmyo, Mema
<i>Myotis emarginatus</i>	Mema	3 calls	Best frequency: > 50kHz, Begin several times > 130 kHz (up to 170 kHz) – 38 kHz (min.30 kHz); Myotis kink = soft at 45-55 kHz Linear calls <sup>1</sup>	Mbec, Mbart, Malc, Mnat
<i>Myotis alcathoe</i>	Malc	3 calls	Frequency: begin < 130 kHz (seldom 145 kHz), end 45 kHz (minimum 40 kHz); Best frequency: > 50 kHz, Myotis kink = 45 – 55 kHz (seldom 60 kHz) <sup>1</sup>	Mbart, Mbec, Mdau, Pmid, Ppyg, Ppip, Mema
<i>Myotis myotis</i>	Mmyo	3 calls	Begin < 100 kHz, end often at 25 kHz, Myotis kink = 30 kHz Best frequency: 30-35 kHz, often flat call with waves <sup>1</sup>	Mdau, Mnat, Eser
<i>Rhinolophus hipposideros</i>	Rhip	> 1 call	CF ca. 110 kHz Up to 60 ms <sup>2</sup>	Rfer ( <i>R.ferruequinum</i> )

## 2.5. Functional groups and urban adaptation

To analyze the influence of the urban landscape structure on the ecological requirements of various bat species, I grouped the validated species into functional groups according to Denzinger and Schnitzler (2013) (Figure 5). In this classification, species are grouped considering preferred habitat, foraging and echolocation behavior, and body morphology (Denzinger and Schnitzler 2013). Five groups described in Denzinger and Schnitzler (2013) were relevant for Vienna, but based on the validated species, I only focused on (i) open space aerial foragers and (ii) edge space aerial foragers because there was not enough data for analyzing the other three groups (i.e., narrow space passive gleaning foragers, edge space trawling foragers, narrow space active gleaning foragers).



**Figure 5: Schematic illustration of the foraging habitat of functional groups according to Denzinger and Schnitzler (2013).**

Bats belonging to the edge space aerial foragers perform echolocation, biotope recognition, avoidance of collisions and prey identification in the proximity of background targets. Therefore, they emit mixed calls with a length of 3 to 10 ms with each wing beat and reduce the call length while increasing call bandwidth when they come closer to the background (Denzinger and Schnitzler 2013). *P. pipistrellus*, *P. pygmaeus*, *P. kuhlii*, *P. nathusii*, *M. schreibersii*, *E. serotinus*, *E. nilsonii*, *H. savii*, *Barbastella barbastellus* and *M. alcaethoe* are members of this group.

Open space aerial foragers navigate and hunt over a large areas and therefore use long, narrowband signals with a low frequency which increase the possibility of finding insects and in a large detection range (Denzinger and Schnitzler 2013). Typical species of this group are *N. noctula*, *N. leiseri*, *E. serotinus*, *E. nilsonii*, *H. savii*, *V. murinus*.

Bats can switch their preferred foraging habitat by modulating their echolocation signals (Schnitzler and Kalko 2001). Species typically hunting in narrow space are able to adapt to edge space habitats and edge space foraging bats may also hunt in open areas. But it is not possible for open space foragers to adapt to narrow habitats because of missing ability of maneuver due to their wing morphology and inability of echolocation behavior adaptation (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013). Therefore, *E. serotinus*, *E. nilsonii* and *H. savii* are members of both edge space aerial foragers and open space aerial foragers.

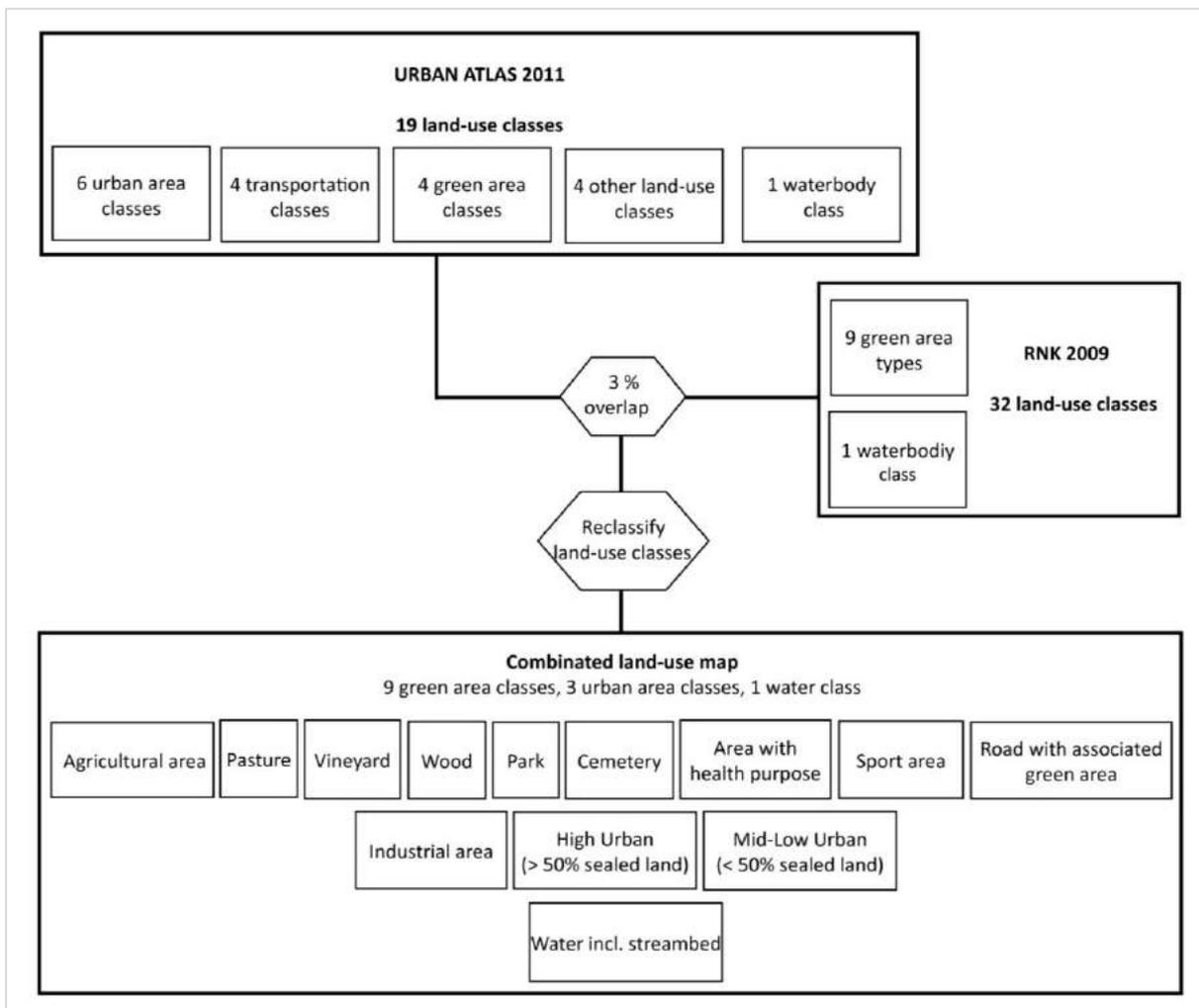
Based on the verified bat species, I also differentiated as rarely detected bats all species occurring at < 30% of the survey points. Using this grouping it was possible to analyze the influence of landscape structure on rare bat species separately. Additionally, I analyzed the influence of the landscape structure on *P. pipistrellus* because it is considered as an urban adapted bat species based on its broad range of habitat exploitation (e.g. Russo and Jones 2003; Dietz et al. 2007, 2014). Consequently, I was able to compare the response of an urban adapted species (*P. pipistrellus*) versus rare bat species to landscape structure.

## 2.6. Landscape analysis

I analyzed the landscape surrounding the survey points using a map which combined the two available land-use maps of Vienna, the Urban Atlas (European Environmental Agency 2011) and the *Realnutzungskartierung 2009* (RNK 2009) (MA 18 2008). Using the combination of both maps (Appendix 1), I merged the advantages and minimized the disadvantages of both maps which would probably influence the results of the analysis.

The Urban Atlas was developed using standardized methodology and categorized Vienna into 19 land-use classes, based on the percentage of sealed land. This seemed more appropriate than the urban classification of the RNK 2009, because it reflects more properly the percentage of land-cover and the remaining amount of non-built area which might be important for bats (for urban exploiters and urban avoiders). However, the RNK 2009 had a much more detailed classification of the various urban green areas which could provide important findings for the diverse use of green areas by bats. Also the available water bodies are mapped in more detailed in the RNK 2009 than in the Urban Atlas, the latter considering only large water bodies like the Danube River and the Danube Channel. Additionally, some survey points were located near the boundary of the RNK 2009 map, so the surroundings included areas outside the RNK 2009. The Urban Atlas had a larger extent, so information about the land-use in these areas was provided by the Urban Atlas.

The more detailed classes of the RNK 2009 (green area types, water bodies) were incorporated into the Urban Atlas using a critical value of > 3 % overlap. The overlapping area in percent of the Urban Atlas classes and the RNK 2009 classes is shown in Appendix 2. Cemeteries, parks, streets with associated green areas, water incl. streambed of the RNK 2009 were always included in the combined map, because the MA 18 had very detailed information about these classes. I reclassified the combined map using the reclassification scheme of Figure 6. So the final land-use map consisted of 13 classes (nine classes reflected green areas, three classes reflected urban areas, one class reflected water bodies) (Appendix 1).



**Figure 6: Classification scheme for the combined land-use map of the Urban Atlas and the RNK 2009 (see Appendix 1) with a critical value of 3 % overlap (see Appendix 2).**

Using the combined land-use map (Appendix 1), I performed the landscape analysis within 0.5 km- and 1 km-radius buffers around survey points using ArcMap v.10.2. (Esri 2011) and FRAGSTATS v.4.2.1. (McGarigal et al. 2012). This two-scale approach accounts for possible scale-dependent differences in the response of bats (e.g., Russo and Ancillotto 2014) due to the high mobility and diverse habitat use of the species (e.g. Dietz et al. 2014).

For each buffer, I measured landscape composition and landscape configuration metrics to assess the effects of urban landscape structure surrounding urban green areas on bats. For landscape composition, I calculated the proportion of the various land-use classes (13 classes; Appendix 1) and the diversity of land-use classes (Simpson Diversity Index) within the buffers. Simpson Diversity Index represents the probability that any two pixels selected randomly would be from different patch types and ranges from 0 to 1 and is a more intuitive measure of diversity than frequently used Shannon Diversity Index (Leitao et al. 2006; McGarigal 2015). Regarding the landscape configuration, I calculated the size of the

green areas (excluding the area of the foundation of buildings), the shape index of the green areas which illustrates the complexity of patch shape and the interspersion and juxtaposition index (IJI) of land-use classes within each buffer. The IJI is based on patch adjacencies, provides information about the interspersion or intermixing of patch types, and is independent on raster resolution (Leitao et al. 2006; McGarigal 2015). The IJI ranges from an uneven (0) to an even spatial arrangement of patches (100) (McGarigal 2014). Also, the Euclidean distances from the survey points to the edges of the nearest green area, water bodies and the city center (i.e., Stephansdom) were measured.

To analyze the influence of building heights on bats, I used a map of the building surface points (*Gebäudeteilflächenpunkte*) provided by the MA 18 which includes information about the relative building height, defined as the cullis of a building minus the elevation level. I considered only buildings with a relative height above 2 m because I assumed that smaller buildings have no influence on bats. Based on this map, I calculated the mean relative building heights and the interspersion and juxtaposition index (IJI) of relative building heights within the two buffers.

## **2.7. Statistical analysis**

I used Welch's ANOVA to test for bat activity and species richness differences among various green area types for all bat groups (i.e., total, edge space aerial foragers, open space aerial foragers, rare species, *P. pipistrellus*). The Welch's ANOVA was needed because of heteroscedasticity among green area types in all groups (assessed with dot plots, R package ggplot2; Wickham and Chang 2015).

Linear models (LM) with total bat activity as dependent variable and generalized linear models (GLM) with total number of species as dependent variable were performed to identify bat response to landscape structure surrounding urban green areas. Additionally, I ran LMs for the activity of edge space aerial foragers and open space aerial foragers and GLMs for the species richness of these two functional groups as well as for species richness of rare species and the occurrence of *P. pipistrellus*. Prior to analysis, variables were transformed to fulfill model assumptions. Total bat activity, the activity of edge space aerial foragers and open space aerial foragers were normalized with a log<sub>10</sub>-transformed. The LMs for bat activity and activity of functional groups were checked for spatial autocorrelation using Moran's I in the Software GeoDa v.1.2. (Anselin 2012) because of occasional overlaps of the 1 km buffers. When spatial autocorrelation was detected, the Queens-based

contiguity spatial weight (order 1) was included in the LMs to account for the autocorrelation (Anselin 2005). The models for the species richness had the same landscape dataset as the models for the bat activity, so Moran's I was identical.

The GLMs for total number of species needed to account for underdispersion, so I used quasipoisson GLMs (Zuur et al. 2009). For the species richness of edge space aerial foragers and the open space aerial foragers Poisson - GLMs were more appropriate (Zeileis et al. 2008; Zuur et al. 2009). To assess the influence of the surrounding landscape on number of rare species, I performed negative binomial GLMs because of the many zero values (Zeileis et al. 2008; Zuur et al. 2009), and binomial GLMs for the occurrence of *P. pipistrellus*.

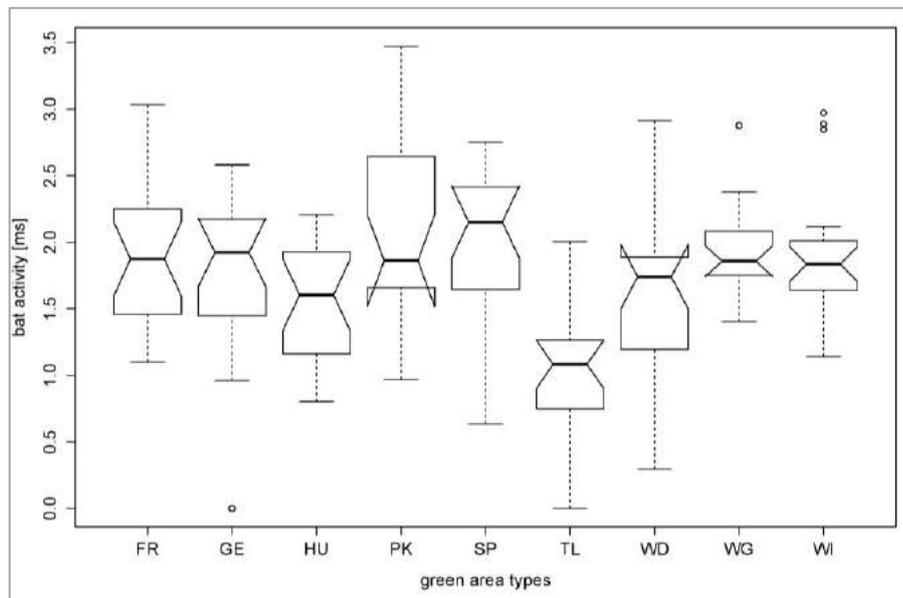
The statistical analyses were performed using R v.3.1.2. (R core team 2014) and all models were fitted using stepwise variable selection based on Akaike's Information Criterion (AIC) (R package MASS; Ripley et al. 2015). Assumptions diagnostics were done using the packages car (Fox et al. 2015), lmtest (Hothorn et al. 2015), MASS (Ripley et al. 2015) and moments (Komsta and Novomestky 2015). Given the high skewness (R package: moments; Komsta and Novomestky 2015) of green area size data, distance to nearest green area, distance to water body, shape index of green area and the percentage of certain land-use classes (agricultural, pasture, woodland, park, sport areas, roads with associated green areas and water bodies), these variables were transformed. Explanatory variables showing high collinearity as assessed with variance inflation factor ( $VIF > 2$ ) (R package: car; Fox et al. 2015) were excluded from the models. All models were performed for each buffer separately to identify scale-dependent effects of the response of bats to landscape structure. The significance level for all tests was 0.05.

### 3. Results

#### 3.1. Bat activity

During the acoustic bat survey the batcorders recorded in total 113 719.52 ms of bat calls (1<sup>st</sup> survey: 28 545.27 ms, 2<sup>nd</sup> survey: 36 546.25 ms, 3<sup>rd</sup> survey: 48 628.00 ms) in 105 076 bat call sequences. Bats could be detected at all survey points except one health area (GE14).

Total bat activity (mean  $\pm$  sd: 1.73  $\pm$  0.62 ms) differed significantly among green area types based on the Welch's ANOVA ( $F = 7.51$ ,  $df = 8$ ,  $p < 0.001$ ). The boxplots using notches indicated probable differences between tree lines and all other green area types (Figure 7). On average, parks had the highest bat activity (2.04  $\pm$  0.63 ms), followed by sport areas (1.97  $\pm$  0.60 ms) and tree lines the lowest (1.04  $\pm$  0.49 ms).

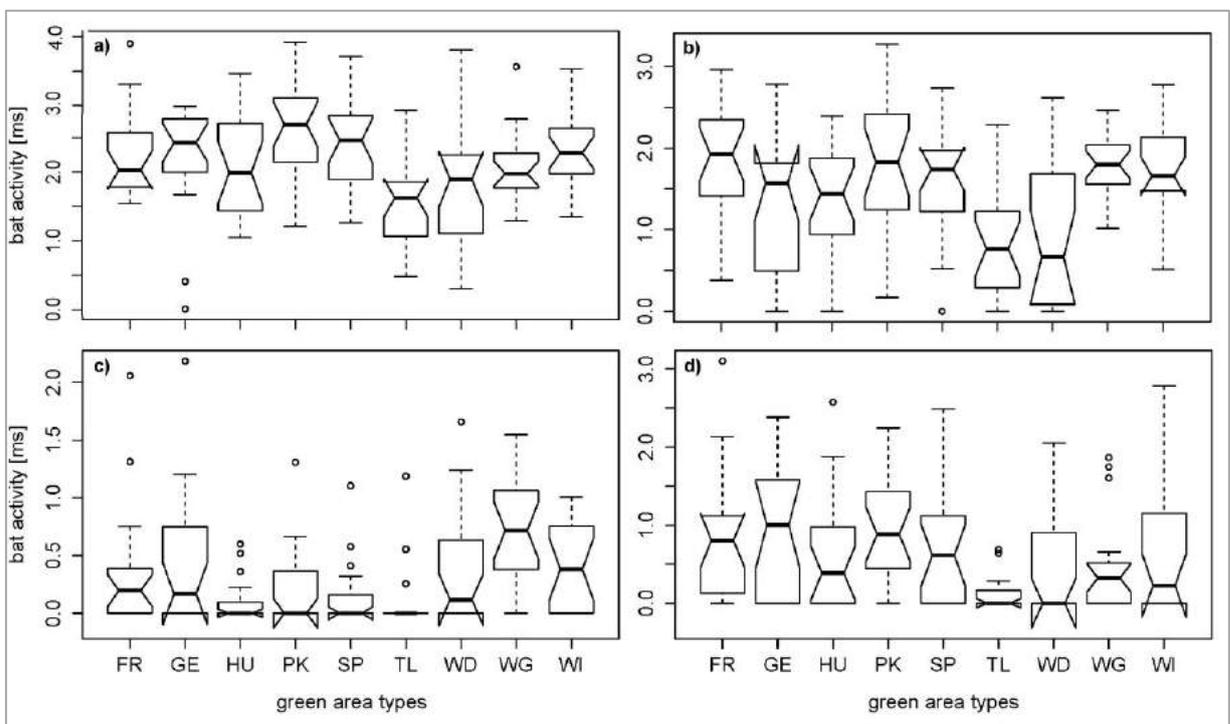


**Figure 7: Total bat activity per green area type using boxplots with notches. Boxes with overlapping notches probably do not have significant different medians (Crawley 2013). FR=cemetery, GE=area with health purpose, HU=housing unit, PK=park, SP=sports area, TL=tree line, WD=woodland, WG=vineyard, WI=pasture.**

Focusing on the functional groups, the activity of edge space aerial foragers (2.13  $\pm$  0.72 ms), open space aerial foragers (1.49  $\pm$  0.77 ms), rare species (0.31  $\pm$  0.44 ms) and *P. pipistrellus* (0.63  $\pm$  0.74 ms) also showed significant differences between green area types according to Welch's ANOVA (edge space aerial foragers:  $F = 4.41$ ,  $df = 8$ ,  $p < 0.001$ ; open space aerial foragers:  $F = 5.85$ ,  $df = 8$ ,  $p < 0.001$ ; rare species:  $F = 6.13$ ,  $df = 8$ ,  $p < 0.001$ ; *P. pipistrellus*:  $F = 7.97$ ,  $df = 8$ ,  $p < 0.001$ ). Similarly to total bat activity, edge space and open space aerial foragers had the highest activity in parks (edge space: 2.61  $\pm$  0.64; open space: 1.80  $\pm$  0.78) and the lowest in tree lines (edge space: 2.20  $\pm$  0.78; open space: 1.34  $\pm$  0.83)

(Figure 8 a, b). The activity of open space aerial foragers differed between tree lines and all other green area types except woods. Also, the activity of edge space aerial foragers differed between tree lines and four green area types (areas with health purpose, parks, sport areas, pastures) but not between tree lines and the other four green areas (woods, vineyards, housing units and cemeteries). In addition, I found differences in the activity of edge space aerial foragers between parks and cemeteries, woods and vineyards and between vineyards and sport areas.

Similar to other groups, activity of rare species and *P. pipistrellus* were lowest in tree lines (rare species:  $0.10 \pm 0.30$ ; *P. pipistrellus*:  $0.11 \pm 0.21$ ). However, the green area with highest activity differed to other groups. Rare species had highest activity in vineyards ( $0.75 \pm 0.45$  ms; Figure 8 c) and *P. pipistrellus* had highest activity in areas with health purpose ( $1.0 \pm 0.83$  ms; Figure 8 d). Rare species showed differences between tree lines and cemeteries, vineyards and pastures. Additionally, the rare species activity at housing units differed to cemeteries, vineyards and pastures and activity at vineyards differed to all other green areas except pastures. *P. pipistrellus* showed also differences between tree lines and all green areas except woods, housing units and pastures. Also, differences between woods and areas with health purpose and parks were detectable.



**Figure 8: Activity of a) edge space aerial foragers b) open space aerial foragers c) rare species d) *P. pipistrellus* per green area type using boxplots with notches. For acronyms refer to Figure 7.**

### 3.2. Species Richness

Based on the validation criteria (Table 1) 77.5 % of the bat call sequences could be identified and validated as bat species (15 species) and three species complex (i.e., Pmid, *Plecotus*, Mbart). The remaining 22.5 % of the bat call sequences were bats, but were not identified as specific species by batIdent or could not be validated. The most common species were *P. kuhlii*/*P. nathusii* (Pmid), *P. pygmaeus*, *N. noctula*, *H. savii*, *P. pipistrellus* and *M. brandtii*/*M. mystacinus* (Mbart). These species occurred at > 30 % of the survey points, whereas the other nine species occurred at < 20 % of the survey points and were denoted as rare species (Figure 9).

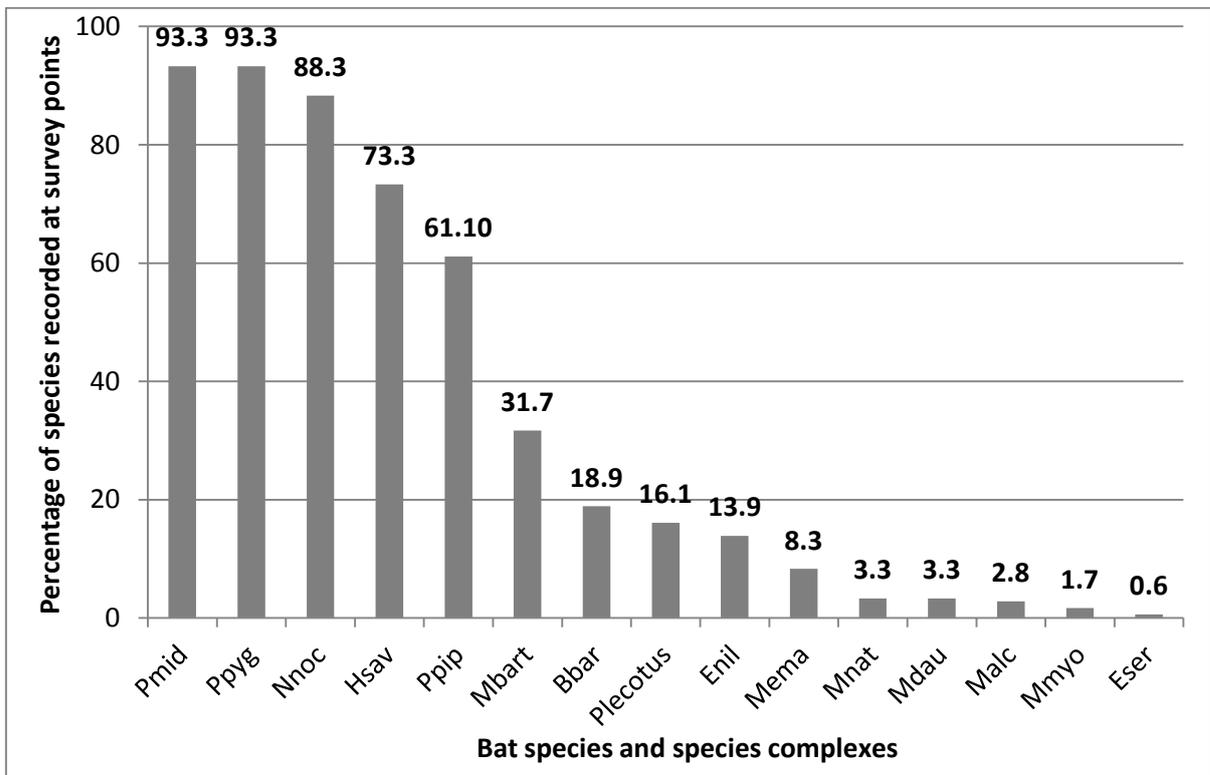
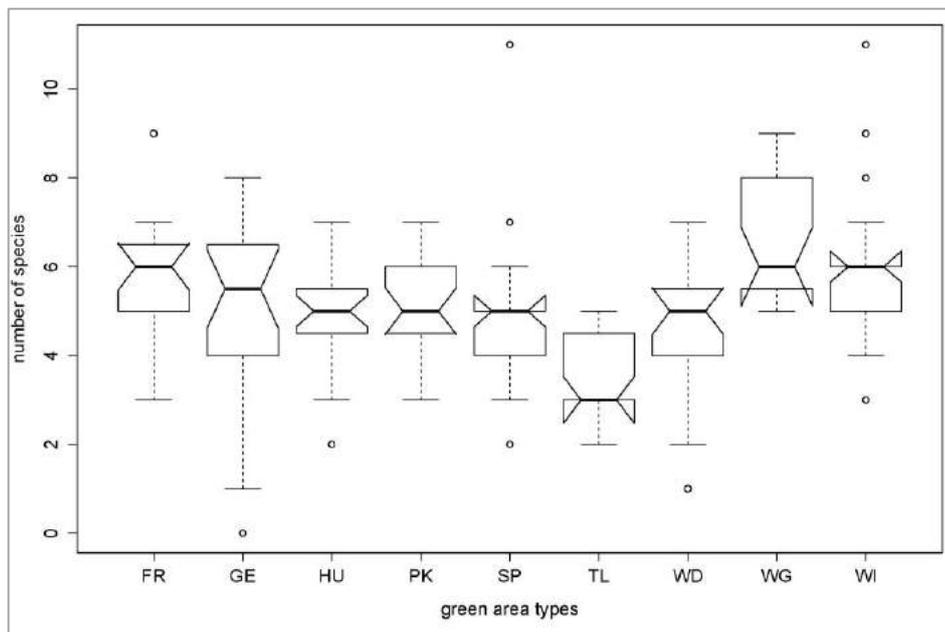


Figure 9: Percentage of species detected at 180 survey points. For acronyms see Table 1.

Like the total bat activity, total number of species ( $5.12 \pm 1.78$ ) varied among green area types ( $F = 9.266$ ,  $df = 8$ ,  $p < 0.001$ ) with lowest number at tree lines ( $3.45 \pm 1.09$ ), but the highest species richness was at vineyards ( $6.6 \pm 1.35$ ). Differences in the total number of species were detected between tree lines and all other green areas, similarly to total bat activity (Figure 10). Additionally, species richness showed differences between sport areas and cemeteries and pastures as well as between woodlands and pastures.

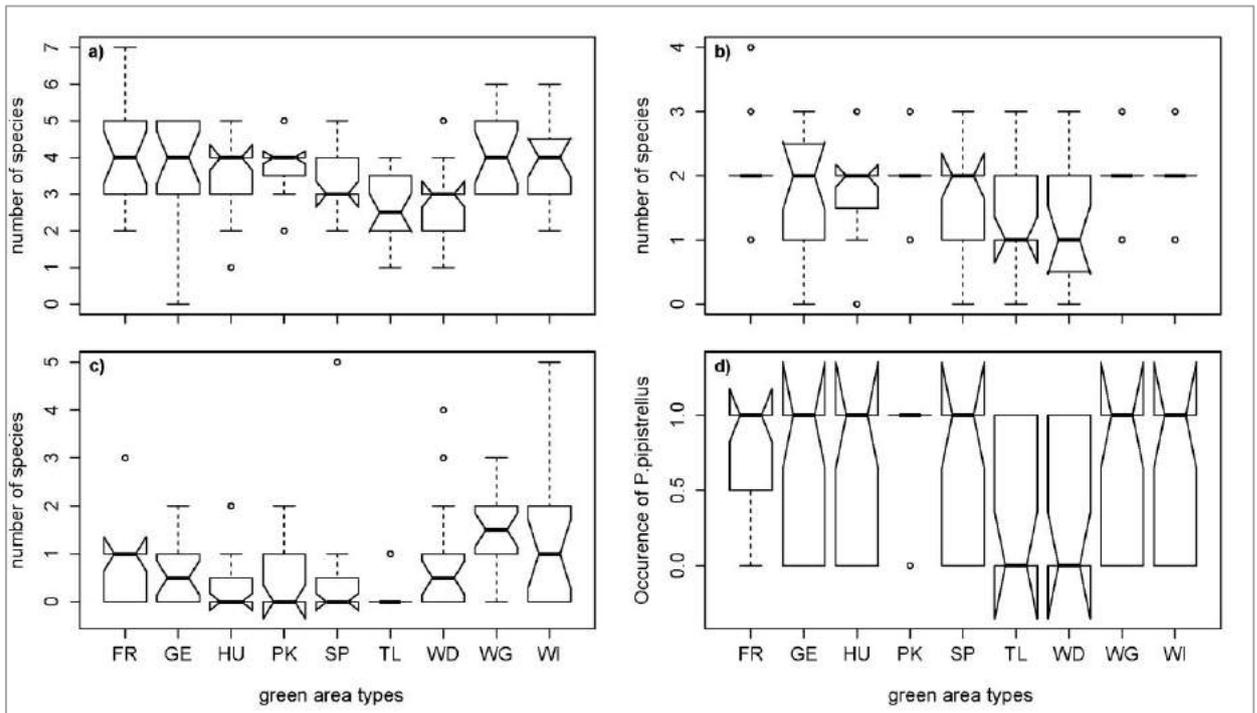


**Figure 10: Total species richness per green area type using boxplots with notches. Boxes with overlapping notches probably do not have significant different medians (Crawley 2013). For acronyms refer to Figure 7.**

When considering functional groups, number of edge space aerial foragers ( $F = 5.40$ ,  $df = 8$ ,  $p < 0.001$ ), open space aerial foragers ( $F = 4.38$ ,  $df = 8$ ,  $p < 0.001$ ), number of rare species ( $F = 7.14$ ,  $df = 8$ ,  $p < 0.001$ ) and occurrence of *P. pipistrellus* ( $F = 2.50$ ,  $df = 8$ ,  $p = 0.019$ ) were significantly different among green area types. In contrast to the bat activity, the species richness of edge space and open space aerial foragers showed different patterns to total species richness (Figure 11 a, b). The highest number of edge space aerial foragers was detected in vineyards ( $4.25 \pm 1.0$ ) followed by cemeteries ( $4.20 \pm 1.24$ ) and the highest number of open space aerial foragers was found in areas with health purpose ( $1.85 \pm 0.93$ ). The lowest number of edge space ( $2.80 \pm 1.10$ ) and open space aerial foragers ( $1.15 \pm 0.88$ ) was detected in woods followed by tree lines (number of edge space:  $3.65 \pm 1.39$ ; open space aerial foragers:  $1.85 \pm 0.93$ ). Species richness of edge space and open space aerial foragers differed between tree lines and all other green area types except woods (for open space aerial foragers) and except woods and sport areas (for edge space aerial foragers). Also, I found differences in the number of open space aerial foragers between woods and all other green area types except tree lines. Additionally, the number of edge space aerial foragers differed between both sport areas and woods and three green area types (housing units, parks, pastures).

Similar to the total number of species and number of edge space aerial foragers, the number of rare species (Figure 11, c) was highest in vineyards ( $1.5 \pm 0.83$ ) and lowest in tree

lines ( $0.15 \pm 0.37$ ). The number of rare species varied between vineyards and all other green area types except pastures and cemeteries as well as between tree lines and five green area types (cemeteries, areas with health purpose, woods, vineyards, pastures). In contrast to the number of species of the other groups as well as the activity of *P.pipistrellus*, the occurrence of *P.pipistrellus* (Figure 11, d) was highest in parks ( $0.85 \pm 0.37$ ) and lowest in woodlands ( $0.40 \pm 0.50$ ). I detected probable differences in the occurrence of *P.pipistrellus* between woodlands and all other green area types except tree lines.



**Figure 11: Species richness of a) edge space aerial foragers b) open space aerial foragers c) rare species and d) Occurrence of *P. pipistrellus* per green area type using boxplots with notches. For acronyms refer to Figure 7.**

### 3.3. Landscape variables

Most survey points were located in green areas of medium size and simple shape with high distance from city center and water bodies but near other green areas (Table 2). The size of green areas ranged from 0.70 to 689.10 ha ( $20.12 \pm 86.15$  ha) and had a shape index between 1 and 11, having on average a simple shape ( $2.42 \pm 1.49$ ). The survey points were at least 620.76 m away from the city center ( $7\ 106.50 \pm 2\ 993.19$  m), on average close to other green areas ( $71.59 \pm 81.07$  m) but farther away from water bodies ( $810.71 \pm 663.93$  m; Table 2).

The landscape within the buffers consisted mainly of urban land-use classes and varied little when comparing the 0.5 km and 1 km scale, only the maximum percentage of

certain land-use classes differed between scales (Table 2). On average the buffers consisted of about 60 % urban areas with different degree of sealed land, 37 % of the different green areas and 3 % water bodies.

Also, the land-use diversity (Simpson's Diversity Index) and the interspersion and juxtaposition index (IJI) of land-use classes were similar at both scales. Land-use diversity ranged from 0.03 to 0.85 at the fine scale ( $0.67 \pm 0.14$ ) and was slightly higher at the broad scale ( $0.71 \pm 0.12$ ), indicating high diversity of land-use classes within the buffers. Interspersion and juxtaposition index (IJI) showed a high intermixture of land-use classes with IJI ranging from 27.56 to 86.63 at the fine scale ( $60.67 \pm 10.88$ ) and similar results at the broad scale ( $60.01 \pm 9.52$ ), illustrating a high intermixture of land-use classes (Table 2).

Focusing on the relative building heights, the measured variables were similar at both buffers. At fine scale, the mean relative building height was on average 7.38 m ( $\pm 4.51$ ) with maximum height about 22 m. The interspersion and juxtaposition index of the relative building heights indicated a high intermixture of different building heights within the 0.5 km buffer ( $61.89 \pm 13.17$ ). These results were similar at the broad scale (Table 2).

**Table 2: Overview of landscape variables; minimum, maximum, mean  $\pm$  standard deviation of untransformed values and transformation method are shown.**

Explanatory variables	scale	min	max	mean $\pm$ sd	transformation
Size of green area (ha)		0.07	686.10	$20.12 \pm 86.15$	Log10
Shape of the green area		1.07	11.08	$2.42 \pm 1.49$	1/shape
Distance to green area (m)		0.28	407.23	$71.59 \pm 81.07$	Square-root
Distance to water (m)		0.32	2955.98	$810.71 \pm 663.93$	Square-root
Distance to the city center (m)		620.76	14954.73	$7106.50 \pm 2993.19$	-
Proportion of agriculture (%)	0.5 km	0.00	74.60	$6.32 \pm 13.54$	Arcsine-root
	1.0 km	0.00	78.59	$7.25 \pm 14.79$	Arcsine-root
Proportion of pasture (%)	0.5 km	0.00	26.93	$3.86 \pm 5.57$	Arcsine-root
	1.0 km	0.00	21.63	$3.84 \pm 3.85$	Arcsine-root
Proportion of vineyard (%)	0.5 km	0.00	77.85	$5.24 \pm 14.57$	-
	1.0 km	0.00	57.44	$4.41 \pm 10.98$	-
Proportion of wood (%)	0.5 km	0.00	98.29	$9.88 \pm 19.49$	Arcsine-root
	1.0 km	0.00	93.03	$11.48 \pm 19.29$	Arcsine-root
Proportion of park (%)	0.5 km	0.00	47.72	$5.42 \pm 7.35$	Arcsine-root
	1.0 km	0.00	31.31	$5.12 \pm 4.84$	Arcsine-root
Proportion of cemetery (%)	0.5 km	0.00	64.74	$2.82 \pm 8.72$	-
	1.0 km	0.00	45.23	$1.96 \pm 5.98$	-
Proportion of areas with health purpose (%)	0.5 km	0.00	35.25	$1.16 \pm 4.44$	-

	1.0 km	0.00	16.75	0.90 ± 2.38	-
Proportion of sport areas (%)	0.5 km	0.00	48.01	5.56 ± 8.51	Arcsine-root
	1.0 km	0.00	25.79	4.98 ± 5.29	Arcsine-root
Proportion of roads with associated green (%)	0.5 km	0.00	26.39	3.02 ± 4.69	Arcsine-root
	1.0 km	0.00	20.98	2.82 ± 3.82	Arcsine-root
Proportion of industrial (%)	0.5 km	0.00	52.90	10.28 ± 11.67	-
	1.0 km	0.00	57.77	11.29 ± 11.19	-
Proportion of high-urban (%)	0.5 km	0.00	74.17	19.31 ± 18.95	-
	1.0 km	0.00	70.56	19.15 ± 16.25	-
Proportion of mid-low urban (%)	0.5 km	0.00	80.87	24.48 ± 19.41	-
	1.0 km	0.00	80.36	24.06 ± 17.13	-
Proportion of water bodies (%)	0.5 km	0.00	60.80	2.66 ± 8.11	Arcsine-root
	1.0 km	0.00	34.56	2.76 ± 6.12	Arcsine-root
Simpson's Diversity Index of the land-use classes	0.5 km	0.03	0.85	0.67 ± 0.14	-
	1.0 km	0.13	0.86	0.71 ± 0.12	-
Interspersion and juxtaposition index of land-use classes	0.5 km	27.56	86.63	60.67 ± 10.88	-
	1.0 km	29.49	82.76	60.01 ± 9.52	-
Interspersion and juxtaposition index of relative building heights	0.5 km	0.00	77.82	61.89 ± 13.17	-
	1.0 km	20.91	83.75	70.38 ± 9.25	-
Mean relative building heights (m)	0.5 km	0.00	21.67	7.38 ± 4.51	-
	1.0 km	0.00	21.68	7.69 ± 4.15	-

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### 3.4. Influence of landscape structure on bat activity

Total bat activity was significantly influenced by landscape composition, configuration, and building height at both scales. At both scales, total bat activity was significantly positive influenced by size and shape of green areas and by mean relative building heights (Table 3). At fine scale, total bat activity was also positively influenced by land-use diversity ( $p = 0.042$ ) and negatively by the proportion of industrial ( $p = 0.020$ ) and high urban areas ( $p = 0.033$ ). Contrary, none of these landscape composition variables showed significant influences on the total bat activity at broad scale. However, the IJI of land-use classes ( $p < 0.001$ ) had a significantly influence on the total bat activity at broad scale. The proportion of mid-low urban areas ( $p = 0.210$ ) remained also in the model of the 1 km buffer and indicated a positive relationship but missed the significance level. The total bat activity was explained by 17.56 % of the variance at the 0.5 km scale and 16.95 % at the 1 km scale. There was no spatial autocorrelation in the broad scale model (Moran's  $I = -1.789$ ,  $p = 0.07$ ).

**Table 3: Best fitted model for total bat activity and landscape variables within 0.5 and 1 km buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	t-value	p-value
Size green area	0.224	0.070	3.201	<b>0.002</b>	0.226	0.064	3.516	<b>&lt; 0.001</b>
Shape green area	0.939	0.233	4.025	<b>&lt; 0.001</b>	0.910	0.232	3.929	<b>&lt; 0.001</b>
IJI* of land-use classes					0.018	0.005	3.505	<b>&lt; 0.001</b>
Land-use diversity	0.745	0.365	2.041	<b>0.042</b>				
Industrial	-0.991	0.422	-2.349	<b>0.020</b>				
High urban	-0.702	0.326	-2.154	<b>0.033</b>				
Mid-low urban					0.333	0.264	1.259	0.210
Mean relative building height	0.035	0.013	2.695	<b>0.008</b>	0.032	0.012	2.630	<b>0.009</b>

\* IJI: Interspersion and juxtaposition

Similarly to total bat activity, activity of edge space aerial foragers was positively influenced by size and shape of green areas and mean relative building heights at both scales (Table 4). However, activity of edge space aerial foragers was neither significantly influenced by land-use diversity nor by IJI of land uses at any scale. Proportion of land-uses had significant influence only at fine scale. Although more land-use classes remained in the model, and contrasting with total bat activity, only proportion of industrial areas ( $p = 0.015$ )

and proportion of woods ( $p = 0.025$ ) had a significantly negative influence on activity of edge space aerial foragers. The activity of edge space aerial foragers had higher explanation power at fine ( $R^2 = 0.15$ ) than at broad scale ( $R^2 = 0.10$ ), and no spatial autocorrelation was detected at broad scale (Moran's  $I = -1.464$ ,  $p = 0.143$ ).

**Table 4: Best fitted model for activity of edge space aerial foragers and landscape variables within 0.5 and 1 km buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	t-value	p-value
Size green area	0.270	0.095	2.844	<b>0.005</b>	0.168	0.078	2.163	<b>0.032</b>
Shape green area	0.817	0.294	2.781	<b>0.006</b>	0.786	0.288	2.729	<b>0.007</b>
IJI* of land-use classes	0.011	0.006	1.728	0.086				
Land-use diversity	0.673	0.542	1.243	0.216	0.657	0.457	1.438	0.152
Agriculture	-0.252	0.307	-0.822	0.412				
Vineyards	-0.734	0.443	-1.657	0.099				
Woods	-0.613	0.270	-2.268	<b>0.025</b>				
Cemeteries	-0.947	0.672	-1.410	0.160				
Sport	-0.547	0.392	-1.395	0.165				
Roads with assoc. green	-0.874	0.515	-1.696	0.092				
Industrial	-1.359	0.555	-2.450	<b>0.015</b>				
Mid-low Urban					0.557	0.330	1.688	0.093
Water					0.649	0.427	1.520	0.130
Mean relative building height	0.044	0.016	2.795	<b>0.006</b>	0.036	0.013	2.672	<b>0.008</b>

\* IJI: Interspersion and juxtaposition

The activity of open space aerial foragers was significantly positively influenced by size and shape of green areas at both scales. But the mean relative building heights showed no significant influence on the activity of open space aerial foragers and did not remain in the models (Table 5). At fine scale, no significant relationship between activity of open space aerial foragers and land-use diversity could be detected ( $p = 0.130$ ), similar to the activity of edge space aerial foragers. Also, the activity of open space aerial foragers was significantly negatively influenced by the proportion of woods, but here not only at fine ( $p = 0.002$ ) but also at broad scale ( $p = 0.004$ ). The other three land-use classes remaining in the fine scale model showed no significant effects on the activity of open space aerial foragers. Alike total bat activity, the activity of open space aerial foragers was positively influenced by IJI of land-

use classes at broad scale ( $p < 0.001$ ). Here, the distance to city center remained in the model but missed the significance level ( $p = 0.623$ ). About 13 % of the variance of the activity of open space aerial foragers could be explained with both models. Here, also no spatial autocorrelation was detected (Moran's  $I = -0.77$ ,  $p = 0.4$ ).

**Table 5: Best fitted model for activity of open space aerial foragers and landscape variables within 0.5 and 1 km buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	t-value	p-value
Size green area	0.310	0.088	3.511	<b>&lt; 0.001</b>	0.172	0.083	2.067	<b>0.040</b>
Shape green area	0.782	0.303	2.580	<b>0.011</b>	0.788	0.292	2.701	<b>0.008</b>
IJI* of land-use classes					0.025	0.006	4.104	<b>&lt; 0.001</b>
Land-use diversity	0.843	0.547	1.540	0.126				
Pasture	0.948	0.499	1.901	0.059				
Woods	-0.839	0.263	-3.186	<b>0.002</b>	-0.670	0.227	-2.953	<b>0.004</b>
Sport	-0.439	0.375	-1.170	0.244				
Industrial	-0.870	0.547	-1.590	0.114				
Distance city center	-0.00001	0.00002	-0.493	0.623				

\* IJI: Interspersion and juxtaposition

### 3.5. Influence of landscape structure on species richness

Total species richness was also significantly influenced by landscape composition and configuration metrics and the buildings, but showed differences to total bat activity (Table 6). Shape of green areas had a significantly positive influence on total species richness at both scales, whereas proportion of industrial and high urban areas had significantly negative effects at both scales. Contrary to total bat activity, the size of green area, the land-use diversity and the IJI of land-use classes had no influence on total species richness and did not remain in the best-fitting model. Also, total species richness showed no relationship to the mean relative building heights, but the IJI of relative building heights ( $p = 0.027$ ) had a significantly positive influence on total species richness at broad scale.

**Table 6: Best fitted model (quasipoisson GLM) for total species richness and landscape variables within 0.5 km and 1 km radius buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	z-value	p-value
Shape green area	0.395	0.116	3.410	<b>&lt; 0.001</b>	0.298	0.114	2.621	<b>0.0095</b>
Industrial	-0.734	0.209	-3.514	<b>&lt; 0.001</b>	-0.567	0.220	-2.578	<b>0.012</b>
High urban	-0.764	0.130	-5.889	<b>&lt; 0.001</b>	-0.990	0.166	-5.959	<b>&lt; 0.001</b>
IJI* of relative building heights					0.006	0.003	2.230	<b>0.027</b>

\* IJI: Interspersion and juxtaposition

In contrast to total species richness, the number of edge space aerial foragers was significantly positively influenced by size ( $p < 0.001$ ) and shape of green areas ( $p = 0.006$ ) only at fine scale. Regarding the influence of the proportion of land-use classes, differences between the two scales occurred (Table 7). The number of edge space aerial foragers was positively influenced by the proportion of mid-low urban areas ( $p < 0.001$ ) at fine scale, whereas the only variable remaining in the model at broad scale was proportion of high urban areas ( $p = 0.001$ ) which showed a significant negative influence. Contrary to activity, the species richness of edge space aerial foragers showed neither relationships to the proportion of industrial areas nor to woods or building heights.

**Table 7: Best fitted model (quasipoisson GLM) for species richness of edge space aerial foragers and landscape variables within 0.5 km and 1 km radius buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	z-value	p-value
Size green area	0.127	0.034	3.772	<b>&lt; 0.001</b>				
Shape green area	0.336	0.121	2.783	<b>0.006</b>				
High urban					-0.483	0.150	-3.228	<b>0.001</b>
Mid-low urban	0.006	0.001	4.629	<b>&lt; 0.001</b>				

Interestingly, the number of open space aerial foragers was neither significantly influenced by the size nor the shape of green areas (Table 8). Also, this bat group showed no interference of building heights. At fine scale, number of open space aerial foragers was positively influenced by the proportion of mid-low urban areas ( $p < 0.001$ ), alike the number of edge space aerial foragers. Additionally, the number of open space aerial foragers was positively influenced by the proportion of agricultural areas at fine scale ( $p < 0.001$ ). At broad scale, the IJI of land-uses ( $p < 0.001$ ) had a significantly positive influence, whereas the

proportion of woods ( $p = 0.001$ ) and parks ( $p = 0.002$ ) had a significantly negative influence on the number of open space aerial foragers.

**Table 8: Best fitted model (quasipoisson GLM) for species richness of open space aerial foragers and landscape variables within 0.5 km and 1 km radius buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	z-value	p-value
IJI* of land-use classes					0.014	0.004	3.718	< 0.001
Agricultural	0.083	0.024	3.427	<0.001				
Woods					-0.500	0.150	-3.338	<b>0.001</b>
Parks					-0.966	0.305	-3.170	<b>0.002</b>
Mid-low urban	0.005	0.002	3.027	<b>0.003</b>				

\* IJI: Interspersion and juxtaposition

The number of rare species was significantly positively influenced by the shape of green areas at both scales, similar to the total species richness (Table 9). In addition, the proportion of industrial ( $p = 0.005$ ) and high urban areas ( $p < 0.001$ ) had a significant negative influence and the distance to city center ( $p = 0.05$ ) had a significantly positive influence only at fine scale. At broad scale, the size of green area had a significant positive influence on the number of rare species ( $p = 0.039$ ), alike the edge space aerial foragers. Additionally, the number of rare species was significantly positively influenced by the IJI of land-use classes ( $p < 0.001$ ) and negatively by the proportion of parks ( $p = 0.047$ ) at broad scale.

**Table 9: Best fitted model (negative binomial GLM) for rare species richness and landscape variables within 0.5 km and 1 km radius buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	t-value	p-value	Estimate	Std.Error	z-value	p-value
Size green area					0.256	0.124	2.068	<b>0.039</b>
Shape green area	1.454	0.480	3.027	<b>0.002</b>	1.126	0.521	2.161	<b>0.031</b>
IJI* of land-use classes					0.039	0.011	3.452	< <b>0.001</b>
Agricultural	-0.137	0.084	-1.627	0.104				
Parks					-1.833	0.923	-1.987	<b>0.047</b>
Industrial	-0.033	0.012	-2.795	<b>0.005</b>				
High urban	-0.035	0.008	-4.530	< <b>0.001</b>				
Distance city center	0.0001	0.00004	1.958	<b>0.050</b>				

\* IJI: Interspersion and juxtaposition

Contrary to rare species, the occurrence of *P. pipistrellus* was not significantly influenced by the shape of green areas at any scale, although shape was included in the best-fitting model (Table 10). Also, the size of green areas showed no significant influence on the occurrence of *P. pipistrellus*. But *P. pipistrellus* was significantly negatively influenced by proportion of agricultural areas ( $p < 0.001$ ), proportion of vineyards ( $p = 0.007$ ), woods ( $p = 0.005$ ) and industrial areas ( $p = 0.021$ ) and the mean relative building heights ( $p = 0.005$ ) at fine scale. Furthermore, *P. pipistrellus* was significantly positively influenced by IJI of relative building heights ( $p < 0.001$ ) at broad scale. Interestingly, distance to water bodies negatively influenced the occurrence of *P. pipistrellus* at both scales.

**Table 10: Best fitted model (binomial GLM, link=logit) for occurrence of *P. pipistrellus* and landscape variables within 0.5 km and 1 km radius buffer. Numbers in bold indicate significance at the 0.05 alpha level.**

Landscape variables	0.5 km				1 km			
	Estimate	Std.Error	z-value	p-value	Estimate	Std.Error	z-value	p-value
Shape green area	1.850	0.100	1.858	0.063	0.994	0.919	1.082	0.279
IJI* of land-use classes	0.053	0.020	2.662	<b>0.008</b>				
Agricultural	-4.330	1.070	-4.047	<b>&lt; 0.001</b>	-1.479	0.794	-1.862	0.063
Vineyards	-3.967	1.464	-2.710	<b>0.007</b>	-1.928	1.715	-1.124	0.261
Woods	-2.547	0.910	-2.799	<b>0.005</b>				
Health areas	26.813	21.986	1.220	0.223	38.579	20.689	1.865	0.062
Sport	-1.861	1.195	-1.557	0.120	0.252	1.581	0.160	0.873
Industrial	-4.084	1.763	-2.317	<b>0.021</b>				
Water					-2.395	1.711	-1.400	0.162
Distance to water	-0.040	0.017	-2.346	<b>0.019</b>	-0.066	0.021	-3.127	<b>0.002</b>
Mean relative building height	-0.147	0.053	-2.799	<b>0.005</b>				
IJI* of relative building heights					0.066	0.023	2.811	<b>0.005</b>

\*IJI: Interspersion and juxtaposition

## 4. Discussion

I investigated the influences of landscape structure surrounding urban green areas on activity and species richness of insectivorous bats in total as well as on functional groups at fine (0.5 km radius) and broad spatial scale (1 km radius). Additionally, I compared the response of rare bat species with the response of an urban adapted bat species (*P. pipistrellus*). My results showed that different landscape composition and configuration variables, and occasionally the proximity to different landscape elements and building height variables, influenced bat activity and species richness.

### 4.1. Response of bat activity to landscape structure

Size and shape of green areas had a significantly positive influence on all measured bat activities (total, edge space aerial foragers, open space aerial foragers) at both scales of analysis. The positive relationship of bat activity with size of green areas agrees with previous findings that larger green areas offer higher prey abundance and therefore are preferred foraging habitats (Avila-Flores and Fenton 2005; Gorresen et al. 2005; Fabianek et al. 2011). The positive influence of simple shape of green areas on bat activity also accords with previous studies claiming that simple forms favored organisms because the disturbance effects of the surroundings are minimized (Forman 1995). These results indicate that large and simple shaped green areas provide more important resources (e.g. prey, roost) than the edge and surroundings of green areas.

Despite size and shape of green areas, total bat activity was influenced by both landscape composition and configuration surrounding urban green areas and this response changed with scale. At fine scale, total bat activity was favored by low proportion of industrial and high urban areas, but these variables did not affect total bat activity at broad scale. Contrary to my expectation that bat activity increases in areas with higher percentage of built-up areas, I found negative effects of industrial and high urban areas on total bat activity within the 0.5 km buffer. Although some species are known to be adapted to human-made structures (e.g. *P. kuhlii*) and choose roosting sites in buildings rather than natural sites (e.g. tree cavities), these species may also need appropriate forage areas in proximity to the roosting sites (e.g. green areas; Kubista 2009). This also agrees with the idea that although bats are adapted to urban structures as roosting sites, they could not adapt their foraging behavior to highly urbanized areas (Russo and Ancillotto 2014). Additionally, the highest total bat activity occurred in parks which are a typical green area type in urbanized

areas and provide forage grounds in proximity to buildings which could be possible roosting sites. My results agree with previous studies that highly urbanized areas reduce bat activity (e.g. Gehrt and Chelsvig 2003; Avila-Flores and Fenton 2005; Johnson et al. 2008; Fabianek et al. 2011; Jung and Kalko 2011; Hale et al. 2012). So, bats use green areas maybe because industrial and high urban areas do not offer adequate foraging grounds (Russo and Ancillotto 2014). However, I could not identify any relations to the proportion of woodland, agricultural or water bodies although these have been suggested as important foraging habitats in a previous study (Gehrt and Chelsvig 2003). This lack of influence of woods, agricultural areas and water sites might be explained by differences in recorded bat species between mine and the previous study. Most of the recorded species in my study use a broad spectrum of habitats (Dietz et al. 2014) and might be not so sensitive to certain urban green area types or water.

Additionally, high land-use diversity favored total bat activity at fine scale, whereas high IJI of land-use classes increased total bat activity at broad scale. These results agree with my hypotheses that a diverse landscape favored overall bat activity because bats use diverse forage grounds (Kunz and Fenton 2003; Dietz et al. 2007, 2014) and that a highly intermixed landscape favored bat activity due to low energy costs to reach essential resources (e.g. prey). However, the scale effects were unexpected. An explanation for the scale-dependent response of recorded bat species might be the preferred forage areas (e.g. Dietz et al. 2014). Because, the majority of recorded bat species has no problem to reach other land-use classes at short distances (e.g. Dietz et al. 2014) the spatial arrangement has no effect on the bat activity at fine scale. At broad scale, a high intermixed landscape might be an indication for the possibility to reach diverse foraging grounds with low energy costs due to short flying distances (e.g. Kubista 2009). In addition, my results agree with the expectation that bats respond to the presence of resources concentrated on fine scale relative to their high mobility (e.g. land-use diversity), as well as to resources offered at broad scale (e.g. intermixture of land-use) (e.g. Gehrt and Chelsvig 2003; Gorresen et al. 2005; Ducci et al. 2015).

Total bat activity and activity of edge space aerial foragers were positively influenced by the mean relative building heights at both scales. These positive relationships could be confounded by high amount of building-dwelling bat species in the survey (e.g. *P. pygmaeus*, *P. pipistrellus*). However, high buildings do not necessarily provide more or adequate roost sites for building-dwelling bats, but rather does the state of the buildings (e.g. cracks,

ornaments, entrance to attic; Kubista 2009). Another explanation for the increase of bat activity with increasing relative building heights is that in areas with high buildings bats might adapt their foraging and flying behavior and hunt near the ground. Thus, the batcorders could record more bats because of the adaption of flying altitude to building height in the surroundings. This might be in context to possibly lower prey availability in higher altitude and the energy cost to modify flying altitude to fly above buildings. Although the energy costs of active flight of bats in relation to flying speed or distance is well studied (e.g. Kunz and Fenton 2003; Dietz et al. 2014; Altringham 2011), the energy cost for modifying altitude during flight is uncertain and requires further study.

Contrary to my expectations, neither total bat activity nor activity of any functional group was significantly influenced by proximity to different landscape elements (i.e., green area, water and city center). The lack of influence is probably related to the measured distances and to the flying abilities of bats: On average, the distance from survey points to the next urban green areas was 71.6 m and therefore easily reachable for the majority of recorded bat species, given their home ranges (e.g. Dietz et al. 2014). Although water bodies were on average farther away from survey points (810.7 m) compared to nearest green areas, these distances probably were still accessible for highly mobile species like bats. Another explanation might be that although water sites are good forage grounds for bats, its foraging advantages (i.e. high prey availability) might be outweighed by diversity of accessible foraging grounds due to high diversity of land-use classes. So, bats might use different foraging areas and the importance of water bodies is minimized. Also, distances could be reduced because private artificial water bodies (e.g. pools) which might provide drinking possibilities and foraging grounds (Razgour et al. 2011; Russo et al. 2012) were not mapped in the Urban Atlas and the RNK 2009. So, although bats are dependent on aquatic habitats (Dietz et al. 2007; Dixon 2012) the proximity to water bodies might not be important for bat activity in urban areas because they find good forage habitats elsewhere which was also confirmed previously (Johnson et al. 2008). Distance to city centre was correlated with proportion of high urban areas thus, was another measure of the degree of urbanization and was outweighed by other variables of landscape composition and configuration (e.g. size and shape of green area).

Contrary to total bat activity, activity of edge space aerial foragers was neither significantly influenced by IJI of land-use, nor by land-use diversity. One explanation for this is that the activity of this group was mainly influenced by urban adapted species (e.g.,

*P. pipistrellus*, *H. savii*). So, this bat group is able to forage also in highly urbanized areas (e.g. around street lamps; Hüttmeir et al. 2010; Dietz et al. 2014), which might be an indication for its ecological plasticity. Therefore the diversity of land-use classes and the spatial arrangement of the land-use have no influence on the activity of edge space aerial foragers because they find appropriate foraging grounds disregarding the land-use class or the spatial arrangement of land-use classes. In addition, this group was negatively influenced by the proportion of woods and of industrial areas at fine scale. Woods might have a negative influence on this group because the vegetation is too cluttered for their echolocation and flying behavior, although edge spaces between wood and surroundings can provide adequate forage habitat (Denzinger and Schnitzler 2013). Contrary to total bat activity, the proportion of high-urban areas had no influence on the activity of edge space aerial foragers. This is not surprising, because this group mainly consist of urban adapted species.

Activity of open space aerial foragers was not influenced by land-use diversity at fine scale. This agrees with findings that open space aerial foragers exploit large habitats due to their echolocation and flying abilities (i.e., fast flight, low frequency; Denzinger and Schnitzler 2013; Ducci et al. 2015). So, land-use diversity at fine scale is not important for this bat group. However, the IJI of land-use classes had a significantly positive influence on the activity of open space aerial foragers similar to the total bat activity. This indicates that open space aerial foragers are also favored by a highly intermixed landscape at broad scale. Contrary to the other bat activities, only the proportion of woods had a significant negative influence on activity of open space aerial forager at both scales. This agrees with previous studies that this bat group cannot adapt its echolocation and flying abilities to cluttered vegetation, consequently, woodlands are inappropriate foraging habitats for this bat group (Denzinger and Schnitzler 2013; Dietz et al. 2014). However, I could only detect a tendency that high amount of pastures affected activity of open space aerial foragers. This disagrees with my hypothesis, because based on the ecology of open space aerial foragers, I expected pastures to have a positive influence on this bat group. Additionally, I found no influence of buildings on the activity of open space aerial foragers. Open space aerial foragers fly in high altitude with low energy costs due to their wing morphology (e.g. Altringham 2011). So, mean relative building height of 7.7 m might be below the normal flying altitude for open space aerial foragers when exploiting an urban landscape.

#### 4.2. Response of species richness to landscape structure

Different patterns for total species richness than for activity were seen regarding the importance of landscape composition and configuration. Total species richness was influenced by shape of green area, but no effect of size of green areas could be found. Similarly to total bat activity, species richness increased with increasing shape simplicity of green area at both scales which agrees with the idea that simple patch shape decreases the influence of disturbances (Forman 1995). Interestingly, size of green areas did not influence species richness as found previously (Avila-Flores and Fenton 2005). The size seems to influence the foraging behavior as indicated by total bat activity but not by the number of species. I assume that for the verified number of species, not the size of green areas (20.1 ha) but their shape was a critical factor. So, the disturbance of green area affected total species richness more than their size, although larger green areas are better foraging grounds. It is noticeable, that species richness was mainly influenced by common urban adapted species and only five species were found on average.

Furthermore, total species richness was negatively influenced by proportion of industrial and of high urban areas, but at both scales contrary to total bat activity. This result confirms my hypothesis that species richness decreases with increasing proportion of built-up areas because the majority of species favors vegetated areas and is not well adapted to human-made areas with high amount of sealed land (e.g. Dietz et al. 2014; Russo and Ancillotto 2014). However, none of the green areas types (e.g. woodlots, cemeteries) had an influence on total species richness. Perhaps the negative impacts of highly urbanized areas (high urban, industrial areas) outweigh the possible positive effects of vegetated areas on total species richness. Nonetheless, green area types differed in total species richness. Green areas which were situated in less urbanized districts of Vienna like vineyards had the highest species richness.

Total species richness was also positively influenced by the IJI of the relative building heights in contrast to total bat activity. With increasing intermixture of different building heights within the 1 km scale, total species richness increases. High intermixture of building heights might facilitate the exploitation of the urban landscape by bats because also small bat species (e.g., *P. pygmaeus*) may pass between tall buildings when they are intermixed with smaller ones which could fly over without high energy cost by modulating altitude or by taken longer routes around the buildings (e.g. Altringham 2011). Thus, intermixed building heights might not be problematic for most bats in exploiting the urban landscape.

Since energy cost of flying altitude adaptation in migrating birds indicates that changes in flying altitude (e.g. due to wind turbulences) cause higher energy cost than flying at a same altitude (e.g. Bowlin et al. 2015) more research on bats is needed to understand possible energy costs associated with exploiting and navigating an urban landscape in context with overcoming possible barriers like high buildings.

The number of edge space aerial foragers was influenced by both size and shape of green areas at fine scale, whereas for the number of open space aerial foragers none of these variables showed any effect. The majority of edge space aerial foragers uses smaller habitats than the open space aerial foragers (e.g. Dietz et al. 2014). Therefore, larger prey abundance within larger green areas (e.g. Avila-Flores and Fenton 2005) and decrease of disturbances due to more simple shaped green areas (Forman 1995) have higher influence on the number of edge space aerial foragers. Contrary, open space aerial foragers exploit large areas due to their echolocation, flying, and foraging behavior (e.g. Denzinger and Schnitzler 2013; Dietz et al. 2014). Thus, size and shape of green areas have no influence on the species richness of this group.

Additionally, number of edge space aerial foragers was positively influenced by the proportion of mid-low urban areas at fine scale. This is reasonable because bats of this group are reported to use human-made structure for roosting (Hüttmeir et al. 2010; Dietz et al. 2014) but also need green areas in the proximity to roosting sites (Kubista 2009; Stürzenbaum 2011). At broad scale, the only variable with influence on the number of edge space aerial foragers was the proportion of high urban areas. This indicates that the negative influence of high urban areas outweigh the other effects of landscape structure at broad scale. Even though this group consists mainly of urban adapted bat species, the negative influence of highly urbanized areas may suggest that although this bat group is adapted to urban structures, a threshold may exist for the acceptable maximum proportion of sealed land.

Contrary, the number of open space aerial foragers was positively influenced by proportion of agricultural and of mid-low urban areas at fine scale which corresponds to the ecology of this group. Both land-use classes provide adequate foraging and roosting habitat for this group. Open space aerial foragers hunt in open agricultural areas or pastures and avoid cluttered vegetation (Denzinger and Schnitzler 2013; Dietz et al. 2014). Considering the roosting preferences, mid-low urban areas provide adequate roosting sites in proximity to foraging areas. The three most common species within the open space aerial foragers (*N.s*

*noctula*, *E. nilsonii* and *H. savii*; all recorded at > 30 % of the survey points) are reported to roost in buildings as well as in single trees with appropriate cavities (Kubista 2009; Hüttmeir et al. 2010; Dietz et al. 2014). At broad scale, the number of open space aerial foragers was negatively influenced by the proportion of woods and parks. This was expected because open space aerial foragers prefer open areas for hunting and fly quickly through the landscape (Denzinger and Schnitzler 2013; Dietz et al. 2014). So, the higher the amount of areas with cluttered vegetation within their forage area, the fewer species of this group occur. Also, the positive influence of highly intermixed landscapes (IJI of land-use classes) is reasonable for this group. Therefore, open space aerial foragers could find more appropriate foraging habitats in a highly diverse (1 km buffer) landscape due to their foraging and flying behavior (Denzinger and Schnitzler 2013; Dietz et al. 2014) than in less diverse landscapes.

Interestingly, neither the number of edge space aerial foragers nor the number of open space aerial foragers were influenced by any of the building height variables. So, both functional groups showed no influence which indicate either no problem to fly over buildings or no need to do this because these bats fly along linear edge structures (edge space aerial foragers) or in higher altitude than the building heights (open space aerial foragers). Thus, the building heights seem to have no barrier effect for edge space and open space aerial foragers and both groups have no problems with different building heights and the spatial arrangement of buildings due to their flying and echolocation abilities.

Regarding the comparison between the occurrence of *P. pipistrellus* and rare species richness, my results agree with previous studies that *P. pipistrellus* is an urban adapted species which uses the urban landscape frequently (e.g. Fabianek et al. 2011; Dietz et al. 2014; Ducci et al. 2015), whereas rare species are influenced by landscape structures which are frequently unavailable in urban areas. These differences are crucial when conserving urban adapted and rare species in urban areas.

Size and shape of the green areas showed no effect on the occurrence of *P. pipistrellus* which indicates that this bat species uses the urban landscape disregarding the size and shape of the green areas where it was recorded. Thus, the influence of urban landscape and disturbances based on shape of green area is irrelevant for *P. pipistrellus*, similar to number of open space aerial foragers. This was expected because *P. pipistrellus* has broad ecological plasticity and explores typical urban structure frequently (e.g. Dietz et al. 2014). *P. pipistrellus* is reported to forage also in man-made structures (e.g. around street lamps; Dietz et al. 2007) and is not dependent on prey availability in green areas. So, the size

of green areas had no influence on *P. pipistrellus*. Additionally, *P. pipistrellus* was one of the most recorded species per survey point in this study which agrees with expectation and previous studies (e.g. Hüttmeir et al. 2010) that this species occurred evenly throughout Vienna. Interestingly, also the urban adapted species *P. pipistrellus* was influenced by the IJI of land-use classes and a highly intermixed landscape at fine scales. Although *P. pipistrellus* is reported to be an opportunistic forager, a highly intermixed landscape might facilitate foraging because of diverse prey availability in diverse land-uses (e.g. Dietz et al. 2014).

Focusing on the proportion of land-use classes, I detected negative influences of proportion of agricultural areas, vineyards, woods and industrial areas at fine scales. So, *P. pipistrellus* dislike the high proportion of agricultural areas, which agrees with the ecology of this species because it prefers hunting in edge spaces and linear structures to hunting in open areas (Denzinger and Schnitzler 2013; Dietz et al. 2014). Although cultivated vine in vineyards and edges of wood provide such linear structures, I detected a negative influence of these land-use classes on the occurrence of *P. pipistrellus* at fine scale. All these land-use classes are mainly located in the outer districts of Vienna and showed higher total species richness. So, woods and vineyards are important for many bats and the concurrence between bat species within these areas might be higher than in highly urbanized areas of Vienna. Also the proportion of industrial areas negative influenced *P. pipistrellus* which indicates that even for an urban adapted bat species industrial areas are no appropriate habitat.

Although the species richness of none of the functional groups showed any influence of distances (green areas, water, city centre), I found for the first time significant influence of the distance to water bodies regarding the occurrence of *P. pipistrellus*. With higher distance to water sites, the occurrence of *P. pipistrellus* decreased. In a previous study, this relationship occurred in context to maternity roosts of *P. kuhlii* (Ancillotto et al. 2015) and was suggested to influence bats of warmer climates because of the danger of dehydration (Russo and Ancillotto 2014). So, for a small bat species which is well adapted to urban areas the hypothesized influence of the availability of water bodies becomes obvious. Additionally, the lack of influence of the distance to city centre and to nearest green areas agrees also with the good adaptation of this bat to urban structure. *P. pipistrellus* occurred also in low distance to the city centre because of its opportunistic use of foraging grounds (e.g. Dietz et al. 2014), making it more independent of green areas than other species.

Notable, *P. pipistrellus* was negatively affected by the mean relative building heights at fine scale, and positively affected by the IJI of relative building heights at broad scale. It is reasonable that a small bat species like *P. pipistrellus* is favored by highly intermixed building heights because it facilitates the exploitation of the landscape and minimizes barrier-effects as described for the richness of edge space aerial foragers. Although *P. pipistrellus* is reported to roost in buildings (e.g. Dietz et al. 2014), the mean building height negatively influenced this species.

Contrary to *P. pipistrellus*, the number of rare species was influenced by the size and shape of green areas. The number of rare species increased with increasing shape simplicity of green areas at both scales. Thus, the shape of the green area has crucial influence on the number of rare species similar to total species richness. The number of rare species was also favored by large green areas. The effects of simple and large green areas indicate that more rare species occur in large green areas with low disturbing influence of the surrounding urban landscape. Interestingly, not the land-use diversity but the IJI of land-use classes positively influenced rare species richness at broad scale. The number of rare species increased with increasing IJI of land-uses which indicates that rare species need evenly intermixed landscape at broad scale. The number of rare species declined with increasing proportion of parks within the 1 km buffer. This could also be influenced by the degree of urbanization because more parks are present in high urban areas than in the outer districts. This was paralleled by the differences between green area types, where the highest rare species richness was recorded in vineyards contrary to total species richness. The higher number of rare species in vineyards, pastures and woods was an indication that rare species favor green areas in lower urbanized areas because these green area types occur more often in the outer districts of Vienna. This agrees with previous studies demonstrating that rare species are less adapted to urbanized landscapes (e.g. Luck et al. 2013), a fact that was also confirmed by the negative influence of proportion of industrial and high urban areas in this study. But these land-use classes also negatively influenced species richness of other bat groups (e.g. total, edge space, *P. pipistrellus*).

Contrary to previous studies (Gehrt and Chelshvig 2003; Avila-Flores and Fenton 2005; Johnson et al. 2008; Razgour et al. 2011; Ducci et al. 2015) no dependency of rare species on the proportion of woods could be detected at any scale. Also, proportion of vineyards had no influence on the number of rare species although I detected most rare species in this green area type. Perhaps the negative influence of highly urbanized areas outweighs the

importance of woods and vineyards. This assertion was confirmed by the increase of rare species in higher distance to city center at fine scale which agrees with previous studies claiming that specialized species are not able to adapt to highly urbanized areas because of their low ecological plasticity (Kurta and Teramino 1992; Gaisler et al. 1998; Jung and Kalko 2011; Luck et al. 2013). Contrary to my expectation, there was no influence of building heights on rare species richness. This lack of influence might be confounded by recording the rare species in places where buildings mainly have lower heights (6 m) and are evenly intermixed at fine scale.

My study contributed to the understanding of the impacts of urbanization on insectivorous bats by providing first indications of the influence of landscape structure surrounding urban green areas on bats in a European city. My study clearly showed the benefits of analyzing landscape effects not only for the whole bat assemblage but also for functional groups to identify the effects of urbanization on bats because the bat fauna is diverse and the species' ecological requirements differ widely. The results clearly demonstrate scale-dependent differences in the response of bats to landscape structure, so including multiple scales (e.g. Gehrt and Chelvig 2003; Gorresen et al. 2005; Fabianek et al. 2011; Luck et al. 2013; Ducci et al. 2015) further improve the knowledge of the response of bats to urban landscape. Also, the study provides first indications about the influence of building heights and their spatial arrangement on bat activity and species richness which should not be neglected in further studies on the assessment of urbanization on bats.

## 5. Conclusion

A major conclusion of this study is that management recommendations for the conservation and protection of bats in urban areas hard to give, because bat groups (total, edge space and open space aerial foragers, *P. pipistrellus*, rare species) differed in their response to landscape structure surrounding urban green areas. Nevertheless, certain landscape characteristics seem to be important for most groups and management efforts need to take these findings into consideration. Bat activity was promoted by size and shape of green areas, the latter also influenced species richness of most functional groups. As well, highly intermixed land-use classes are important for the species richness and bat activity of the many analyzed bat groups. And industrial areas were demonstrated to have negative effects on most bat groups and even on the occurrence of the urban adapted *P. pipistrellus*. The assessment of the influence of building heights on the bat assemblage gave first indications that building heights affected bat activity and species richness.

An important message of these results for urban planners is that large and simple shaped green areas are vital to mitigate the impact of urbanization on bats. Also, landscape management should focus on preserving and maintaining a diverse and intermixed land-use within urban areas which might be crucial for bat species to find essential resources. Focusing on the negative impacts of industrial areas on most bat groups, urban planners need to consider these effects especially when authorizing new industrial areas in the outer districts of Vienna. In respect to the conservation of rare species, landscape managements should maintain large, simple shaped green areas in the outer city districts and especially minimize development of industrial areas in these areas. Regarding the influence of building height on species richness, it is important for bats to maintain intermixed building heights in highly urbanized areas to be able to travel the urban landscape with low energy cost.

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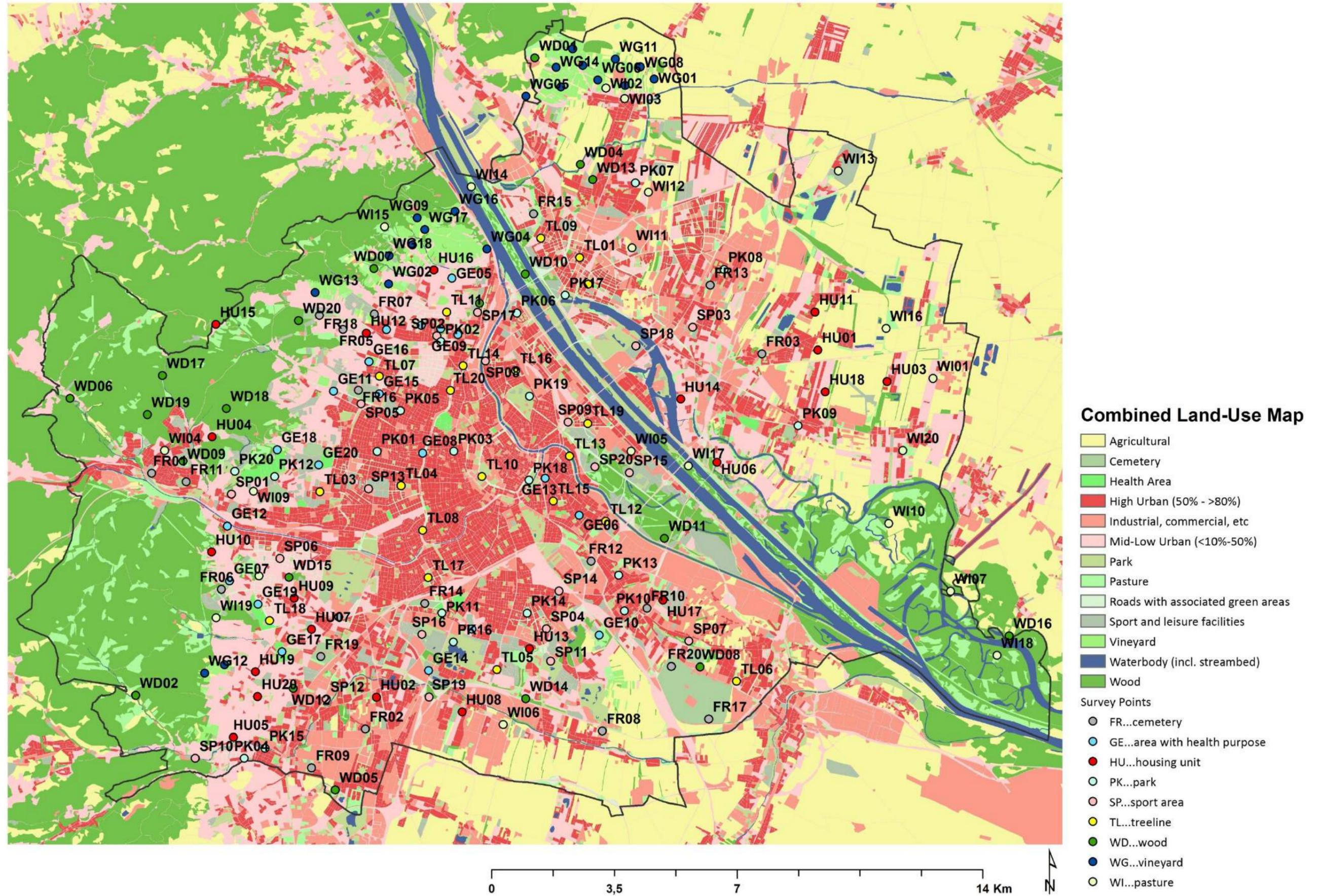
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## Appendices

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Appendix 1: Combined land-use map of Urban Atlas and RNK 2009 based on classification scheme (Figure 6) including survey points.



**Appendix 2: Overview of the overlap between the land-use classes of the Urban Atlas and the RNK2009. The critical value for the integration of the green area types of the RNK2009 is >3% overlap.**

		Urban Atlas																			
		20000	13300	11100	11210	11230	11220	11240	12210	30000	14100	12100	11300	13400	13100	12220	12300	12230	14200	50000	
		Agricultural + Semi-natural areas + Wetlands	Construct ion sites	Continuous Urban Fabric (S.L. > 80%)	Discontinuous Dense Urban Fabric (S.L. : 50% - 80%)	Discontinuous Low Density Urban Fabric (S.L. : 10% - 30%)	Discontinuous Medium Density Urban Fabric (S.L. : 30% - 50%)	Discontinuous Very Low Density Urban Fabric (S.L. < 10%)	Fast transit roads and associated land	Forests	Green urban areas	Industrial, commercial, public, military and private units	Isolated Structure	Land without current use	Mineral extraction and dump sites	Other roads and associated land	Port areas	Railways and associated land	Sports and leisure facilities	Water bodies	
Total Area Urban Atlas [ha]		6946,82	221,59	2793,76	3735,19	1026,45	3467,55	40,97	213,19	7579,29	3185,95	4757,43	40,47	187,07	36,70	2564,87	228,22	668,65	1522,93	1472,34	
RNK 2009	27	Acker	60,98%	1,28%	0,07%	0,34%	0,24%	0,37%	0,01%	0,87%	0,29%	0,33%	0,73%	6,15%	6,98%	3,49%	1,09%	0,00%	0,66%	0,49%	0,02%
	22	Bahnhöfe und Bahnanlagen	0,60%	6,85%	0,30%	0,39%	0,11%	0,29%	0,00%	1,73%	0,05%	1,41%	3,94%	0,52%	2,96%	0,00%	2,00%	7,87%	78,62%	0,75%	0,06%
	12	Bildung	0,03%	2,03%	1,09%	0,99%	0,33%	0,42%	0,02%	0,00%	0,01%	0,56%	5,94%	0,00%	0,42%	0,00%	0,10%	0,00%	0,00%	0,94%	0,00%
	5	Büro- und Verwaltungsviertel	0,01%	1,31%	1,70%	0,21%	0,00%	0,06%	0,00%	0,08%	0,00%	0,15%	3,34%	0,00%	0,20%	0,00%	0,09%	0,00%	0,13%	0,01%	0,00%
	3	dichtes Wohn(misch)gebiet	0,03%	6,99%	66,28%	25,66%	1,89%	5,61%	0,24%	0,01%	0,02%	1,06%	3,12%	0,00%	0,44%	0,00%	0,71%	0,00%	0,11%	0,40%	0,00%
	16	Energieversorgung u. Rundfunkanlagen	0,06%	0,15%	0,13%	0,02%	0,01%	0,05%	0,00%	0,09%	0,01%	0,11%	3,18%	0,48%	0,00%	0,00%	0,02%	0,00%	0,06%	0,10%	0,07%
	26	Friedhof	0,05%	0,01%	0,02%	0,03%	0,03%	0,02%	0,00%	0,00%	0,04%	0,71%	10,45%	0,97%	0,57%	0,00%	0,04%	0,00%	0,01%	0,07%	0,00%
	2	Gartenstadt	0,10%	5,98%	3,23%	24,23%	28,07%	26,58%	0,50%	0,00%	0,24%	1,39%	1,30%	2,02%	1,81%	0,00%	0,91%	0,00%	0,04%	0,75%	0,00%
	29	Gärtnerei, Obstplantagen	2,69%	0,69%	0,04%	0,58%	0,43%	0,56%	0,00%	0,01%	0,22%	0,58%	3,21%	8,04%	5,32%	7,00%	0,14%	0,00%	0,02%	0,34%	0,00%
	7	Geschäfts-, Kern- u. Mischgebiete	0,00%	0,38%	1,81%	0,00%	0,00%	0,00%	0,00%	0,00%	0,00%	0,00%	0,12%	0,00%	0,00%	0,00%	0,02%	0,00%	0,00%	0,00%	0,00%
	11	Gesundheit und Einsatzorg.	0,00%	0,00%	0,13%	0,10%	0,26%	0,15%	0,00%	0,02%	0,02%	0,69%	2,88%	0,00%	0,00%	0,00%	0,06%	0,00%	0,00%	0,07%	0,00%
	32	Gewässer inkl. Bachbett	1,21%	0,06%	0,01%	0,15%	0,45%	0,18%	2,56%	0,32%	2,82%	4,28%	0,22%	0,53%	2,60%	5,79%	1,09%	2,04%	0,43%	1,04%	95,52%
	4	großvolumiger, solitärer Wohn(misch)bau	0,00%	7,49%	1,86%	7,04%	0,10%	1,43%	0,00%	0,00%	0,00%	0,46%	1,01%	0,00%	1,20%	0,00%	0,19%	0,00%	0,00%	0,15%	0,00%
	9	Industrie, prod. Gewerbe, Großhandel inkl. Lager	0,20%	2,11%	1,73%	0,54%	0,05%	0,13%	0,00%	0,26%	0,04%	0,57%	26,47%	2,43%	2,51%	6,40%	0,41%	57,65 %	1,55%	0,32%	0,00%
	15	Kläranlage, Deponie	0,01%	0,00%	0,01%	0,00%	0,00%	0,00%	0,00%	0,00%	0,00%	0,00%	0,05%	0,00%	0,08%	1,32%	0,00%	0,00%	0,05%	0,00%	0,00%
	10	Kultur, Freizeit, Messe	0,07%	0,14%	0,40%	0,17%	0,21%	0,32%	0,00%	0,03%	0,06%	0,81%	3,19%	1,16%	0,07%	0,00%	0,12%	0,48%	0,05%	2,22%	0,23%
	1	locker bebautes Wohn(misch)gebiet	0,88%	5,63%	0,92%	20,01%	52,77%	51,51%	85,04%	0,06%	1,02%	2,57%	1,26%	40,00%	3,45%	0,00%	3,51%	0,00%	0,73%	42,99%	0,13%
	14	Militärische Anlagen	0,06%	0,00%	0,33%	0,03%	0,00%	0,03%	0,00%	0,00%	0,00%	0,25%	1,30%	0,00%	2,64%	0,00%	0,01%	0,00%	0,00%	0,25%	0,00%
	8	Mischnutzung wenig dicht	0,14%	0,53%	0,53%	5,15%	2,50%	2,12%	0,00%	0,00%	0,00%	0,23%	0,64%	0,76%	0,91%	0,00%	0,15%	0,00%	0,00%	0,06%	0,00%
	24	Park, Grünanlage	0,02%	1,69%	0,33%	1,52%	0,76%	0,38%	0,00%	0,80%	0,08%	29,67%	1,21%	1,49%	1,91%	0,00%	0,77%	0,02%	1,12%	1,56%	0,77%
	21	Parkplätze u. Parkhäuser	0,04%	0,75%	0,14%	0,43%	0,04%	0,16%	0,00%	0,18%	0,03%	0,45%	3,14%	0,00%	1,11%	0,00%	1,20%	3,39%	0,98%	1,17%	0,00%
	6	solitäre Handelsstrukturen	0,04%	1,23%	0,63%	0,35%	0,01%	0,09%	0,00%	0,01%	0,00%	0,04%	5,31%	0,00%	0,60%	0,00%	0,24%	0,00%	0,22%	0,23%	0,00%
	13	Sport und Bad (Indoor)	0,00%	0,01%	0,03%	0,02%	0,00%	0,00%	0,00%	0,00%	0,00%	0,05%	0,22%	0,00%	0,00%	0,00%	0,01%	0,00%	0,03%	0,93%	0,00%
	25	Sport und Bad (Outdoor), Camping	0,13%	1,69%	0,07%	0,29%	0,71%	0,25%	0,00%	0,09%	0,07%	2,81%	1,10%	0,00%	0,06%	0,00%	0,16%	0,00%	0,22%	37,06%	0,04%
	19	Straßenraum begrünt	0,19%	1,23%	2,28%	2,59%	1,41%	1,76%	0,27%	27,26%	0,02%	2,36%	1,44%	0,00%	3,56%	0,44%	13,35%	0,00%	0,36%	0,94%	0,02%
	20	Straßenraum unbegrünt	1,14%	7,52%	15,53%	8,20%	4,27%	5,96%	4,53%	63,59%	0,48%	4,09%	6,35%	2,68%	4,87%	1,30%	70,82%	4,75%	3,31%	3,84%	0,45%
18	Transformationsfläche, Baustelle, Materialgew.	1,22%	39,81%	0,19%	0,13%	0,01%	0,07%	0,00%	0,31%	0,03%	0,71%	2,25%	2,59%	9,82%	62,18%	0,24%	0,13%	3,10%	0,16%	0,09%	
23	Transport und Logistik inkl. Lager	0,15%	0,94%	0,11%	0,09%	0,00%	0,06%	0,00%	1,96%	0,01%	0,30%	3,92%	1,10%	1,58%	0,26%	0,17%	21,08 %	5,39%	0,18%	0,01%	
30	Wald	3,82%	0,23%	0,01%	0,24%	2,44%	0,45%	2,81%	1,12%	89,57%	26,44%	0,61%	10,48%	1,69%	4,91%	1,09%	1,55%	1,65%	1,04%	1,38%	
17	Wasserversorgung	0,22%	0,00%	0,00%	0,01%	0,06%	0,04%	0,00%	0,00%	0,04%	0,22%	0,24%	0,56%	0,00%	0,00%	0,01%	0,00%	0,00%	0,10%	0,00%	
28	Weingarten	9,71%	0,23%	0,00%	0,01%	0,53%	0,17%	0,21%	0,00%	0,10%	0,07%	0,04%	8,16%	0,00%	0,00%	0,17%	0,00%	0,00%	0,05%	0,00%	
31	Wiese	16,21%	3,04%	0,08%	0,48%	2,34%	0,78%	3,83%	1,20%	4,74%	16,61%	1,81%	9,89%	42,64%	6,91%	1,13%	1,04%	1,16%	1,81%	1,19%	