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STRUCTURAL COMPLEXITY AS A PREDICTOR OF BAT ACTIVITY AND SPECIES RICHNESS IN AN URBAN AREA: A COMPARISON OF DIGITAL IMAGES AND A FIELD METHOD

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ABSTRACT

In the face of rapidly expanding urbanization, time- and cost-effective tools for assessment of wildlife habitat quality are needed in urban areas. Structural complexity is known to affect habitat quality for bats, an ecologically important group of vertebrates, but information about their response to habitat complexity in urban environments is scarce. This master thesis investigates the ability of structural complexity derived from digital images at the microhabitat scale to predict bat activity and species richness, functional groups and representative species. The mean information gain (MIG) was calculated from the images and included as a proxy for habitat heterogeneity, for the first time in an urban environment. Moreover, this method was compared to a standard field method for recording vegetation structure. Sampling effort included 180 locations within green areas distributed over Vienna. Bat activity and species richness were assessed with ultrasonic monitoring during spring and summer 2014 using Batcorders. Results suggest MIG is a useful, time- and cost-effective tool to measure habitat complexity and also partly replaced field data. Contrary to my expectations, total bat activity and species richness were negatively correlated with structural complexity measured by MIG of the top view. This outcome suggests that canopy cover, which is represented by MIG top view, may hinder maneuverability and echolocation for bat species using canopy height for flight and foraging. Consistent with previous findings, responses to structural complexity were group- and species-specific. The negative response of functional groups to increased complexity was strongest for the open space foragers and weaker for the edge space foragers, while the Myotis group exhibited a positive response to structural complexity. Myotis was the only group showing a significant positive influence of MIG, indicating the relevance of structure-rich habitats like woodlands on species of this genus. As Myotis species were clearly underrepresented, probably due to scarce complexity of green areas, conservation and restoration of structurally complex areas with forest cover in urban environments may be crucial for this group. *Nyctalus noctula*, a species foraging in open space, showed a negative response to MIG, whereas *Pipistrellus pygmaeus*, an edge space forager, was positively influenced by MIG. The group- and species-specific response to structural complexity points at the importance of maintaining habitat heterogeneity within the urban matrix to fulfill their differing requirements.

ZUSAMMENFASSUNG

Im Angesicht rapide zunehmender Urbanisierung sind zeit- und kosteneffiziente Werkzeuge zur Qualitätsbewertung von Wildtierhabitaten in urbanen Räumen notwendig. Es ist bekannt, dass strukturelle Komplexität die Qualität von Fledermaushabitaten beeinflusst, einer ökologisch wichtigen Gruppe von Vertebraten, jedoch existiert wenig Information hierzu für urbane Gebiete. Diese Masterarbeit untersucht die Strukturkomplexität digitaler Fotografien als Prädiktor von Fledermausaktivität und -artenreichtum, funktionellen Gruppen sowie repräsentativen Arten. Hierfür wurde der sogenannte Mean information gain (MIG) von den Fotos berechnet und als Lokalparameter und Schätzer für Habitatkomplexität zum ersten Mal in einem urbanen Raum eingesetzt. Des Weiteren wurde diese Methode mit einer Standard-Feldmethode zur Aufnahme der lokalen Vegetation verglichen. Es wurden 180 Grünräume in Wien während der Frühjahrs- und Sommermonate 2014 aufgenommen. Fledermausaktivität und Artenreichtum wurden mit Hilfe von Ultraschallgeräten (Batcorder) aufgezeichnet. Die Ergebnisse legen nahe, dass MIG ein nützliches, zeiteffizientes und kostengünstiges Werkzeug zur Messung von Habitatkomplexität darstellt, welches zum Teil Felddaten ersetzen konnte. Gesamtaktivität und Artenreichtum der Fledermäuse nahmen, entgegen meiner Erwartung, mit steigender Strukturkomplexität der Baumkronen-Perspektive (MIG top) ab. Diese Ergebnisse deuten auf durch Baumkronen bedingte Flug- und Echolokationsnachteile für Arten hin, deren Flughöhe sich mit dem Kronendach von Bäumen überschneidet. Der Einfluss der Strukturkomplexität war gruppen- und artspezifisch, in Übereinstimmung mit früheren Untersuchungen. Der höchste negative Einfluss wurde bei der Gruppe der Offenlandarten festgestellt, gefolgt von jener der Grenzlandarten, welche schwächer negativ beeinflusst wurden, während die Myotisgruppe eine positive Korrelation zu MIG zeigte. Der positive Einfluss von Habitatkomplexität auf Myotisarten weist auf die Relevanz von strukturreichem Waldcharakter für diese Gruppe hin. Da Myotisarten in meinen Aufnahmen deutlich unterrepräsentiert waren, potentiell eine Folge unzureichender Strukturkomplexität von Grünräumen, könnte die Erhaltung und Wiederherstellung strukturreicher Waldflächen in urbanen Räumen entscheidend für diese Artengruppe sein. *Nyctalus noctula,* eine Offenlandart, zeigte eine negative Korrelation zu MIG, während *Pipistrellus pygmaeus,* eine Grenzlandart, positiv davon beeinflusst wurde. Der gruppen- und artenspezifische Einfluss der Strukturkomplexität zeigt indes auf, dass die Erhaltung von Habitatheterogenität innerhalb der urbanen Matrix nötig ist um den unterschiedlichen Habitatansprüchen gerecht zu werden.

1. INTRODUCTION

Natural ecosystems throughout the world are subject to an increasing pressure by human-generated impacts. Habitat loss or degradation due to anthropogenic activities represent critical threats to biodiversity (Jones et al., 2009; Pimm et al., 1995), potentially resulting in a loss of ecosystem functions and services (Boyles et al., 2011; Maas et al., 2013). One group that provides essential ecosystem services, which are considered of economic value, like pollination, seed dispersal and the top-down control of insects are bats, the second largest mammalian order of our planet (Dietz et al., 2007; Kunz et al., 2011). Hence, conservation and management of bats is of growing importance, not only because of their contribution to global biodiversity and ecosystem functioning, but also due to their role as bio-indicators and their vulnerability to declines (Jones et al., 2009; O'Shea et al., 2003).

Bat population declines have been ascribed to human-induced land use changes such as reduction, fragmentation and transformation of natural habitats (Fenton, 1997; Guest et al., 2002; Lane et al., 2006). It has been demonstrated that urbanization, as an extreme example of habitat modification, has negative impacts on insectivorous bat populations, by for example reducing species richness, altering species composition and habitat use, and reducing reproductive success (Avila-Flores and Fenton, 2005; Kurta and Teramino, 1992). Nevertheless, urban environments are recurrently shown to be frequented by flying and foraging bats, by potentially providing essential habitat requirements for bats such as roosting and hunting sites (Bartonicka and Zukal, 2003; Dietz et al., 2007; Gaisler et al., 1998). In fact, bats may be among the most abundant wild mammals in urban areas around the world (Avila-Flores and Fenton, 2005). Therefore, particular species are able to take advantage of human-modified landscapes by using roosting sites in houses (Gaisler et al., 1998; Bihari, 2004) or by exploiting insects around street lights for example (Jung and Kalko, 2010), whereas others cannot (Jung and Kalko, 2011).

It has been shown that habitat quality for bats is related to habitat heterogeneity, whose description is particularly dependent on variation of structural parameters at the microhabitat level (McElhinny et al. 2005). Rising habitat complexity has resulted in increased species richness (Milne et al., 2006; Sánchez-Cordero, 2008) and higher activity levels (Jung et al., 2012). Bat activity has been demonstrated to be significantly higher around structural elements than in open areas (Frey-Ehrenbold et al., 2013), while a loss of structural elements in a habitat had negative impacts on activity (Boughey et al., 2011). Thus, structurally poor habitats seem to be less attractive for the majority of foraging bats (e.g. Walsh and Harris, 1996; Lesiński et al., 2000).

Heterogeneous habitats showing higher structural complexity provide more niches and resource accessibility through enlarged microhabitat segregation (MacArthur et al., 1966; MacArthur and MacArthur, 1961; Tews et al., 2004; Wilson, 2002). In this way, vegetation structural complexity increases insect prey diversity and abundance (Grüebler et al., 2008; Jung et al., 2012; Ober and Hayes, 2008), provides roosts as well as protection against wind and shelter from predation for bats (Verboom and Spoelstra, 1999). However, some bat species have been shown to avoid habitats with dense vegetation when foraging presumably for easing navigation (Brigham et al., 1997; Loeb and O'Keefe, 2006). Differential use of habitat types related to structural complexity has been linked to the maneuverability and the echolocation characteristics of species, dividing the bat assemblage into different functional groups with diverging habitat requirements (Aldridge and Rautenbach, 1987; Crome and Richards, 1988; Frey-Ehrenbold et al., 2013).

Bats are still representing earnestly understudied vertebrates and although urbanization likely represents a serious compromise to many of them (Hale et al., 2012; Luck et al., 2013), studies that attempt to characterize their response to vegetation structural attributes in urban areas are rare (Bader et al., 2015; Coleman and Barclay, 2012). Knowledge on specific habitat requirements and diversity patterns of bats in cities is required to identify areas of high conservation priority, propose adequate conservation strategies and to forecast local extinction risks (Threlfall et al., 2012). Although there are some investigations recording vegetation complexity at fine scales and their influence on bats, they were mainly based on field data including often varying parameters, hampering comparison of studies among each other.

Measuring structural complexity from digital images has been recently developed for assessing site heterogeneity (Proulx and Parrott, 2008, 2009). The mean information gain (MIG) is used to describe image heterogeneity which represents a reasonable estimate of habitat complexity in natural scenes (Proulx and Parrott, 2008) as it contains spatial and structural information about the represented objects (St-Louis et al., 2006). Therefore, if image-derived spatial heterogeneity reflects complexity of habitats, greater species richness and presumably also higher activity levels would be expected for bats in areas of greater image heterogeneity. Image complexity has already been linked to biodiversity patterns for vascular plants in temperate forests (Proulx and Parrott, 2008) and savannahs (Oldeland et al. 2010), fishes in coral reefs (Mellin et al., 2012) and birds in semiarid landscapes (St-Louis et al., 2006; Bellis et al., 2008). However, it is uncertain whether this method will be useful to assess habitat complexity in urban environments. In the face of rapidly expanding urbanization worldwide (e.g. Baker and Harris, 2007; Seto et al., 2011), time- and cost-effective indicators for biodiversity and its drivers are needed in these areas. Habitat complexity is known to enhance biodiversity (e.g. Huston, 1979), whereby complexity assessment based on digital images is a simple, rapid, cost-effective and objective method working at any spatial scale (Mellin et al., 2012). Hence, it represents a promising tool for complementing existing methods which is easy to standardize.

The aim of this study was to analyze the ability of MIG measured from digital images to predict bat activity and species richness and compare it to the predictability of parameters recorded using a field method at the microhabitat scale. To my knowledge, there exists no similar study measuring structural complexity from digital images in the context of bat habitat associations in urban environments. The comparison of this method to a standard field method is also a novel contribution. The following hypotheses were tested: (1) Bat activity and species richness rise with increasing structural complexity of sites, represented by increasing MIG. Sites of greater vegetation complexity support greater insect productivity, wherefore bats would prefer structurally complex areas as foraging sites (Kalcounis and Brigham, 1995). Structural complexity as proxy of habitat diversity provides more niches and thus higher variety of species than a structurally poor habitat (Tews et al., 2004). (2) Functional groups (i.e. edge space aerial foragers, open space aerial foragers, Myotis species) and representative species (i.e. *Pipistrellus pygmaeus, Nyctalus noctula*) differ in their response to structural complexity (MIG). Bat functional groups have been found to show diverging tolerances to structural clutter due to different morphological constraints (Crome and Richards, 1988; Denzinger and Schnitzler, 2013). Therefore, species foraging at edges or inside vegetation (edge space aerial foragers, Myotis species) are expected to show a positive response to structural complexity, while species hunting in open space should be negatively influenced by increasing MIG. (3) Measuring structural complexity from digital images and the standard field method provide complementary information. I assume that variables of both methods have effects on bat activity and species richness as MIG calculated from images reflects vegetation parameters recorded in the field. MIG therefore is presumably best used as complementary predictor to the parameters recorded using the field method, improving the models for bat activity and species richness.

2. MATERIALS AND METHODS

2.1 Study organisms

Approximately 70 % of recent bat species are insectivorous, including all European species. Insects, with their tremendous diversity and abundance as well as their high nutrition value, represent an attracting energy reservoir. The great availability of nocturnal insects is viewed as an initiator for development of the hunting type "bat" and the driver for the evolution of the suborder microbats (Microchiroptera) with its high species richness itself. Being the only mammals capable of active flight, bats were the first flying nocturnal hunters to effectively use this reservoir by means of their echolocation system (Richarz and Limbrunner, 1992). This echolocation system allowed them to exploit night with its reduced predator risk and has led to the high ages they reach in comparison to land living mammals of the same size – living up to ten times longer (Dietz et al., 2007), making them inter alia interesting study organisms.

The bat fauna of Austria consists of 28 species, from which 22 are occurring in the city of Vienna (Hüttmeir et al., 2010; personal communication Hüttmeir, 2015). All of them are listed in the Habitats Directive of the European Union and severely protected, many of them being classified as endangered species (Dietz et al., 2007). Bats are today one of the most endangered vertebrate groups throughout Europe (Hüttmeir et al., 2010). Urbanization and implicated habitat loss, fragmentation and alteration (Guest et al., 2002), and various disturbance factors like light pollution (Stone et al., 2015), noise pollution (Bennett and Zurcher, 2013; Bunkley et al., 2015) and direct road mortality (Medinas et al., 2013) are detrimental for certain bat species. Furthermore, the insertion of pesticides, insecticides and other chemicals threaten European bats by reducing prey availability, leading to infertility and causing damages to their nervous system (Dietz and Kiefer, 2014).

Bats have undergone numerous adaptations as an evolutionary outcome of competition avoidance. They occupy different sectors of a habitat, which allows the coexistence of the variety of insectivorous species in Europe (Jung et al., 2012). Although certain species are able to adapt to urban environments, forests are their major natural habitat and the main portion of bat species depends on woodlands whether for roosting, foraging, or both (Dietz et al., 2007). Bats have developed differing hunting strategies that are connected to the habitat structure of their hunting sites. Fast flying species have evolved long and narrow wings, while slowly flying maneuverable species show short and broad wing morphology (Richarz and Limbrunner, 1992). The latter are capable of flying through dense vegetation and hunting in slow or stationary flight, while larger less agile species are adapted to hunting in open environments (Dietz et al., 2007).

Bat species with similar adaptations were grouped in the present study based on Denzinger and Schnitzler (2013) to investigate response of functional groups to habitat complexity. Habitat type and foraging mode were used to divide European chiropterans into different functional groups (i.e. open space aerial foragers, edge space aerial foragers, edge space trawling foragers, narrow space flutter detecting foragers, narrow space passive gleaning foragers). Open, edge and narrow space represent the different habitat types defined according to their specific echolocation behavior. The frequency of a call determines the structure resolution a bat perceives. Smaller species hunting in edge or narrow space, whose calls reach high frequencies, have a high resolution which enables them to efficiently detect even small insects near to or on vegetation (Aldridge and Rautenbach, 1987). Larger bat species foraging in open space generally emit deeper frequencies as they are in search for larger prey (Siemers and Schnitzler, 2004). In this manner, a *Pipistrellus pygmaeus* (edge space forager), calling up to 60 kHz, has a three times higher resolution than a *Nyctalus noctula* (open space forager), calling with < 21 kHz, while the resolution of species adapted to narrow space like the *Myotis emarginatus* (up to 170 kHz) is even substantially higher. Adversely, these high frequency calls have just short ranges (Lawrence and Simmons, 1982), being only efficient in narrow space.

Furthermore, the duration of a call is niche dependent. Open space foragers emit long calls because of the greater distances between obstacles. Calls of narrow space foragers are shorter as distances between structures are also and have to be perceived in time. Echolocation calls also vary depending on situation (Schnitzler and Kalko, 2001). Bats change signal structure when they approach background targets through increasing bandwidth and reducing call duration. Searching flights in obstacle-poor space are characterized by longer and deeper narrowband calls, while the approach to prey is indicated by a higher amount of shorter and broadband calls per time period. Hunting ends in a so called “final buzz”, where the bat either catches its prey or misses it in the last moment (Dietz et al., 2007). Narrow space foragers in addition to echolocation also use passive listening when detecting prey (Schnitzler and Kalko, 2001).

Niche affiliation of bat species is reflected through their diverging prey spectra, although they are often overlapping (Aldridge and Rautenbach, 1987; Dietz et al., 2007). Open space foragers hunt in flight and consume airborne insects (butterflys, dipteran, cadisflys). Main prey of edge and narrow space foragers consists of flying (e.g. truebugs, cicadas, earwigs, bush crickets) as well as non-flying arthropods (spiders, harvestmen, larvae). Nevertheless, what nearly all bats have in common is that they also flexibly hunt within certain ranges while surplus supply of prey is present, e.g. outbreaks of easily catchable insect species (Dietz et al., 2007).

2.2 Study area

The study area covers the city of Vienna (northern latitude 48° 07' 06" - 48° 19' 23" eastern longitude 16° 10' 58" - 16° 34' 43"), the capital of Austria. With a total surface of 41487 ha, it elevates from 151 m to 543 m above sea level. Being part of the transition zone from the alpine to the continental climate region, Vienna offers a great diversity in vegetation and habitat types. Humid beech groves in the west alternate with arid oak forests in the north, the eastern Pannonia dry grasslands and the floodplain forests in the southeast (Hüttmeir et al., 2010). Also remarkable is the proportion of green areas compared to other European metropolises, which composes of approximately 50 % of the total surface, reaching from 2-15 % in the inner districts up to 70 % in the western part of the city (Hoffert et al., 2008; Fig. 1).

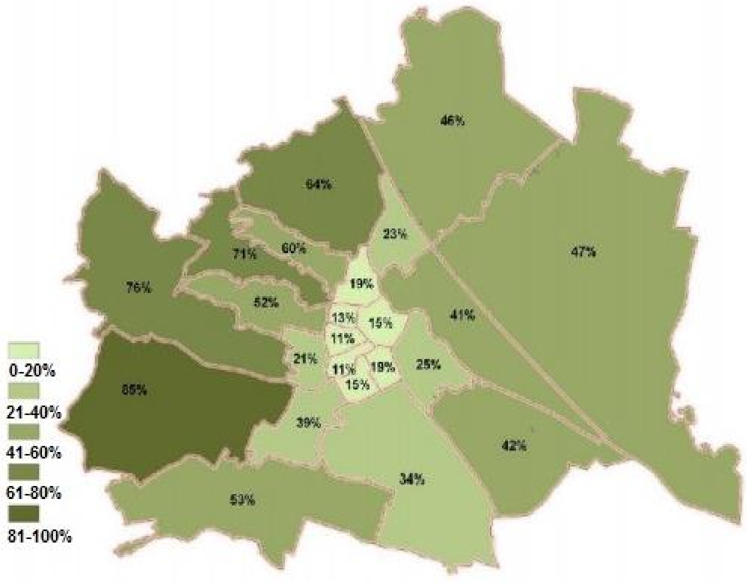


Figure 1: ***Proportion of green areas in the 23 districts of Vienna***. Figure from "Grünraummonitoring Wien 2005" (Hoffert et al. 2008).

2.3 Selection of sampling points

A total of 180 points were selected on the basis of the "Realnutzungskartierung 2009", a map of land use of the Vienna administration department MA18. This map defines different areas in terms of land utilization from which I chose in total nine classes referring to green areas, including cemeteries (FR), health areas (GE), housing units (HU), parks (PK), sport areas (SP), tree lines (TL), forests (WD), vineyards (WG) and pastures (WI). Only green areas of more than 0.25 ha were included for selection of the sampling points. To gain a gradient of patch sizes, these patches were divided into quartiles and separated in four different size classes (0-25 %, 25-

50 %, 50-75 % and 75-100 %). Five points were randomly chosen for each size class, resulting in 20 data points for each category (Fig. 2). Sampling points had a minimum distance of 200 m from each other to decrease likelihood of spatial autocorrelation.

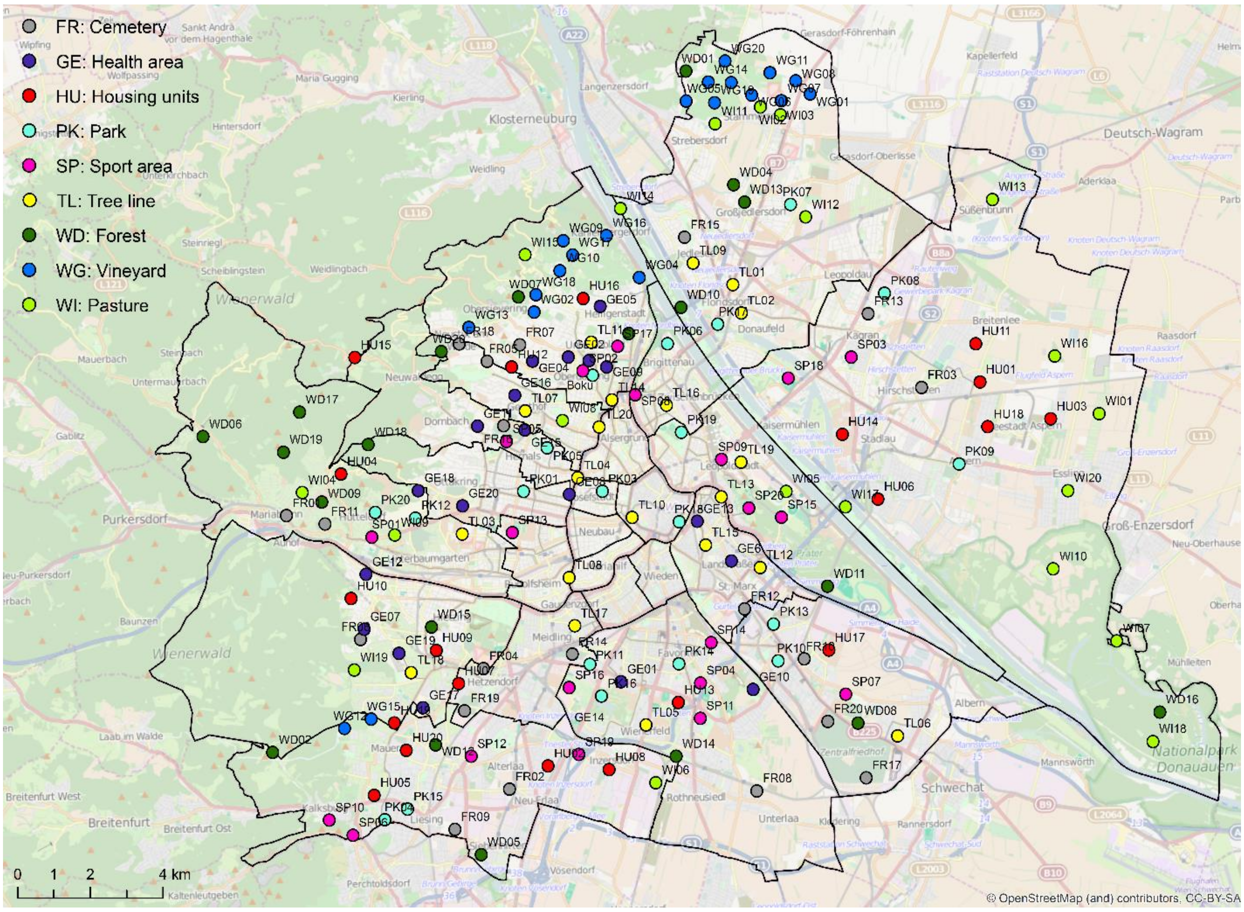


__Figure 2: Location of the 180 sampling points distributed over Vienna.__ The affiliation to the respective green area type is illustrated by different colors.

2.4 Acoustic sampling

Bat surveys were conducted from April 28th and to September 27th 2014. Each point was recorded three times, which led to a total of 540 recording nights. Bat calls were digitally recorded with bio-acoustical measurement devices called Batcorder 2.0 from ecoObs (Runkel, Marckmann & Schuster GbR). A timer function allows fully automatic recording of ultrasonic sounds over a previously settled time period, here beginning one hour before sunset and ending an hour after sunrise. Surveys were only conducted during suitable weather conditions for bats, i.e. excluding rainy and cold nights (temperature below 10 °C). GPS-devices (Garmin GPS map 62st) were used to localize the sampling points accurately. The Batcorder was placed on an attachment rod at approximately 2 m height with a minimum distance of 2 m from any vegetation or anthropogenic structure in each direction to avoid echo recordings.

2.5 Call analysis

Bat activity was defined as the length of the call sequences, summed up for each night and the median taken of the three surveys. Activity can also be measured by number of calls, which is usually highly correlated to length of sequence, as was in our case ($r^2 = 0.90$). Species richness was defined as the total number of species recorded during all three surveys, which is regarded as more appropriate for the establishment of management recommendations.

The recordings were processed with the software bcAdmin, batIdent & bcAnalyze from ecoObs. Data were imported and organized with bcAdmin, bat species were automatically identified on the basis of advanced algorithms with batIdent, while bcAnalyze served for the manual call analysis with sonograms and extended playbacks of bat calls. With this software it is possible to handle great data sets efficiently. However, the occurrence of species has to be manually verified. As the frequencies of certain species overlap, it is necessary to inspect if the species identified by the software are essentially plausible. Also background noises residing in the frequency range of bat calls, like cricket calls or public transport noises, have to be deleted manually. To identify noises, sonograms and the playback function of the program were used.

To assess the plausibility of species occurrences, I used as a basis the guidelines from the “Koordinationsstelle für Fledermausschutz in Bayern" (Hammer and Zahn, 2009), which describe the characteristics of the species-specific echolocation calls. Call sonograms were compared with typical calls for respective bat species in the guideline, describing maximum, best and minimum frequencies as well as other distinctive call features, like the typical kink of Myotis species. The guideline was initially established for first determination of a species presence in an area. As I already had a current list of species in Vienna from which evidence exists about their occurrence, I modified the criteria (Table 1) for species with easy distinguishable call characteristics, which were the majority of them. Nevertheless, for species with a high confusion rate, I used the original criteria as their call frequencies are similar which complicates the differentiation. The following species with quasi identical call characteristics were combined as reliable differentiation was not possible: Pmid = *P.kuhlii* and *nathusii,* Mbart = *M.mystacinus* and *brandtii*, Plecotus = *P. auritus* and *P. austriacus*. Criteria for certain species which were not included in the original guideline were established following Dietz and Kiefer (2007).

Table 1: Criteria for bat call verification based on frequencies from the guideline by Hammer & Zahn (2009). * indicates that frequencies refer to Dietz & Kiefer (2014). A species was verified when criteria were fulfilled and confusion species were excluded. CL=call length, TCF=typical call frequency, CF=constant frequency, QCF=quasi-constant frequency, BF=best frequency, MK="Myotis kink", LH=lower harmonic, UH=upper harmonic.

Species	Acronym	Typical call characteristics	Criteria	Confusion species
Pipistrellus pipistrellus	Ppip	43-51kHz, CL up to 10ms	min. 1 call >46kHz	Ppyg, Pmid
Pipistrellus pygmaeus	Ppyg	53-over 60kHz, CL up to 12ms	min. 2 calls with TCF	-
Pipistrellus kuhlii/ nathusii	Pmid	36-41kHz	3 calls, min. 1 call >41kHz	Hsav
Miniopterus schreibersii	Misch*	49-53kHz, CL up to 18ms, shorter calls 50-58kHz	>25 calls with p >70% in >5 sequences and CL over 12ms	Ppyg, Ppip
Hypsugo savii	Hsav	32-36kHz	2 calls with TCF	Pmid, Enil
Plecotus auritus/ austriacus	Plecotus*	*P. austriacus:* LH 48-55 to 27-17kHz, UH >80 to 35-40kHz *P. auritus:* LH 40-44 to 19-25kHz, UH 70-80 to 38-40kHz	3 calls with clear harmonics	Bbar, Eser, Vmur
Barbastella barbastellus	Bbar	Deep call: 28-35kHz, high call: 32-45kHz	2 calls with both call types visible	-
Nyctalus noctula	Nnoc	Deep CF calls with <21kHz	1 call	Nlei, Vmur, Eser
Nyctalus leisleri	Nlei	Short calls with 24-26kHz, long calls up to 20ms with 21-24kHz	>15 calls with p >70% in >5 sequences	Nnoc, Vmur, Eser, Enil
Eptesicus serotinus	Eser	CF calls with 24-27kHz	>30 calls with p >90% in >5 sequences	Nnoc, Vmur, Enil
Eptesicus nilssonii	Enil	CF calls with short CL >30kHz, long CL: 26-29kHz	10 calls with long CL	Hsav, Eser, Vmur
Verspertilio murinus	Vmur	CF calls with 22-24kHz, others with variable TCF and CL	>30 calls with p >70% in >10 sequences	Nnoc, Eser
Rhinolophus hipposideros	Rhoch	Long CF calls with 110kHz	1 call	-
Myotis myotis	Mmyo	<100 (max. 110) – 25kHz	3 calls with BF 30-35kHz,MK 30kHz	Mbart, Mdau, Mnat

Myotis daubentonii	Mdau	<100 - <30 (min. 25)kHz	3 calls with BF 47kHz, MK <40kHz	Malc, Mbart, Mbec, Mnat
Myotis dasycneme	Mdas*	65-85kHz – 25-35kHz with CL 4-8ms, QCF calls 32-37kHz with CL up to 15-25ms	10 calls with TCF and QCF-calls in between	not defined
Myotis brandtii/ mystacinus	Mbart	>100kHz (max. 125) – 26kHz	3 calls with BF 47.5kHz, MK 40kHz	Malc, Mbec, Mdau, Mmyo, Mema
Myotis bechsteinii	Mbec	120-130kHz (max. 140) - >30kHz (min. 22)	MK >50kHz for steep calls, 34kHz for flat calls	Malc, Mbart, Mdau, Mmyo, Mnat, Mema
Myotis nattereri	Mnat	>135kHz (max. 175) - <20 (often 17, min. 7kHz)	3 calls with BF 47kHz	Mbart, Mbec, Mdau, Mmyo, Mema
Myotis emarginatus	Mema	>130kHz (max. 170) - 38kHz (min. 30)	3 calls with BF > 50kHz, MK 45-55kHz	Mbec, Mbart, Malc, Mnat
Myotis alcathoe	Malc	<130kHz (max. 145) - >45kHz (min. 40)	3 calls with BF >50kHz, MK 45-55kHz (max. 60)	Mbart, Mbec, Mdau, Mema, Ppip

2.6 Structural complexity of digital images

Photographs were taken with a commercial digital camera (Nikon CoolpixS220) to record the vegetation structure of each sampling point. The images were taken simultaneously with data of the field method to ensure equal conditions and between 09:30 and 15:30 to ensure similar illumination. The camera was installed at the center of the sampling point with the tripod placed at a fixed height of 1 m above the ground. Images were taken with the automatic mode (focal length 35 mm) and the camera pointing outwards in four cardinal directions (north, east, south and west), with the (imaginary) horizon parting the scene horizontally in half. Additionally, one photograph was taken upwards to account for the canopy cover. Five images per sampling point resulted in a total of 900 images taken.

Commercial digital cameras, as the one I used, record images in the red, green, blue (RGB) color space. Following Proulx and Parrott (2008), the RGB color space of all images was converted to hue, saturation, value (HSV) color space to separate the pure color component (hue) from chroma (saturation) and intensity (value). Color represents the dominant wavelengths in the light signal, while intensity is the grey tone, the departure of a color from black. Chroma describes how much the light spectrum differs from the pure color component and the intensity. The conversion was necessary because of the considerable overlap of transmittances among the three spectral bands (RGB) in commercial cameras, which is not present in the HSV system. Also it is more natural to a human observer as it reproduces more effectively how the human brain represents color, without information loss of within- and among-image variation of the RGB color space (Mellin et al., 2012). For the analysis, I used the V-layer of the images, which Proulx and Parrott (2008, 2009) have used and identified as a robust value for quantification of structural complexity in natural scenes.

Among the various metrics available to describe digital images, mean information gain (MIG) was chosen, as it is a well-established measure of spatial complexity patterns in natural scenes (Wackerbauer et al. 1994, Gell-Mann and Lloyd 1996, Proulx and Parrott 2008, 2009). This index is used as an ecological indicator for quantifying structural heterogeneity of vegetation in photographs. MIG was calculated using the V-layer of the digital images based on Shannon´s equation for entropy and the relative distribution of pixel values. MIG determines the amount of spatial heterogeneity in an image, i.e. joint entropy (JE), and excludes the fraction of aspatial heterogeneity, i.e. marginal entropy (ME). Joint entropy of an image is calculated on a probability matrix that represents the chances of getting a specific pair of pixel values, while marginal entropy is calculated for individual pixel values indifferently of their location in the image.

Joint Shannon Entropy:

$$H[\chi] = -\sum_{i=1}^{N^4} p(\chi_i) \log p(\chi_i) \tag{eq. 1}$$

Marginal Shannon Entropy:

$$H[\gamma] = -\sum_{i=1}^{N} p(\gamma_i) \log p(\gamma_i) \tag{eq. 2}$$

where $p(\chi_i)$ is the probability of finding a specific spatial configuration χ_i made of four neighboring pixels in the image (2x2-pixel neighborhood, eq. 1). $p(\gamma_i)$ denotes the probability of observing a pixel´s intensity value γ_i independently of its location in the image (eq. 2). I computed MIG for the intensity band (V) in the HSV image as follows:

$$\mathrm{MIG} = \frac{H[\chi] - H[\gamma]}{\log \mathrm{N}^4 - \log \mathrm{N}^1} = \frac{\mathrm{JE} - \mathrm{ME}}{\log \mathrm{N}^4 - \log \mathrm{N}^1} \tag{eq. 3}$$

where N is the number of frequency bins of pixel values, ($\log N^4 - \log N^1$) represents the maximum number of possible pixel configurations in a four-pixel neighborhood and serves to normalize MIG (eq. 3). MIG ranges from 0 for completely uniform spatial patterns across pixels (order), which would represent a single color, to 1 for completely random patterns (disorder). Thus, images of undifferentiated, uniform habitats are expected to have a low MIG, while images of random or highly differentiated habitats should have high MIGs. Intermediate values of MIG are associated with more spatially heterogeneous data, hence they are correlated with habitat complexity in images taken within natural ecosystems (Parrott, 2010). MIG was processed for each of the five images per sampling point. I used the mean to combine the images per sampling location into one index as suggested by Proulx and Parrott (2008) and Mellin (2012). MIG of all five images was used as individual parameter and also separated into MIG of side views and MIG of the top view as MIG top rather reflects canopy cover. All digital images were processed with R v. 3.2.1 (R Core Team, 2015), package “imagemetrics” (Massicotte, 2014).

2.7 Field sampling

A set of structural parameters at the microhabitat scale was recorded from June 27th to September 8th 2014 to investigate their influence on the bat fauna of Vienna: vegetation profile, understory coverage, canopy coverage, vegetation height, Shannon index, number of trees with a diameter at breast height (DBH) > 0.3 m, DBH of these trees, tree density, and presence of a water body. I chose a radius of 20 m for the sampling plot as it corresponds to the mean distance of bat ultrasound detection (Rodrigues et al., 2008; Bach, 2002). To record the vegetation parameters, I used the cover-board method (Nudds 1977; Fig. 3). This method served as basis for evaluating vegetation profile, understory coverage, canopy coverage and vegetation height. The measurements started at the initial sampling point and were repeated in 5, 10, 15 and 20 m distance from the sampling point along the cardinal directions (north, south, east and west). Percentage of understory and canopy coverage was estimated. For the vegetation profile , vegetation touching a 2 m pole at the following intervals: 0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-5, 5-7, 7-10, 10-15 and > 15 m was recorded. The pole was marked every 0.5 m and aided estimating also higher layers and the height of the vegetation. The Shannon diversity index (Shannon & Weaver, 1948) was included to describe complexity of vegetation. The index is usually used as an indicator for species diversity considering species richness and abundances (Peet, 1974). I used the Shannon index for the vegetation profile, whereat the different "species" were represented by the 10 layers. The index was calculated with R v. 3.2.1 (R Core Team, 2015), package "vegan" (Oksanen et al., 2015).

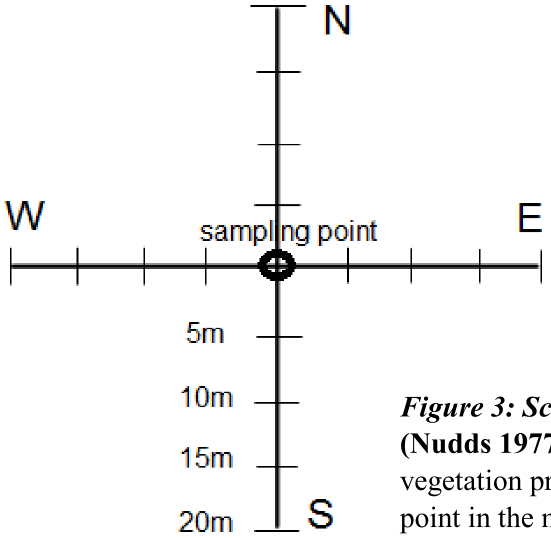


Figure 3: Schematic representation of the cover-board method* (Nudds 1977)*: Understory, canopy coverage, vegetation height and vegetation profile (10 layers), were recorded starting from the sampling point in the middle to 20 m along four cardinal directions.

For evaluating tree density, the number of trees with DBH > 0.16 m within the sampling plot was counted. I excluded smaller trees as those show bush character rather than the properties of mature trees. DBH of trees > 0.3 m was measured because they could offer roosts and protection from predators for bats (personal communication Kubista, 2015). In addition to the vegetation parameters, I registered the presence of a water body, whereby a water body was defined as any kind of permanent water being potentially available for bats. Hereinafter parameters recorded using the field method are referred to field parameters.

2.8 Statistical analysis

To investigate if MIG reflects vegetation complexity of sampling points correlations between MIG and recorded field parameters were examined with Pearson´s coefficient (correlation threshold $r^2=0.5$). To test my first hypothesis if MIG was correlated with bat activity and species richness, Pearson´s was used. Analysis of variance (ANOVA) were done to test for significant differences in bat activity, species richness and MIG between green area types, while Tukey test was used to locate the differences. Influence of the independent parameters (i.e., vegetation parameters, water, MIG) on bat activity and species richness was examined.

Generalized linear models were used to determine which parameters are the best predictors of bat species richness. Linear models were conducted to analyze which parameters influence bat activity. Models were also performed for the following functional groups according to Denzinger & Schnitzler (2013): edge space aerial foragers (*P. pipistrellus, P. pygmaeus, P. kuhlii/ nathusii, B. barbastellus, M. alcathoe, E. serotinus, E. nilssonii, H. savii*) and open space aerial foragers (*N. noctula, E. serotinus, E. nilssonii, H. savii*). As the species *E. serotinus, E. nilssonii* and *H. savii* show characteristics of both groups they were included in both. I also analyzed Myotis species richness because this genus represented partly the remaining three functional groups (i.e., narrow space passive gleaning foragers, narrow space flutter detecting foragers and edge space trawling foragers). Species from this genus are often grouped for investigations, as there is evidence for similar habitat requirements among them (e.g. Dixon, 2012). To examine potential differences between individual species, activity of representative species, i.e. *Nyctalus noctula* and *Pipistrellus pygmaeus,* was analyzed.

To test for homogeneity of variances for the linear models, the non-constant variance score test, package “car” (Fox and Weisberg, 2011), was performed. Square root, Log10 and Yeo-Johnson-transformations, package “car” (Fox and Weisberg, 2011), were done to reach normality of parameters if required. Parameters showing correlation were removed according to variance inflation factor (VIF) to avoid multi-collinearity, package “usdm” (Naimi, 2015; threshold for correlation coefficients th=0.8, threshold for VIF th=7). All models were performed with only field parameters, only MIG parameters and both combined. Models were conducted first with MIG of all views, and again with MIG sides and MIG top, as MIG sides and MIG top potentially, but not necessarily, contain information with different relevance for bats. Fitting of the models was based on Akaike’s Information Criterion AIC and evaluated through stepwise model selection, package “MASS” (Venables and Ripley, 2002), preferring the smallest AIC value for the final model. Best models were selected according to AIC and R-squared. All statistical analyses were performed in R v. 3.2.1 (R Core Team, 2015). Where Poisson GLM revealed underdispersion of data, correction of standard errors was done using a quasi-GLM.

3. RESULTS

3.1 Bat activity

A total of 105,076 call sequences were recorded during all surveys (1st survey: 24,912, 2nd survey: 33,036, 3rd survey: 47,128 sequences). Mean length of sequence lasted 1.08 ± 0.81 s (min: 0 s, max: 20.058 s). The average number of calls per sequence was 6.44 ± 8.09. Highest number of call sequences was recorded at a cemetery (FR09) during the 2nd survey with 4,383 calls, whereas a health area (GE14) showed the lowest activity with no recordings during all surveys. In total during 15 nights no bats were recorded. The average bat activity for all sampling points was 139 ± 283 s, while the maximum activity with 2,965 s was recorded at a park (PK13). Differences in bat activity according to green area type were highly significant (ANOVA: F=6.378, df=8, p<0.001, Fig. 4). Sport areas displayed the highest average bat activity (171 ± 155 s), followed by health-purpose areas (108 ± 106 s). Lower activity was recorded at housing units (53 ± 50 s), while tree lines showed the least activity (19 ± 26 s).

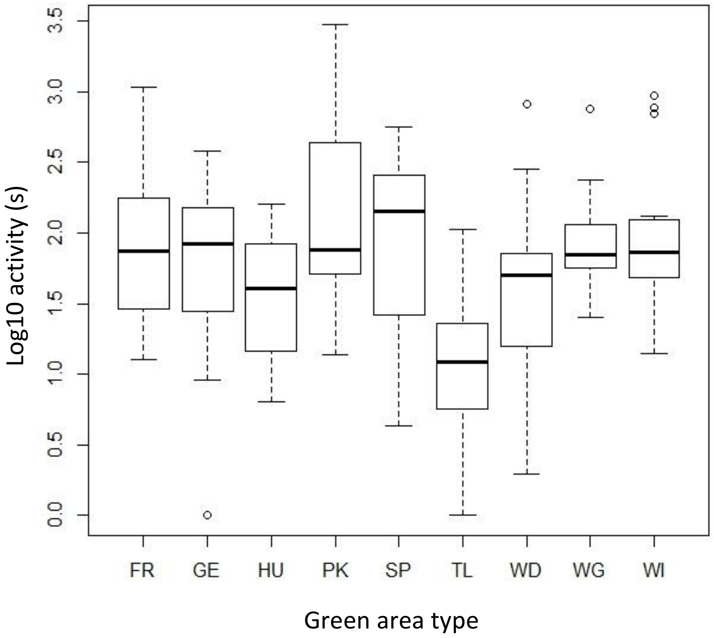


Figure 4: Total bat activity of different green area types. Acronyms: FR=cemetery, GE=health area, HU=housing unit, PK=park, SP=sport area, TL=tree line, WD=forest, WG=vineyard, WI=pasture. Log10-transformation was used to reach normality (Shapiro-Wilk-Test, p=0.150). ANOVA (N=180, F=6.378, p<0.001). Post-hoc-test: Tukey, significant differences between TL and FR, GE, PK, SP, WG, WI.

3.2 Species richness

I was able to verify 18 of the 22 species occurring in Vienna according to KFFÖ (Hüttmeir et al., 2010; personal communication Hüttmeir, 2015, Table 2). Among them were the three grouped species which were not distinguishable, from which I assume that both were present, as they are already known to occur in Vienna. The three most commonly recorded species were *Pipistrellus pygmaeus*, *Pipistrellus kuhlii* and *Pipistrellus nathusii* occurring at 93 % of all sampling points (as mentioned before Pmid represents here two species). The common noctule *Nyctalus noctula* was found at 88 % of the sampling points, followed by Savi's pipistrelle *Hypsugo savii* with an occurrence of 73 %. The common pipistrelle *Pipistrellus pipistrellus* was recorded at 61 % of all sites. Only two species of the genus Myotis were yet relatively common, occurring at one third of the sites, namely the whiskered bat *Myotis mystacinus* and Brandt's bat *Myotis brandtii* (grouped to Mbart). The following four species were recorded infrequently between 14-19 % of the sampling points: *Barbastella barbastellus,* the two *Plecotus* species *P. auritus* and *P. austriacus,* and *Eptesicus nilssonii*, while six species occurred even more rarely and could be detected at less than 10 % of the sites (Fig. 5).

Data base for species richness consisted of 77.5 % of all original recordings as only sequences with species identified by the program and verified afterwards were used for analysis. The average species richness among all sampling points was 5.1 ± 1.8 species. Maximum species richness was detected at a sport area SP10 and at a pasture WI15 where 11 species were recorded during all surveys. Differences in species richness among green area types were highly significant (ANOVA: F=6.418, df=8, p<0.001, Fig. 6). Vineyards (6.6 ± 1.4), cemeteries (5.9 ± 1.7) and pastures (5.9 ± 1.9) showed the highest average species richness, whereas tree lines were the green areas with the lowest species richness (3.5 ± 1.1).

Table 2: ***Verified species at the sampling points.*** Scientific and common names, acronyms and conservation status of the FFH-directive and of the Red list of Austrian´s endangered mammals (Spitzenberger 2005) are included: EN (endangered), VU (vulnerable), NT (near threatened), LC (least concern), DD (data deficient), NE (not evaluated), -- (not listed).

	Species	**Common name**	**Acronym**	**FFH-directive**	**Red List**
1	*Pipistrellus pygmaeus*	Soprano pipistrelle	Ppyg	IV	DD
2	*Pipistrellus kuhlii*	Kuhl's pipistrelle	Pmid	IV	VU
3	*Pipistrellus nathusii*	Nathusius' pipistrelle	Pmid	IV	NE
4	*Nyctalus noctula*	Common noctule	Nnoc	IV	NE
5	*Hypsugo savii*	Savi's pipistrelle	Hsav	IV	EN
6	*Pipistrellus pipistrellus*	Common pipistrelle	Ppip	IV	NT
7	*Myotis mystacinus*	Whiskered bat	Mbart	IV	NT
8	*Myotis brandtii*	Brandt's bat	Mbart	IV	VU
9	*Barbastella barbastellus*	Barbastelle	Bbar	II,IV	VU
10	*Plecotus auritus*	Brown/Common long-eared bat	Plecotus	IV	VU
11	*Plecotus austriacus*	Grey long-eared bat	Plecotus	IV	LC
12	*Eptesicus nilssonii*	Northern bat	Enil	IV	LC
13	*Myotis emarginatus*	Geoffroy's bat	Mema	II,IV	VU
14	*Myotis daubentonii*	Daubenton's bat	Mdau	IV	LC
15	*Myotis nattereri*	Natterer's bat	Mnat	IV	VU
16	*Myotis alcathoe*	Alcathoe Whiskered bat	Malc	IV	--
17	*Myotis myotis*	Greater mouse-eared bat	Mmyo	II,IV	LC
18	*Eptesicus serotinus*	Serotine bat	Eser	IV	VU

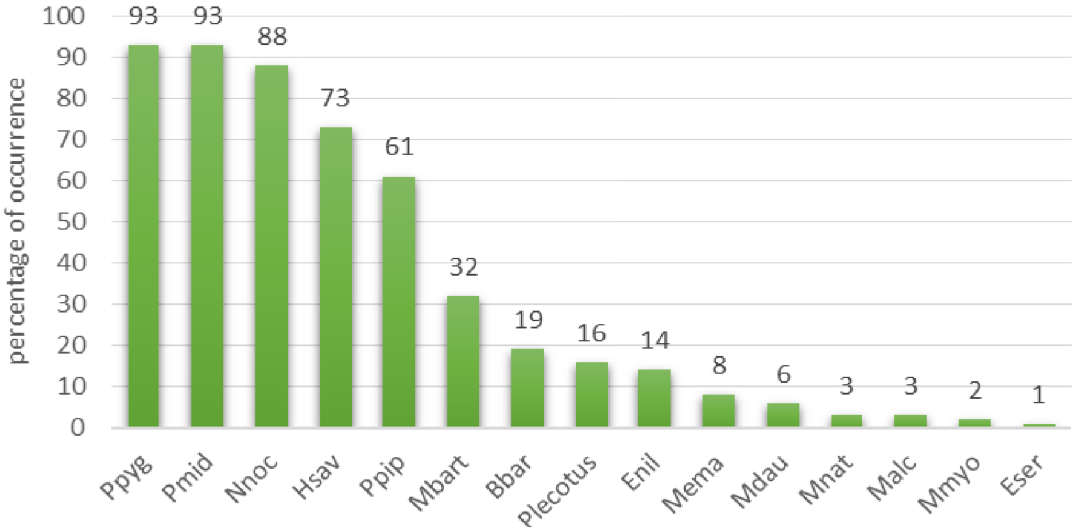


Figure 5: Percentage of occurrence of verified bat species at the 180 sampling points. For species acronym please refer to Table 2.

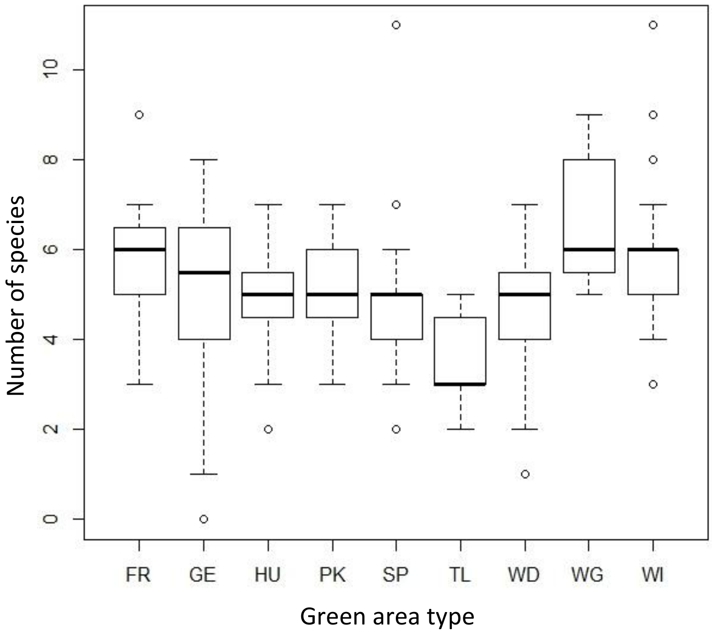


Figure 6: Total bat species richness of different green area types. Acronyms: FR=cemetery, GE=health area, HU=housing unit, PK=park, SP=sport area, TL=tree line, WD=forest, WG=vineyard, WI=pasture. ANOVA (N=180, F=6.418, p<0.001). Post-hoc-test: Tukey, differences between TL and FR, GE, PK, WG, WI and between WG and HU, SP, WD.

3.3 Local parameters of field method

Vegetation profile showed that the first layer (0-0.5 m) was the most frequent, whereas layers between 0.5 to 3 m were less often present at the sampling points. Highest vegetation layers (10-15 and >15 m) were uncommon. Average understory cover was 46.7 %, while average canopy cover was 31.9 %. Mean vegetation height was almost 5 m and there were six trees per sampling plot on average (Table 3).

Table 3: ***Summary of field parameters and MIG parameters.*** Minimum, maximum, mean and standard deviation values are shown. Transformations used to approach normality for operating linear models are given in the last column; YJ designates Yeo-Johnson-transformation (respective λ-values in parenthesis).

Parameter	Min	Max	Mean ± SD	Transformation
Foliage profile (presence/absence):				
Layer 0-0.5 m	0.000	1.000	0.507 ± 0.288	-
Layer 0.5-1 m	0.000	1.000	0.173 ± 0.169	Square root
Layer 1-1.5 m	0.000	0.824	0.144 ± 0.143	Square root
Layer 1.5-2 m	0.000	0.824	0.130 ± 0.133	Square root
Layer 2-3 m	0.000	0.647	0.159 ± 0.151	Square root
Layer 3-5 m	0.000	0.882	0.249 ± 0.189	Square root
Layer 5-7 m	0.000	0.882	0.309 ± 0.240	Square root
Layer 7-10 m	0.000	1.000	0.286 ± 0.261	Square root
Layer 10-15 m	0.000	1.000	0.170 ± 0.256	YJ (λ= -5.07837)
Layer >15 m	0.000	1.000	0.059 ± 0.197	-
Understory coverage (%)	0.0	98.6	46.7 ± 24.8	Square root
Canopy coverage (%)	0.0	91.8	31.9 ± 25.2	Square root
Vegetation height (m)	0.10	35.56	4.96 ± 5.19	Log10
Shannon index	0.000	2.261	1.711 ± 0.380	YJ (λ= 3.93581)
Tree density (No. of trees/m^2)	0.0000	0.0708	0.0093 ± 0.0098	YJ (λ= -79.95304)
DBH (m)	0.00	0.88	0.40 ± 0.18	YJ (λ= 2.685285)
Number of trees	0.0	43.0	6.0 ± 6.3	YJ (λ= 0.1053379)
Presence of water body	0.000	1.000	0.089 ± 0.285	-
MIG all views	0.377	0.604	0.489 ± 0.050	-
MIG side views	0.422	0.639	0.526 ± 0.053	YJ (λ=2.304512)
MIG top view	0.049	0.594	0.342 ± 0.129	Log10

3.4 Structural complexity of digital images

MIG side views was lowest at a pasture WI11 with 0.422 ± 0.036 and highest at WG04 with 0.639 ± 0.068, which was a highly structured sampling point at a fallow vineyard near the edge of the city. Lowest MIG top (0.049) was recorded at a health area GE02 with no canopy cover and therefore of a pure sky image, while HU09, a housing unit with an idle highly vegetated garden, had the highest MIG top (0.594). MIG of the top view in general was on average smaller due to sky images than MIG of the four side views (Table 3).

MIG was correlated with several field parameters (Fig. 7). MIG of all five views (four side views and top view) was correlated with canopy cover (r^2= 0.67), tree density (r^2= 0.64), vegetation height (r^2= 0.64), Shannon diversity of vegetation layers (r^2= 0.58), and the number of trees of the sampling points (r^2=0.54). MIG of the four side views was correlated with Shannon (r^2= 0.54) and to a lesser extent with tree density (r^2= 0.47), canopy cover (r^2= 0.44), vegetation height (r^2= 0.43) and slightly to the number of trees (r^2= 0.36). MIG of the top view showed correlation to the canopy cover (r^2= 0.59), as well as to vegetation height (r^2= 0.54) and to a lower extent to tree density (r^2= 0.46) and to the number of trees (r^2= 0.46), while a weak negative correlation was also detected to understory coverage (r^2= -0.32).

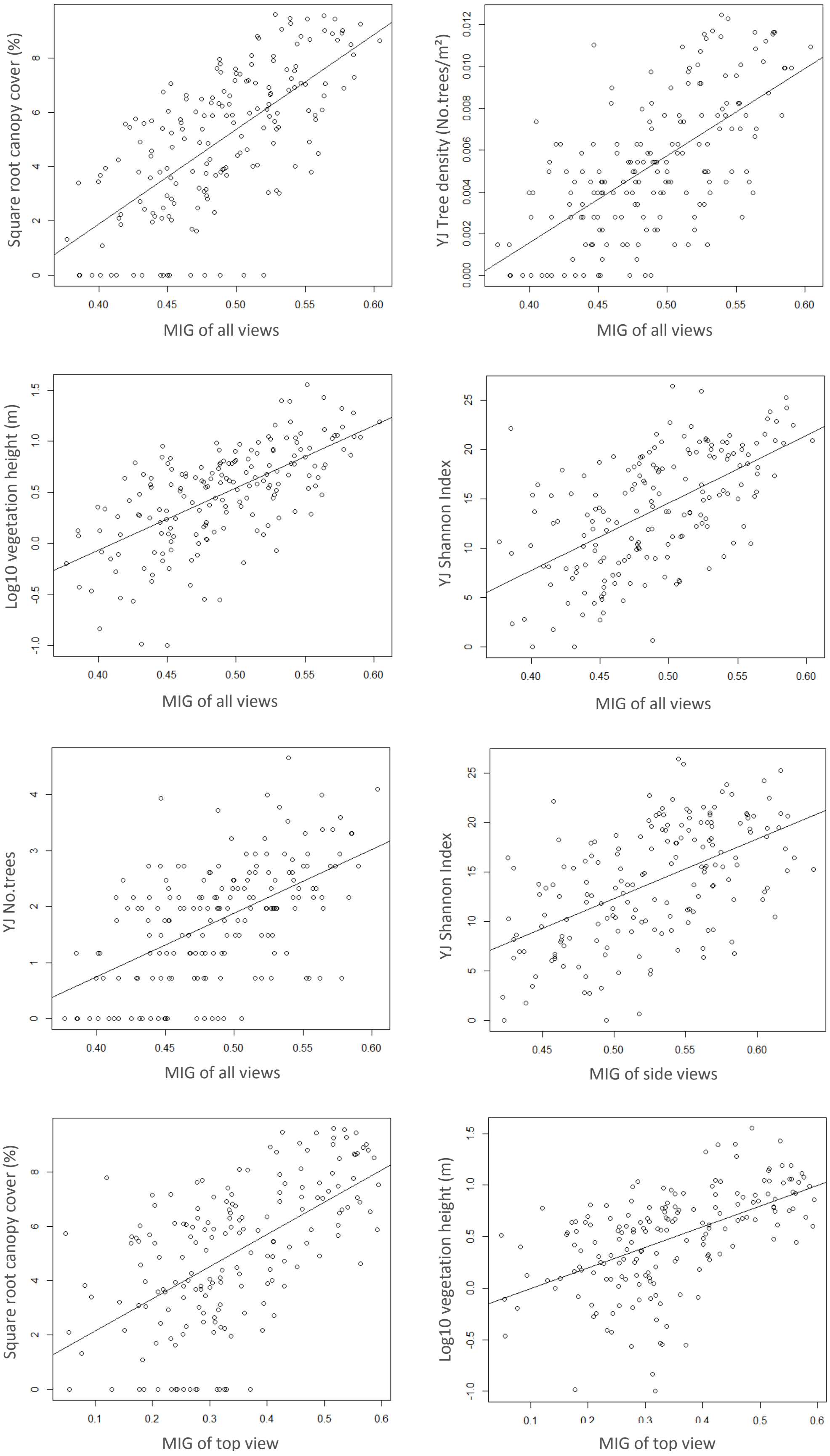
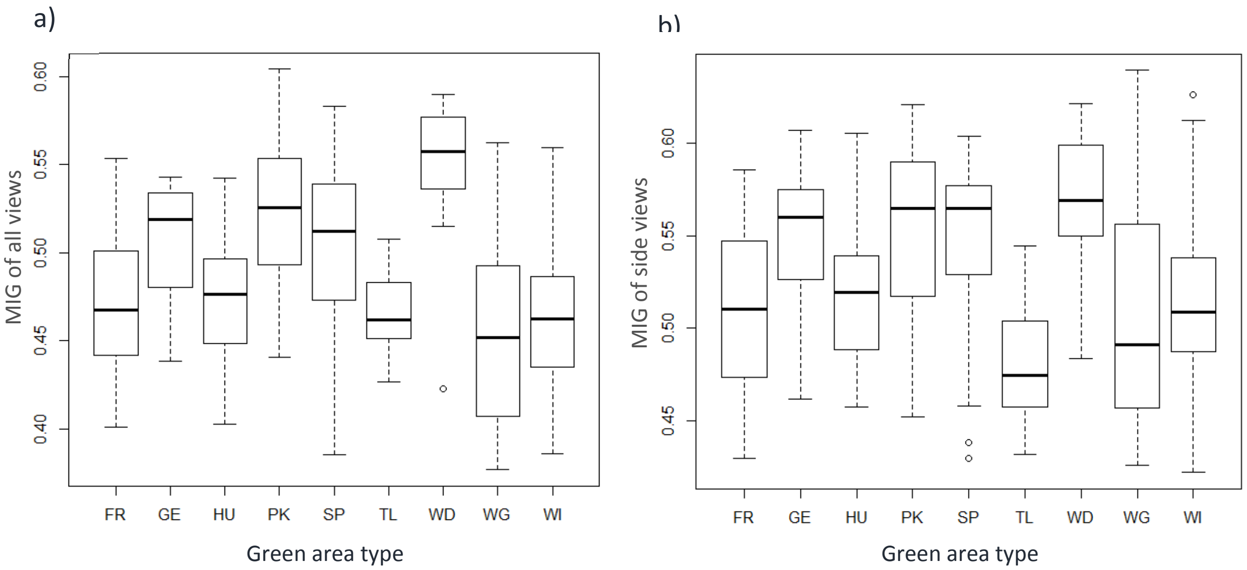


Figure 7: ***Correlation between MIG and vegetation parameters.*** Parameters correlated more than r^2=0.5 are shown.

Differences in MIG among green area types were highly significant for MIG including all five views (ANOVA: F=11.98, df=8, p<0.001, Fig. 8a) as well as MIG of the four side views (ANOVA: F=11.98, df=8, p<0.001, Fig. 8b) and MIG of the top view (ANOVA: F=11.98, df=8, p<0.001, Fig. 8c). As expected, forests had the highest average complexity of vegetation obtained by all three MIGs: MIG all views (0.549 ± 0.038), MIG side views (0.570 ± 0.035), and also MIG top view of the sampling sites (0.467 ± 0.096). Pastures (0.464 ± 0.046), tree lines (0.466 ± 0.024) and vineyards (0.452 ± 0.052) showed lower complexity according to MIG all views (Fig. 8a).



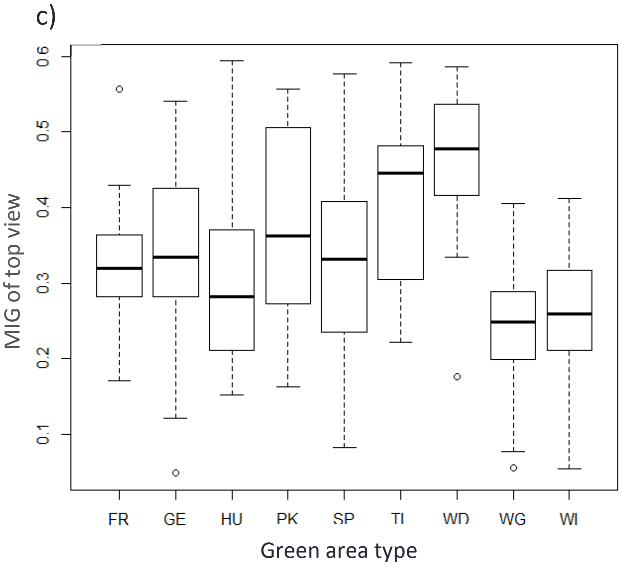


Figure 8: Mean information gain (MIG) for each green area type. Highly significant differences of MIG including all views, MIG side views and MIG top view between the nine green area types. a) MIG all views: ANOVA (N=180, F=11.98, p<0.001). Post-hoc-test: Tukey –significant differences between WD and FR, GE, HU, SP, TL, WG, WI; between WG and GE, PK, SP; PK and WI, TL, FR, HU; GE and WI. b) MIG side views: ANOVA (N=180, F=8.06, p<0.001). Tukey – significant differences between WD and TL, WG, FR, WI, HU; TL and SP, GE, PK; PK and WG, FR. c) MIG top view: ANOVA (N=180, F=7.71, p<0.001). Tukey – significant differences between WD and WG, WI, HU, FR, SP, GE; WG and PK, TL; WI and PK, TL.

Complexity of green area types for MIG side views and MIG top view was similar to MIG all views, with the exception of MIG top regarding tree lines. In contrast, tree lines had the second highest MIG top after forests. This is understandable as they consisted mainly of big mature trees with well-developed canopy, filling the photographs as the camera was always placed directly under them. Apart from that, tree lines generally were characterized by scarce or no vegetation at all, which is reflected by the lowest average MIG of side views for this green area type.

No correlation could be detected between MIG of all views and bat activity (r^2= -0.07) nor species richness (r^2= -0.14), neither between MIG of the side views and bat activity (r^2=0.12) nor species richness (r^2=0.05). Indeed, slight negative linear correlation was found for bat activity and MIG of top view (r^2= -0.32) as well as species richness and MIG of top view (r^2= -0.35; Fig. 9).

When evaluating the influence of only MIG parameters on total bat activity (Table 4), MIG top was negative significant, while MIG of side views stayed almost positive significant in the model (p= 0.058). Similar pattern was found for activity of the edge space aerial foragers, where MIG top had a negative significant effect and MIG sides curtly missed the significance level (p=0.051). Activity of open space aerial foragers was only affected by MIG top, which had a significant negative impact. Same result was asserted for *N.noctula.* In contrast, for activity of *P.pygmaeus* MIG sides had a significant positive effect, while MIG top had no influence. Most of the variance in activity was explained by models for *N.noctula* (17.0 %) and for the open space foragers (16.6 %), followed by total bat activity (12.2 %), the edge space guild (8.5 %) and *P.pygmaeus* (4.1 %). AIC for total bat activity was smallest (321.6), followed by *N.noctula* (371.9), the edge space group (382.5), the open space group (393.3) and ending again with *P.pygmaeus* (681.8).

When models for total species richness were conducted only with MIG parameters (Table 4), MIG top had a significant negative influence, while MIG sides had no effect. Same result was obtained for edge space and the open space aerial foragers. In contrast, for the Myotis species the model with MIG of all views was the best, revealing a significant positive influence on their species richness. AIC was smallest for Myotis species (360.1), followed by the open space group (494.9), the edge space group (626.4) and total species richness with the highest AIC (727.3).

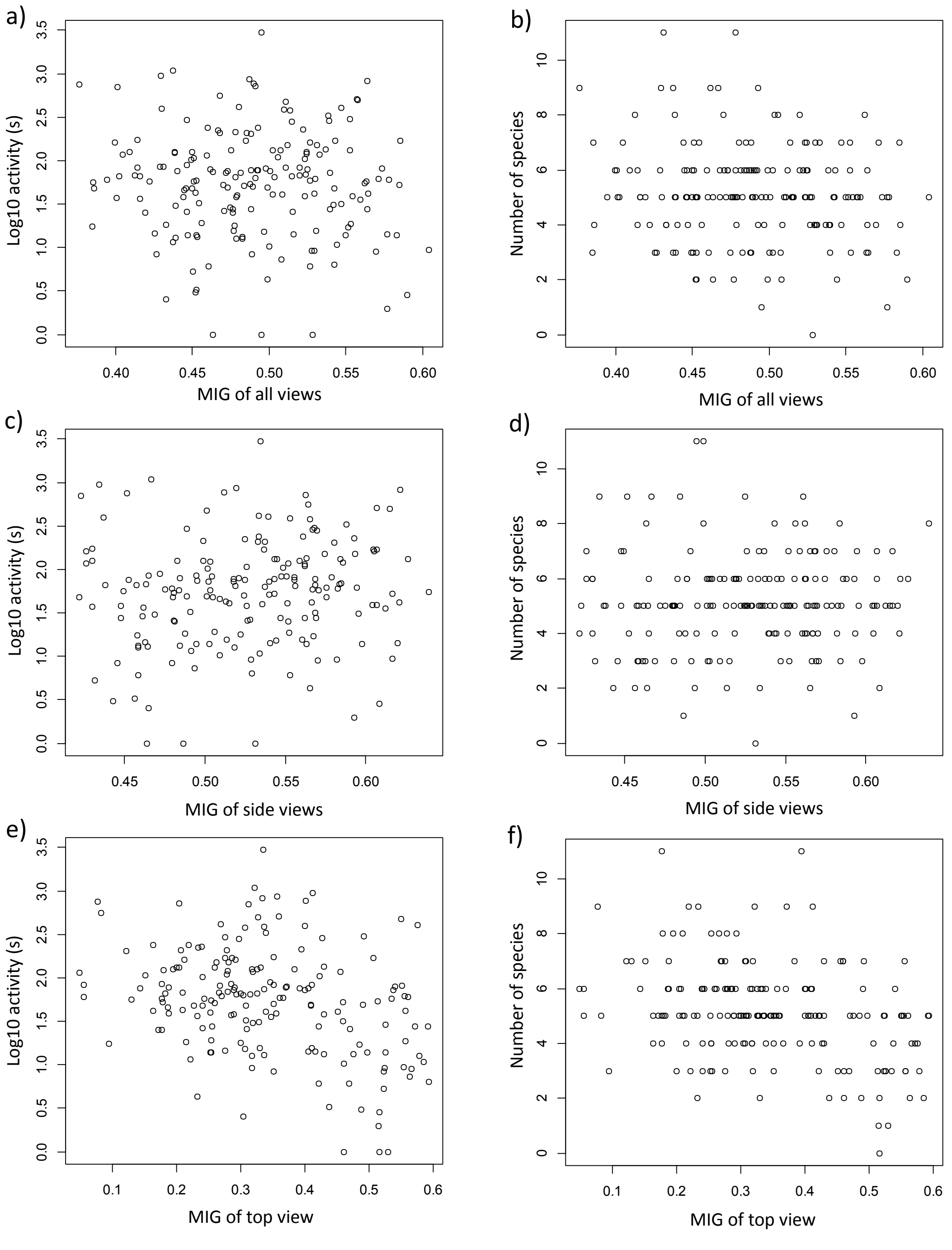


Figure 9: ***Relationship between log-transformed bat activity on left panels, species richness on the right panels and MIG all views (a, b), MIG sides (c, d) and top view (e, f)***.

3.5 Influence of MIG and field parameters on bat activity

Models concerning bat activity were conducted excluding the following parameters as they showed high collinearity: canopy coverage, vegetation height, layers 1-1.5, 1.5-2 and 7-10 m. When evaluating influence of only field parameters on total bat activity (Table 5), layers 0.5-1 m and 5-7 m, and tree density had a significant negative effect on bat activity, while understory cover and Shannon had a significant positive influence. Tree density showed the highest influence on bat activity (Coefficient = -47.39) compared to the other parameters. When including MIG in the model, tree density was excluded from the best fitted model and MIG top view was a negative significant factor, improving the model (AIC only field parameters = -221.5, including MIG parameters = -227.1) and explaining approximately three per cent more of the variance (R^2 only field parameters = 29.0, including MIG parameters = 31.9). Also MIG top showed the highest influence of the remaining significant parameters (Coefficient = -3.09).

Results for the linear model of the edge space aerial foragers were similar to total bat activity (Table 5). In the model including only field parameters, tree density and layer 0.5-1 m had a significant negative influence on activity of this group, while understory cover, Shannon and number of trees had a significant positive impact. Tree density had the highest influence (Coefficient = -82.40) also in this model. After inclusion of MIG, layer 2-3 m was additionally positive significant and MIG of top view negative significant, while Shannon was excluded. Values for AIC and R-squared were improved, although here to a smaller extent (AIC only field parameters = -140.5, including MIG parameters = -143.6; R^2 only field parameters = 17.3, including MIG parameters = 18.7). MIG top showed the highest influence (Coefficient = -3.12) after tree density (Coefficient = -77.70). For activity of open space aerial foragers only with field parameters, tree density and layer 0.5-1m had a significant negative effect, while understory cover and Shannon were positive significant. Similarly, tree density had the highest influence (Coefficient = -83.52) compared to the other parameters. When MIG was included, MIG top was negative significant, improving the model slightly (AIC only field parameters = -151.8, including MIG parameters = -156.5; R^2 only field parameters = 32.5, including MIG parameters = 34.3). MIG top also had the highest influence (Coefficient = -3.57) after tree density (Coefficient = -81.76).

Activity of *N. noctula* when including only field parameters was significantly affected by layer 5-7 m and understory cover, with the former having a negative and the latter a positive influence on activity of this species. Inclusion of MIG five views delivered the best fitted model with a significant negative impact of this parameter, also showing the highest influence (Coefficient = -2.55) and improving the model (AIC only field parameters = -175.78, including

MIG parameters = -177.6; R² only field parameters = 33.9, including MIG parameters = 36.0). Activity of *P. pygmaeus* was negatively influenced by layer 0.5-1 m and 5-7 m, while layer 0-0.5 m, understory cover, Shannon and number of trees positively affected activity of this species. Hereby layer 0.5-1m showed the highest influence (Coefficient = -2.55). MIG parameters had no influence on the fitted model of this species (AIC = 143.67, R² = 20.3).

3.6 Influence of MIG and field parameters on species richness

Models for species richness were calculated excluding canopy coverage, vegetation height and layer 7-10 m due to collinearity. When analyzing the influence of only field parameters on total species richness (Table 5), layer 5-7 m showed a negative significant effect, while understory cover had a significant positive influence. When including MIG, MIG of top view was negative significant, showing also the highest influence (Coefficient = -0.46), although the model was not improved compared to the model of field parameters only (AIC only field parameters = 718.8, including MIG parameters = 718.6).

Species richness of the edge space foragers when including only field parameters was negatively influenced by tree density, with the highest significant influence (Coefficient = -8.66), while understory cover had a significant positive impact. When MIG was added to the model, MIG top showed a significant negative and understory cover a significant positive impact on species richness of this group, with MIG top having the highest influence (Coefficient = -0.76). Slight model improvement was reached when including MIG (AIC only field parameters = 625.3, including MIG parameters = 623.7). Species richness of open space aerial foragers was negatively influenced by the layers 5-7 m and 10-15 m, while understory cover had a significant positive effect when only field parameters were included. Layer 10-15 m showed the highest influence (Coefficient = -0.48). When adding MIG, layers 5-7 m and >15 m were negative significant, with layer 5-7 m having the highest influence (Coefficient = -0.68). Including MIG did not improve the model for the open space foragers (AIC only field parameters = 489.8, including MIG parameters = 490.2). Myotis species richness was positively affected by layer 1.5-2 m, >15 m and understory cover, with layer 1.5-2 m having the highest influence (Coefficient = 1.77). Incorporation of MIG did not change the outcome (AIC = 339).

Table 4: ***Results of models conducted only with MIG parameters for bat activity and species richness, respectively.***

	Only MIG parameters			
	Estimate	Standard error	t value	*P*
Total bat activity				
MIG sides	0.912	0.478	1.91	0.058
MIG top	-4.820	1.037	-4.65	**<0.001**
Activity edge space aerial foragers				
MIG sides	1.083	0.566	1.91	0.057
MIG top	-4.483	1.229	-3.65	**<0.001**
Activity open space aerial foragers				
MIG sides	-0.075	0.583	-0.13	0.898
MIG top	-7.497	1.266	-5.92	**<0.001**
Activity *Nyctalus noctula*				
MIG sides	-0.808	0.550	-1.47	0.143
MIG top	-6.893	1.193	-5.78	**<0.001**
Activity *Pipistrellus pygmaeus*				
MIG sides	3.362	1.300	2.59	**0.011**
MIG top	-2.878	2.822	-1.02	0.309
Total species rich richness				
MIG sides	0.389	0.471	0.83	0.410
MIG top	-0.951	0.193	-4.92	**<0.001**
Species richness edge space aerial foragers				
MIG sides	0.331	0.433	0.77	0.445
MIG top	-0.933	0.177	-5.26	**<0.001**
Species richness open space aerial foragers				
MIG sides	-0.214	0.585	-0.37	0.715
MIG top	-1.506	0.241	-6.24	**<0.001**
Myotis species richness				
MIG all views	4.032	2.053	1.96	**0.049**

Table 5: ***Results of models conducted only with field parameters and models including MIG for bat activity and species richness, respectively.***

	Only field parameters				Including MIG parameters			
	Estimate	Standard error	t value	*P*	Estimate	Standard error	t value	*P*
Total bat activity								
0.5-1m	-1.017	0.239	-4.25	**<0.001**	-1.007	0.235	-4.28	**<0.001**
5-7m	-0.658	0.243	-2.71	**0.007**	-0.508	0.245	-2.07	**0.040**
Understory cover	0.153	0.021	7.17	**<0.001**	0.138	0.022	6.37	**<0.001**
Shannon index	0.040	0.011	3.70	**<0.001**	0.039	0.011	3.60	**<0.001**
Tree density	-47.386	23.863	-1.99	**0.049**	-36.355	23.783	-1.53	0.128
No. of trees	0.132	0.071	1.87	0.063	0.130	0.070	1.87	0.063
MIG top					-3.089	1.136	-2.72	**0.007**
Activity edge space aerial foragers								
0.5-1m	-0.936	0.300	-3.12	**0.002**	-0.780	0.277	-2.82	**0.005**
2-3m					0.566	0.285	1.98	**0.049**
5-7m	-0.453	0.304	-1.49	0.138				
Understory cover	0.136	0.027	5.10	**<0.001**	0.124	0.027	4.51	**<0.001**
Shannon index	0.034	0.014	2.49	**0.014**				
Tree density	-82.395	29.891	-2.76	**0.006**	-77.703	30.315	-2.56	**0.011**
No. of trees	0.219	0.089	2.47	**0.015**	0.252	0.088	2.87	**0.005**
MIG top					-3.124	1.404	-2.23	**0.027**
Activity open space aerial foragers								
0.5-1m	-0.840	0.290	-2.90	**0.004**	-0.777	0.281	-2.77	**0.006**
5-7m	-0.428	0.286	-1.50	0.136				
Understory cover	0.165	0.025	6.60	**<0.001**	0.152	0.026	5.94	**<0.001**
Shannon index	0.034	0.013	2.55	**0.012**	0.027	0.012	2.25	**0.026**

Tree density	-83.519	22.908	-3.65	**<0.001**	-81.754	20.808	-3.93	**<0.001**
MIG top					-3.565	1.353	-2.64	**0.009**
Activity *Nyctalus noctula*								
0.5-1m	-0.333	0.228	-1.46	0.146	-0.451	0.276	-1.64	0.104
5-7m	-0.735	0.193	-3.80	**<0.001**	-0.717	0.250	-2.87	**0.005**
10-15m	-1.383	0.728	-1.90	0.059	-1.221	0.802	-1.52	0.130
Understory cover	0.137	0.024	5.78	**<0.001**	0.142	0.024	5.99	**<0.001**
Water	0.268	0.159	1.69	0.094	0.224	0.159	1.41	0.159
Shannon index					0.019	0.013	1.52	0.130
MIG all views					-2.549	1.257	-2.03	**0.044**
Activity *Pipistrellus pygmaeus*								
0-0.5m	1.279	0.624	2.05	**0.042**	1.279	0.624	2.05	**0.042**
0.5-1m	-2.548	0.755	-3.38	**<0.001**	-2.548	0.755	-3.38	**<0.001**
5-7m	-1.496	0.655	-2.28	**0.024**	-1.496	0.655	-2.28	**0.024**
Understory cover	0.219	0.073	2.98	**0.003**	0.219	0.073	2.98	**0.003**
Shannon index	0.070	0.029	2.39	**0.018**	0.070	0.029	2.39	**0.018**
No. of trees	0.391	0.154	2.54	**0.012**	0.391	0.154	2.54	**0.012**
Total species richness								
5-7m	-0.373	0.102	-3.67	**<0.001**	-0.254	0.116	-2.19	**0.030**
Understory cover	0.005	0.001	4.78	**<0.001**	0.004	0.001	4.13	**<0.001**
MIG top					-0.464	0.222	-2.09	**0.038**
Species richness edge space aerial foragers								
Understory cover	0.004	0.001	4.10	**<0.001**	0.003	0.001	3.06	**0.003**
Tree density	-8.664	2.593	-3.34	**0.001**				
MIG top					-0.760	0.183	-4.16	**<0.001**

Species richness open space aerial foragers								
5-7m	-0.438	0.148	-2.97	**0.003**	-0.608	0.131	-4.64	**<0.001**
10-15m	-0.480	0.153	-3.14	**0.002**				
>15m					-0.569	0.204	-2.79	**0.006**
Understory cover	0.005	0.001	4.92	**<0.001**	0.005	0.001	4.35	**<0.001**
Species richness Myotis species								
1.5-2m	1.773	0.716	2.48	**0.014**	1.773	0.716	2.48	**0.014**
>15m	1.684	0.367	4.59	**<0.001**	1.684	0.367	4.59	**<0.001**
Understory cover	0.012	0.005	2.53	**0.012**	0.012	0.005	2.53	**0.012**

4. DISCUSSION

This study represents the first attempt to apply structural complexity measured from digital images at the microhabitat scale in an urban area. We tested the mean information gain (MIG) calculated from digital images as a predictor for bat activity and species richness, functional groups and representative species, and combined it with field data for comparison.

4.1 Influence of MIG and field parameters on total bat activity and species richness

Contrary to my expectations, structural complexity measured by MIG had no significant positive effect, neither on total bat activity nor on species richness when analyzing only the influence of MIG parameters. MIG side views had only a marginal positive impact on total bat activity, with this parameter curtly missing the significance level (p=0.058), while MIG top view showed a considerable negative influence (Table 4). This result indicates that areas with open canopy represent microhabitats where foraging activity for some bat species is facilitated. This is supported by previous findings where bat activity decreased with the relative area of canopy closure and increased with open canopy area (Ford et al., 2006; Kusch et al., 2004). Clutter in general, such as foliage and branches, has been shown to affect bat foraging behavior by complicating prey detection and pursuit (Brigham et al., 1997; Crome and Richards, 1988; Schnitzler et al., 2003). Nevertheless, heterogeneous vegetation captured by the images of the side views may have also played a role in the selection of the hunting sites as activity was almost positively associated with rising values of MIG sides.

Positive effect of vegetation elements for bat hunting grounds became also apparent when evaluating MIG and field parameters together, which indeed was limited by presence of canopy cover again. This is supported by the significant positive, although relative low influence of understory cover, Shannon and the almost positive significant number of trees. MIG top, representing canopy cover, was the strongest predictor, and had together with layer 5-7 m a significant negative influence, with layer 5-7 m also reflecting a strata belonging to tree canopy. Understory cover and Shannon likely contribute to higher insect availability. This has been confirmed by previous studies where understory cover and vegetation elements like hedgerows, and single trees have been shown to enhance insect abundance (Di Giulio et al., 2001; Grüebler et al., 2008), while trees were additionally found to offer shelter from wind and predation (Verboom and Spoelstra, 1999). The negative influence of MIG top and layer 5-7 m points at potential maneuvering and echolocation disadvantages due to tree canopy cover. Indeed, single scattered trees are likely favorable elements for bat hunting grounds, supported by the almost significant positive influence of number of trees. Scattered trees have been shown to be valuable habitat components for foraging insectivorous bats (Lumsden and Bennett, 2005). Foliage-free spaces between tree crowns were found to be more suitable for hunting bats as they combine high insect abundance and obstacle free spaces needed for foraging, while still providing some protection from aerial predators (Marques et al., 2015).

Similarly to total bat activity, MIG top also had a negative significant influence on total species richness when analyzing only MIG parameters, while MIG sides had no significant impact (Table 5). Canopy cover therefore seems to be disadvantageous to the majority of recorded species likely due to maneuverability and echolocation issues (Kusch et al., 2004). Results for total species richness might be influenced by the high occurrence of edge space foragers in this study (Fig. 5). Although species belonging to this group show intermediate wing morphology and therefore to some extent niche flexibility (Dietz et al., 2007), results suggest them to be associated with open canopy areas or canopy gaps. This is also supported by the outcome for total species richness when analyzing MIG and field parameters together. There MIG top was the strongest predictor, affecting species richness negatively together with layer 5-7 m, which represents also part of tree canopy. Understory cover was the only positive predictor, although with an evanescent low influence.

The negative relationship between species richness and structural complexity was surprising since heterogeneous environments are thought to comprise more niches and therefore cause rising number of species (Huston, 1979). Highest species richness was found at vineyards and cemeteries in this study, from which the majority were located at the city outskirts and characterized by decreased surrounding urbanization, while lowest species richness was detected in the inner city at the highly urbanized tree lines (Fig. 6). Hence, urbanization and with it habitat fragmentation and disturbance may be an important factor influencing species richness in urban areas, potentially at a greater scale than microhabitat heterogeneity. Same pattern was found in previous studies where species richness was shown to vary along the urban gradient, to diminish towards the core city area and to increase towards city-outskirts, peaking at forest outlying the urban area (Jung and Kalko, 2011). To date, only a few publications have demonstrated a positive relationship between image-derived habitat complexity and species richness (Proulx and Parrott, 2008; Mellin et al. 2012), indeed they were carried out in natural environments in contrast to the present study.

Another aspect of urbanization is dominance of bat species which may be reflected in my recordings where only six of 18 bat species occurred frequently, with five of them belonging to edge space foragers, while the rest was recorded at less than one third of sampling points (Fig. 5). Evidence for urbanization increasing dominance of a few bat species comes from former studies, with this factor leading to homogenization of urban species assemblages (Coleman and Barclay, 2012; Hourigan et al., 2010; Jung and Kalko, 2011; Kurta and Teramino, 1992; Loeb et al., 2009; Oprea et al., 2009). The high occurrence of edge space foragers presumably is reasoned by their broader niche flexibility in comparison to other functional groups and might be also a sign for homogenization. It is known that unpredictable or severe environments force organisms to have broader niches, which benefits fewer species and causes greater extinction dangers for marginal populations (Slobodkin, 1969; Usher and Pielou, 1976).

4.2 Influence of MIG and field parameters on functional groups

MIG sides had a clear positive tendency on activity of edge space foragers when evaluating only MIG parameters, curtly missing the significance level (p=0.057), while it had no effect at all on activity of open space aerial foragers (Table 4). Also, negative influence of MIG top was clearly higher for the open space foragers (Coefficient= -7.50) than for the edge space group (Coefficient= -4.48). Therefore, the negative response of functional groups to increased structural complexity was strongest for the open space foragers and weaker for the edge space foragers, with this group being less affected in its activity by structural clutter, as awaited. Bats belonging to the open space group hunt for airborne prey in open areas, are less agile and therefore morphologically not adapted to hunt within vegetation clutter as they need more space for collision avoidance (Denzinger and Schnitzler, 2013). In contrast, species of the edge space group are adapted to hunt in gaps but in the vicinity of background clutter, for which higher maneuverability is necessary for obstacle avoidance (Adams et al., 2009).

A similar trend was seen when both MIG and field parameters were analyzed together. Tree density, representing the strongest predictor, and MIG top had a higher negative impact on activity of the open space than on the edge space group. A former study has revealed the open space foragers to show higher avoidance of closed canopy areas than edge space foragers, which was ascribed to their different physiological tolerances to structural clutter (Crome and Richards, 1988). Also, layer 2-3 m and number of trees had a significant positive influence on activity of edge space foragers, again likely a sign for their hunting strategy in the vicinity of vegetation, with the stratum 2-3 m presumably representing bushes and juvenile trees.

Caution should be taken when interpreting the significant negative influence of tree density on functional groups as it potentially was induced by tree lines. Tree lines investigated as individual green area type could have been influential as they were characterized by high tree densities but had the lowest bat activity and species richness among all green area types. Though, they were located in the highly urbanized inner districts, wherefore the low activity and number of species recorded there might be rather caused by urbanization accompanied by its various disturbance factors than because of their high tree density.

Species richness of the functional groups followed a pattern similar to activity when analyzing only MIG parameters. MIG top had a greater negative impact on open space foragers (Coefficient= -1.51), again pointing at their lower tolerance to structural complexity of tree canopy compared to the edge space group (Coefficient= -0.93). Models analyzing MIG and field parameters together did not show this trend that clearly, but while species richness of the edge space aerial foragers was negatively affected only by one parameter (MIG top), the open space group showed negative impacts by two upper vegetation layers (5-7 m, >15 m), potentially also indicating a lower tolerance to vegetation clutter of tree canopy. This might be reasoned by greater flight heights of species belonging to the open space aerial foragers in comparison to the edge space group (Dietz et al., 2007; O´shea and Vaughan, 1980).

In contrast, a positive response to structural complexity was found for the Myotis group when evaluating influence of MIG parameters alone, confirmed by the significant positive influence of MIG all views (Coefficient=4.03). The Myotis genus contains only members of narrow and edge space foragers hunting within or near to vegetation. Consequently, they also share similar morphological traits like large-surfaced and broad wing morphology, making them agile flyers (Dietz et al., 2007), supporting the result that structural complexity has a positive effect on them. This outcome fits to previous findings where species with this morphology were found to occur in habitats of high structural complexity like forests (Estrada-Villegas et al., 2010; Bader et al., 2015). Also vegetation layer 1.5-2 m and >15 m increased their species richness when including both MIG and field parameters, with the former pointing at the positive effect of scrub vegetation, like bushes, and the latter at canopy of large mature trees. Species from this genus have already been shown to occur in areas with a high percentage of bushland cover (Threlfall et al., 2012) and tree cover (Dixon, 2012; Fabianek et al., 2011; Lesiński et al., 2000). Thus, urban woodlands are likely to be of major interest for conservation of Myotis species, which was also supported by my results. Threlfall et al. (2012) have revealed that areas with rich structured vegetation and high hollow density such as riparian forests are of importance for roosting habitats, which is known to be correlated with bat species richness (Basham et al., 2011). Wooded and riparian habitats have also been demonstrated to enhance bat foraging activity (Lesiński et al., 2000) and along the way to generally increase urban biodiversity (Savard et al., 2000).

Myotis species were clearly underrepresented in the present study. Except the grouped species *M. mystacinus/brandtii*, which together occurred at 32 % of sampling sites, they were only found at 8 % to 2 % of the sampling points (Fig. 5). Species sharing morphological characteristics of this group may be therefore of conservation priority. Also previous studies found them to be associated with higher extinction risk (Jones et al., 2003) and decreased occurrence in urban areas, which has been linked to their reduced mobility (Bader et al., 2015; Safi and Kerth, 2004) and light aversion (Rydell, 1992; Stone et al., 2012). Clutter-adapted species appear to be less adaptable and more sensitive to urbanization (Luck et al., 2013) and generally to habitat fragmentation (Frey-Ehrenbold et al., 2013). Therefore, future urban planning has to consider the restoration or the maintenance of particularly rich structured near-natural forests (Hüttmeir et al., 2010), serving as refuge for rare bat species like members of the Myotis group. Moreover, it might be necessary to take the reduced mobility of vulnerable bat species into account. To preserve species diversity in fragmented environments like urban matrices, conservation management should assure spatial proximity to source populations in larger areas of continuous forest and enable functional connectivity of green spaces (Hale et al., 2012; Meyer et al., 2007).

4.3 Influence of MIG and field parameters on single species

Pipistrellus pygmaeus was one of the most recorded species, occurring at 93 % of our sampling points (Fig. 5), although this species is very small and agile and therefore potentially shares morphology traits with rare bat species like Myotis sp. Park et al. (2012) already revealed this pattern in urban green spaces, where bat activity was primarily comprised of *P. pygmaeus,* appearing at 86 % of sites. The authors reason that the species is able to use even small patches of wooded green space in the urban matrix independently of the urbanization around it. *Pipistrellus pygmaeus* inhabits wooded riparian areas, but also roosts in human settlements, e.g. in house sidings (Dietz et al., 2007), which may be one main cause of its high occurrence in urban areas and also in the present study.

When analyzing only influence of MIG parameters, *P. pygmaeus* showed a positive response to vegetation complexity as MIG sides was positive significant for activity of this species. *Pipistrellus pygmaeus* is a member of the edge space guild and one of the smallest European species, morphologically highly maneuverable. It is known to be capable of hunting within or near to vegetation and to occur in urban woodland interior or edge habitat (Dietz et al., 2007; Lintott et al., 2015; Park et al., 2012). A similar trend was found when evaluating both MIG and field parameters, where *P. pygmaeus* showed a positive response to several vegetation elements. Its activity was positively influenced by understory cover, Shannon, number of trees and layer 0-0.5 m. Layer 0.5-1 m was representing the strongest predictor and had, together with 5-7 m a negative influence on activity of this species. A species´ tolerance to individual vegetation layers may depend on its ordinary flight height. Hence, layer 5-7 m is potentially overlapping with its average hunting altitude, consequently being disadvantageous. For *P.*

pygmaeus literature does not offer information on flight heights as it has only recently been discovered as individual species through genetic analyses and was not distinguished from the morphologically highly similar *P. pipistrellus* before (Hüttmeir et al., 2010). Nevertheless, it presumably hunts at lower altitudes (Plank et al., 2012) like *P. pipistrellus,* from which it is known that it does between two and six meters height (Richarz and Limbrunner, 1992). Therefore, layer 0.5-1 m might disturb echolocation for *P. Pygmaeus* as it is in the vicinity of its lower hunting threshold.

Nyctalus noctula was recorded at 88 % of all sampling points, also representing one of the most successful species in occurrence probability (Fig. 5). Although it is originally an inhabitant of riparian areas and deciduous forests, using hollow bearing trees, it also makes use of human settlements (Dietz et al., 2007). The good roosting possibilities in housing estates, consisting of prefabricated panel buildings, likely contribute to the success of *N. noctula* in urban areas (Bihari, 2004).

By contrast to *P. pygmaeus*, *N. noctula* was found to have a negative response to structural complexity, supported by the negative impact of MIG top when evaluating only influence of MIG parameters. This result suggests that areas with dense tree canopy are no suitable foraging grounds for this species. *Nyctalus noctula* belongs to the open space aerial foragers and is one of the largest species, hunting mainly at higher altitudes in open areas (Richarz and Limbrunner, 1992), wherefore presence of canopy likely is unfavorable. *Nyctalus noctula* was also found to be negatively affected by structural complexity when analyzing influence of MIG and field parameters together. Here, inclusion of MIG five views had a stronger effect than MIG sides and MIG top. MIG five views represented the strongest predictor and had, together with layer 5-7 m a negative influence on activity of this species, while understory cover was the only vegetation parameter with a positive effect. Layer 10-15 m was almost negative significant in the model analyzing only field parameters. *Nyctalus noctula* flies at heights of more than 100 meters, but hunts within a range of five to twenty meters (Richarz and Limbrunner, 1992), wherefore particularly the two upper layers 5-7 m and > 15 m belonging to the tree canopy may be unfavorable.

4.4 Comparison of digital images and field method

I hypothesized that incorporation of MIG into models conducted only with field parameters should result in improved predictive power. This was the case for all models concerning bat activity (except for *P. pygmaeus*), where a higher percentage of variance was explained and a lower AIC obtained when including MIG into the model. Yet, model improvement was slight, reaching from 0.8 % for activity of *N. noctula* to 2.9 % for total bat activity (Table 4). There are different possible reasons why model improvement was not better. I showed that MIG´s performance to depict vegetation structures was by approximation quite good as MIG was correlated with canopy cover, tree density, vegetation height, the Shannon index of vegetation layers, and number of trees (Fig. 7). These correlations suggest that MIG satisfyingly captures vegetation complexity. But, MIG may here not contain relevant additional information about vegetation complexity to data collected in the field, therefore underlying data redundancy. MIG top indeed included information about the canopy and had a significant effect in most models, but presumably replaced the parameter canopy cover which was removed in the forefront of the modelling approaches due to high collinearity. An exception was the model for *N. noctula*, where MIG of all views remained negative significant in the fitted model. Models conducted singly with field data in general showed higher explanatory power compared to models analyzing only MIG. Field parameters have presumably therefore behaved better because they contain potentially differing information which is summed up in the MIG in a few photographs, but worthy to divide here, as shown in the diverging influence of single vegetation layers for example.

Potential limitations of MIG in urban areas could downgrade its efficiency compared to the field method. Field data here contained measurements at every five meters of the sampling plot, while images were taken only from one point in the middle. In this manner, field data may contain more information depending on the sampling point and its structural arrangement. The relative size of vegetation or anthropogenic structures to each other can have an undesirable influence on MIG, potentially causing “masking effects” described hereafter. If directly adjacent structures of any kind are larger in relation to others located behind them or if they completely cover the image, they are concealing structural attributes which can be of totally different appearance in a highly fragmented area like a metropolis, in contrast to natural areas. In such cases, part of the structural characteristics of a site is not captured by MIG, but with data of the field method. It is also possible that anthropogenic structures occurring in urban environments influence the performance of MIG as a predictor. I have sampled green areas of Vienna, yet that does not mean they contain only vegetation. Buildings, cars, fences and other human-made artificial structures, especially in the scenery of housing units and tree lines, potentially alter heterogeneity of digital images and therefore MIG. Digital images take every structure of the scenery into account, while data collected with the field method takes only vegetation into account. If and to what extent anthropogenic structures change image heterogeneity remains to be further investigated but supposedly depends on their size, form, distance from the camera as well as their abundance. MIG as a measure of structural complexity was originally applied to forests (Proulx and Parrott, 2009, 2008) and also in marine habitats (Mellin et al., 2012), while other complexity metrics (e.g. second moment, homogeneity) were used in semi-arid landscapes (Bellis et al., 2008; Oldeland et al., 2010; St-Louis et al., 2006). All these represent natural environments, wherefore the potentially different efficiency of image-derived complexity measures in highly fragmented and modified urban areas in comparison to natural environments calls for further research.

Nevertheless, the strengths of structural complexity measured from digital images were apparent. MIG parameters analyzed separately were found to have profound effects on bat activity and species richness of Vienna´s bats and to show considerable explanatory power in comparison to models including only field parameters. It is still remarkable that models performed with only MIG parameters accounted for almost one fourth (*P.pygmaeus*) up to half (open space foragers) of the variance explained by models evaluating only field parameters for bat activity (Table 4), given the relative small effort for its sampling. While photographs were taken in a very brief time period, record of field data lasted up to two hours for forest sites e.g., depending on the vegetation at the sampling points. My results suggest MIG, as complexity measure for the microhabitat scale, is potentially a useful tool in assessing species-habitat relationships, also in urban environments. To improve this method, I indeed recommend enlarging the amount of images taken per site to enhance information content and reduce potential masking effects occurring in urban areas. To the basis of the four images taken outwards from the middle of a sampling plot, photographs could also be taken from the outer borders inwards for example, or depending on the site-specific structure arrangement at different distances in the buffer, similar to the recordings of the field data. Furthermore, the investigation of different spatial scales may be advantageous and likely enhancing model explanatory power. Habitat selection and distributional patterns of bats are known to be influenced by a complex interplay of multiple spatial scales, including attributes from the local or microhabitat scale up to those from the geographic or landscape scale (Ford et al., 2006; Gehrt and Chelsvig, 2003; Loeb and O’Keefe, 2006). In addition, MIG might worth being tested in combination with remotely sensed imagery in urban environments, as it would deliver multi-scale information with relative little effort. This approach has been successfully tested in the Great Barrier Reef, where MIG has been shown to work scale-independently (Mellin et al., 2012).

4.5 Conclusions

I have demonstrated that MIG, as image-derived complexity measure, can be a useful predictor of bat activity and species richness at the microhabitat scale in urban environments. My results suggest that image-derived structural complexity is a time- and cost-effective tool for depicting complexity of vegetation. I have shown its ability to at least partly replace field data with the advantage of considerable time saving. Still, models analyzing only MIG parameters had a lower predictive power than those conducted with parameters of the field method alone, while including MIG only slightly improved them. Therefore, I recommend to increase the amount of images per site to enhance information content and with it potentially model predictive power. MIGs efficiency in human-modified urban areas in comparison to natural environments indeed remains to be further investigated as anthropogenic structures and habitat fragmentation might affect it. Moreover, my results indicate that responses of bats to structural complexity are group- as well as species-specific, consistent with existing literature. Edge and open space foragers were negatively influenced by MIG of the top view, which illustrates structural complexity of canopy cover. Hereby, open space foragers showed a stronger negative response than edge space foragers, indicating a lower tolerance to structural complexity of this group. In contrast, species of the Myotis genus exhibited a positive response to increasing MIG of all views, suggesting a high tolerance to structural complexity and the importance of structure-rich areas like forests. Myotis species occurred rarely, which may be because insufficient structural complexity of green areas, pointing at the need for conservation management to maintain or restore structurally complex areas with forest cover for this genus. *Nyctalus noctula,* an open space forager, showed a negative response to structural complexity, whereas *Pipistrellus pygmaeus,* an edge space forager, was positively influenced by increasing complexity. The group- and species-specific response to structural complexity of microhabitat points at the importance of maintaining habitat heterogeneity within the urban matrix for conservation of total bat diversity.

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