Universität Greifswald

Bioacoustic survey of habitat use of bats in a protected Central European floodplain forest and its adjacent human-dominated landscape

Bioakustisches Monitoring zur Habitatnutzung von Fledermäusen in einem geschützten Auwald in Mitteleuropa und der angrenzenden, vom Menschen geprägten Landschaft

Master thesis in master's Program 'Landscape Ecology and Nature Conservation' to obtain the academic degree "Master of Science" (M.Sc.)

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Abstract

Bat populations are at risk of declining due to a variety of factors, including landuse change. Nature reserves can help to increase or stabilize species diversity. In agricultural areas, landscape elements can have this effect to a smaller extent. For this study I conducted a bioacoustic monitoring to measure bat activity and species richness for different habitats inside a national park and in surrounding landscape elements. In the study area (*Nationalpark Donau-Auen),* a floodplain forest along the Danube and the agricultural landscape around, a total of 352 points were sampled. Besides analysing the possible benefits for species diversity in a protected area, the impacts of a flooding event on bat activity levels, in the protected floodplain forest, were examined. The question whether a mosaic landscape is beneficial for bat occurrence in comparison to a contiguous forest was studied as well. Results show that activity levels differed significantly between the protected forest and the agriculturally used landscape around. Also inside the national park significant differences in bat activity between some habitats were found. The same applies to the non-protected habitats. In both sample areas, densely vegetated habitats were the ones with lowest bat species richness and activity. Generally guild and species-specific preferences in habitat use were found. The examined flooding event had no measurable effect on bat activity. The study showed that a well protected mosaic landscape, as it is found in the *Nationalpark Donau-Auen*, can contribute to higher species richness.

Zusammenfassung

Fledermauspopulationen sind durch eine Vielzahl von Faktoren, unter anderem durch Landnutzungswandel, vom Rückgang bedroht. Naturschutzgebiete können dazu beitragen, die Artenvielfalt zu erhöhen oder zu stabilisieren. In landwirtschaftlich genutzten Gebieten können Landschaftselemente in kleinerem Maß für eine solche Wirkung sorgen. Für diese Studie habe ich ein bioakustisches Monitoring durchgeführt, um die Fledermausaktivität und den Artenreichtum in verschiedenen Habitaten innerhalb eines Nationalparks, sowie in Landschaftselementen in der Umgebung zu messen. Im Untersuchungsgebiet (Nationalpark Donau-Auen), einem Auwald entlang der Donau und der umgebenden Agrarlandschaft, wurden insgesamt 352 Punkte beprobt. Neben der Analyse des möglichen Nutzens eines Schutzgebiets für die Artenvielfalt, wurden auch die Auswirkungen eines Hochwasserereignisses auf die Fledermausaktivität im geschützten Auwald untersucht. Auch die Frage, ob eine Mosaiklandschaft im Vergleich zu einem zusammenhängenden Waldgebiet für das Vorkommen von Fledermäusen von Vorteil ist, wurde untersucht. Die Ergebnisse zeigen, dass sich die Aktivität zwischen dem geschützten Auwald und der umliegenden landwirtschaftlich genutzten Fläche deutlich unterscheidet. Auch innerhalb des Nationalparks wurden signifikante Unterschiede in der Fledermausaktivität zwischen einigen Habitaten festgestellt. Das Gleiche gilt für die nicht geschützten Lebensräume. In beiden Untersuchungsgebieten waren die dicht bewachsenen Habitate diejenigen mit dem geringsten Artenreichtum und der geringsten Aktivität von Fledermäusen. Es wurden gilden- und artspezifische Präferenzen bei der Habitatnutzung festgestellt. Das untersuchte Hochwasserereignis hatte keinen messbaren Einfluss auf die Aktivität. Eine gut geschützte Mosaiklandschaft, wie sie in den Donau-Auen vorzufinden ist, kann zu einem höheren Artenreichtum beitragen.

1 Introduction

With more than 1400 species worldwide bats belong to the second largest order of mammals (Lu et al., 2021). Although they play an important role for our ecosystems and 15 % of the world´s bat species are endangered or not enough data on their status are available (18 %) (IUCN 2022), publications on conservation measures are insufficiently represented (Voigt & Kingston, 2016). Bats have occupied diverse niches on every continent except for Antarctica (Jones et al., 2009) whereas the highest species richness can be found in the tropics (Dietz & Kiefer, 2020).

Besides protecting bats out of ethical reasons they fulfil several monetary benefits to humans, which are defined as ecosystem services (Voigt & Kingston, 2016; Russo et al., 2016). In the tropics they contribute to pollination of economically important fruits, they serve as top-down predators for insects in tropical and temperate forests and play an important role for pest control, which can be an important benefit in agricultural regions (Voigt & Kingston, 2016; Jones et al., 2009; Russo et al., 2018; Heim et al., 2018; Park, 2015).

Bats reproduce slowly. A female usually gives birth to one or two young that she will nurse for up to ten weeks. Additionally, most species in Europe do not reach sexual maturity until the first year of age (Dietz & Kiefer, 2020). Therefore, bats are susceptible to degradation of their habitats. Forest loss, habitat fragmentation, urbanization, intensive agriculture, light pollution and declining water quality are the biggest threats to bat populations in Europe (e.g. Jones et al., 2009; Park, 2015; De Conno et al., 2018). The main problem they cause is the loss or at least reduction of potential roosting sites and a reduced prey availability. In Europe, all bat species have an insectivorous diet and feed, amongst others, on moths and chironomides (Skiba, 2009). With an intensification of agriculture accompanied by a higher use of pesticides, the insect populations in agricultural areas decrease (Wickramasinghe et al., 2004). As shown by Wickramasinghe et al., bat activity is generally higher on organic farms with a lower use of pesticides in comparison to conventional farming (2003). Besides pesticides the loss of structures like hedgerows and field margins contribute to lower bat activity. These vertical landscape features not only support insect density, but also serve as flight paths and foraging spaces for bats in agricultural regions. Even in protected areas the insect biomass is shrinking. With a decline of 76 % in the last 27 years, prey availability for bats is shrinking drastically, as not only vulnerable insect species decline, but the whole insect community (Hallmann et al., 2017).

To prevent bat populations from further decline they were included in the EU Habitats Directive 92/43/CEE. They are listed under the Annexes II and IV. In Austria – where the study was conducted – 28 different bat species are native. In comparison to the world's red list status most Austrian bats are not directly threatened by extinction. Still, nearly 13 % need further protection to increase their population levels to not become extinct (IUCN 2022). According to the IUCN the biggest hazard to bats in Austria are humans by intruding their habitats for agriculture, recreational and forestry purposes (2022).

1.1 Sate of research on bats

In research there is an increasing interest of using bats as bioindicators for land-use changes (e.g. Russo & Jones, 2015; Jones et al., 2009). Due to their slow reproduction rates, high species diversity and habitat requirements, they are assumed to be an optimal taxa to indicate habitat changes that will affect the whole species composition, as population declines in bats are observed rapidly (e.g. De Conno et al., 2018; Jones et al., 2009). To collect information on bats several options exist. For species identification they can either be caught by mist netting, roosts are controlled either personally, with photo traps or acoustic monitoring methods are used in foraging areas. Acoustic sampling, as it was used for this study, is very cost effective and can provide a huge amount of data in a short time. Still the method has disadvantages, like inaccurate species determination if not conducted properly. Bat echolocation calls of some species are hard to determine as their calls vary from age, sex and geographic location (Russo & Voigt, 2016).

1.1.1 Bats and wetlands

Wetlands only comprise around 6 % of the worlds land masses but play an ecologically important role (for comparison: forests cover 30 % of the land mass) (Mas et al., 2021). Besides providing habitat refugia and foraging grounds to many animals, wetlands are important for humans as well. They contribute to nutrient cycling, food production, water supply and flood mitigation to only name a few of their biggest advantages (Kingsford et al., 2016). In a recently published paper by Froidevaux et al., the concept of guilds is applied to a study in a floodplain landscape in the Mediterranean that is agriculturally used (2022). Studies on bats in floodplain areas and generally wetlands rarely exist, in comparison to other ecosystems (Salvarina, 2016). Wetlands mostly influence bat activity and species richness in a positive way, as they provide foraging grounds rich in prey and serve as drinking sites (Mas et al., 2021; Straka et al., 2016). The wetland size, vegetation cover and water quality play a decisive role for bat activity and species richness (Mas et al., 2021; Torrent et al., 2018). Generally, tree cover in or around wetlands favours bat activity, only species that are less manoeuvrable like *N. noctula* or *N. leisleri* tend to avoid these areas (Straka et al., 2016). In definition, 'wetlands' is already a term compromising many forms of aquatic habitats that are shaped completely different, e.g. a lagoon and a floodplain forest are not comparable in most respects. This makes it harder to generalize implementations for bat conservation (Mas et al., 2021). Nevertheless, there is no doubt about the importance of the preservation of wetlands as a unique biotope and as a measure for bat conservation.

1.1.2 Conservation measures for bats

Knowing what threatens bats the most is critical to implement effective conservation measures. Since species diversity in bats is huge and thus includes different habits, the answer to the question is not simplistic (Dietz & Kiefer, 2020; Jones et al., 2009). Setting focus on e.g. roost preferences or foraging, it gets obvious that requirements vary greatly between species (Russo et al., 2016). While forest bats like *B. barbastellus* or *M. bechsteinii* prefer cavities in living trees or deadwood, other species, e.g. *P. auritus* or *P. pipistrellus,* live close to humans and can be found in roof trusses and behind house fronts (Russo et al., 2016). Therefore every implemented conservation measure is useful for a particular species but not all will benefit from it alike.

Landscape elements

Landscape elements and their preservation are important biodiversity conservation measures in managed agricultural areas. Examples for such elements are hedgerows, single trees or water bodies (Ancillotto et al., 2019; Heim et al., 2015). Besides source of nutrition and shelter, they serve as corridors for animals by linking fragmented habitats. Although bats are very mobile they still benefit greatly from the protective function, as they can hide from strong winds or using the elements as a shelter from predators. Especially bats that use high echolocation calls for foraging avoid wide open areas and preferably hunt close to vegetation (Heim et al., 2015) and particularly profit from landscape elements. Several studies on agriculture and bat activity showed, that intensive farming reduces the activity mainly due to shrinking insect populations (Froidevaux et al., 2022; Park, 2015; Wickramasinghe et al., 2003). To counteract this trend more heterogeneous fields (Barré et al., 2018), a more wildlife-friendly farm management (Wickramasinghe et al., 2003) and landscape elements (Heim et al., 2015) can help to increase bat activity even in intensively used agricultural areas. Some bat species are adapted to forage in vegetation, like almost all *Myotis* species, and therefore benefit of high hedges and trees more than open-space foragers like e.g. *N. noctula* (Toffoli, 2016). The same was observed for vegetation around ponds and other water bodies (Ancillotto et al., 2019; Heim et al., 2018). The latter ones serve as important landscape elements themselves. Especially rivers and creeks are features that are not as easily changed by agricultural practices as e.g. a hedgerow (Lundy & Montgomery, 2010). Bat activity around water bodies is high and they are crucial for bats in intensified agricultural areas. Besides foraging grounds (due to an increased prey availability) they also serve as drinking sites (Heim et al., 2018).

Protection areas

Better than only small patches of intact vegetation, are huge areas with little or no human interference. Several studies have demonstrated that species richness is higher in protected nature reserves than in the surroundings that are often highly urbanized or agriculturally used (Buckman-Sewald et al., 2014; Kerbiriou et al., 2018; Smith et al., 2016). To evaluate the exact effect, a conservation area has on bats, a closer look has to be taken on each bat species as their habitat requirements are highly variable. Still the study conducted by Kerbiriou et al. on bats in Natura 2000 areas across Europe has shown that both, the bat activity and the species richness were higher in the Natura 2000 areas, than in the surrounding non-protected landscape (2018). The

study of Zehetmair et al. on the other hand showed no significant increase of bats in a protected beech forest in comparison to an economically used one (2015). A reason for the low effectiveness could be the short protection time range of the beech forest as habitat quality only starts to increase after decades (Zehetmair et al., 2015).
In Europe and North-America a lot of studies on bats and forests exist (Drake et al., 2020; Russo et al., 2010, 2016) but as not all bats live and forage in woodlands, it is important to see, whether other protected habitats than mere forests have a positive impact on bat conservation as well and if different bat species could be targeted by it. For insectivorous bats riparian habitats are of greatest importance, as they serve as major foraging grounds and drinking sites (Jones et al., 2009). With the Ramsar Convention and Natura 2000 some effective protection already exists in Europe but many ecosystems, e.g. wetlands are still degrading worldwide (Mas et al., 2021).

Mosaic landscape vs. continuous forest

Despite their small size bats can travel long distances (Heim et al., 2015). Therefore, one may question whether a contiguous forested area is of greater importance to bat species diversity than a fragmented mosaic landscape of meadows, forest and agriculture. Bat species that preferably forage at vegetation edges, like *P. pygmaeus,* could benefit of fragmented forest patches as their foraging area is increasing and their paths from roosting to foraging ground is shorter in comparison to a huge continuos forest (Ethier & Fahrig, 2011). The study of ETHIER & FAHRIG conducted in North-America came to the conclusion that a moderately fragmented landscape with diverse land cover types can increase bat activity and species diversity (2011). Besides quantity, the quality of the existing mosaic patches has a huge influence on bats. This valuation is shared by CIECHANOWSKI who found out that besides forest cover, riparian vegetation, water quality and tree lines in agricultural fields are of relevance for bat protection (2015). Also typical forest-dwelling bats like *B. barbastellus* can profit from open spaces as shown by ANCILLOTTO ET AL. (2015). Rocky and riparian sites, agricultural and even urban areas were used by the observed bats for foraging. The amount of use was closely linked to prey availability (Ancillotto et al., 2015). When talking about fragmentation, urbanized areas also need to be taken into account as urbanization is a still ongoing process. Several studies on bats and urbanization exist (e.g.Hale et al., 2012; Li & Kalcounis-Rueppell, 2018). Due to habitat loss, barrier effects, chemicals, light illumination and an increased predator density (especially cats) urban areas do not favour bat occurrence (Russo & Ancillotto, 2015). Still the responses are species-specific whereas flexible species dominate in urban areas at the expense of more specialized ones (Russo & Ancillotto, 2015). Synanthropic species like *P. kuhlii* or *H. savii* can profit to a certain degree of urban structures as more roosts are available around buildings and bridges (Russo & Ancillotto, 2015). In general, highly urbanized areas have a negative influence on bat activity and abundance.

1.2 Hypothesis and question

To investigate the relevance of protected floodplain forests for species diversity in comparison to the, human shaped surrounding landscape, a bat monitoring was conducted. The aim was to examine whether a protected area shows higher activity levels and species richness in comparison to the agriculturally used surrounding. Additionally more data on habitat preferences of bat species should be gained. Only with this knowledge useful conservation measures can be implemented to protect certain species. With this objective several hypothesis and aims were formulated and investigated in the course of this thesis.

(1) I expect higher bat species richness and activity in the national park in comparison to the landscape elements in the agricultural buffer zone.

(2) Higher activity rates south of the dam after a flooding event, due to higher prey availability with an increase of standing water puddles. The northern part of the national park does not get flooded because of the dam.

(3) Is it beneficial for bats to keep areas, like meadows, artificially open in a floodplain forest?
I expect a species-specific, or at least guild specific, reaction to meadows and other open water areas in comparison to closed forest cover.

(4) Are some landscape elements outside the NP more advantageous for bats than others?
I expect gravel pits to be more beneficial for bats than all other landscape elements as they are mostly surrounded by vegetation, filled with water (Fig. 2c) and fulfil the requirements to serve as optimal foraging ground for bats in the *Marchfeld.*

(5) Do different echolocation guilds prefer different foraging grounds?
I would expect LRE to preferably forage in open areas like meadows, Sutten and around water while SRE prefer forest tracks. MRE I expect to be found most around vegetation edges, so also on forest tracks and meadow borders close to forest.

2 Material and Methods

To investigate and answer the questions/ hypothesis postulated before, a bioacoustic monitoring was conducted in the Danube floodplains in Lower Austria.

2.1 Study site

The studied area is located in Austria, east of Vienna. The floodplain forest located along the Danube is protected as a national park until the Slovakian border (Fig. 1).

2.1.1 *Nationalpark Donau-Auen*

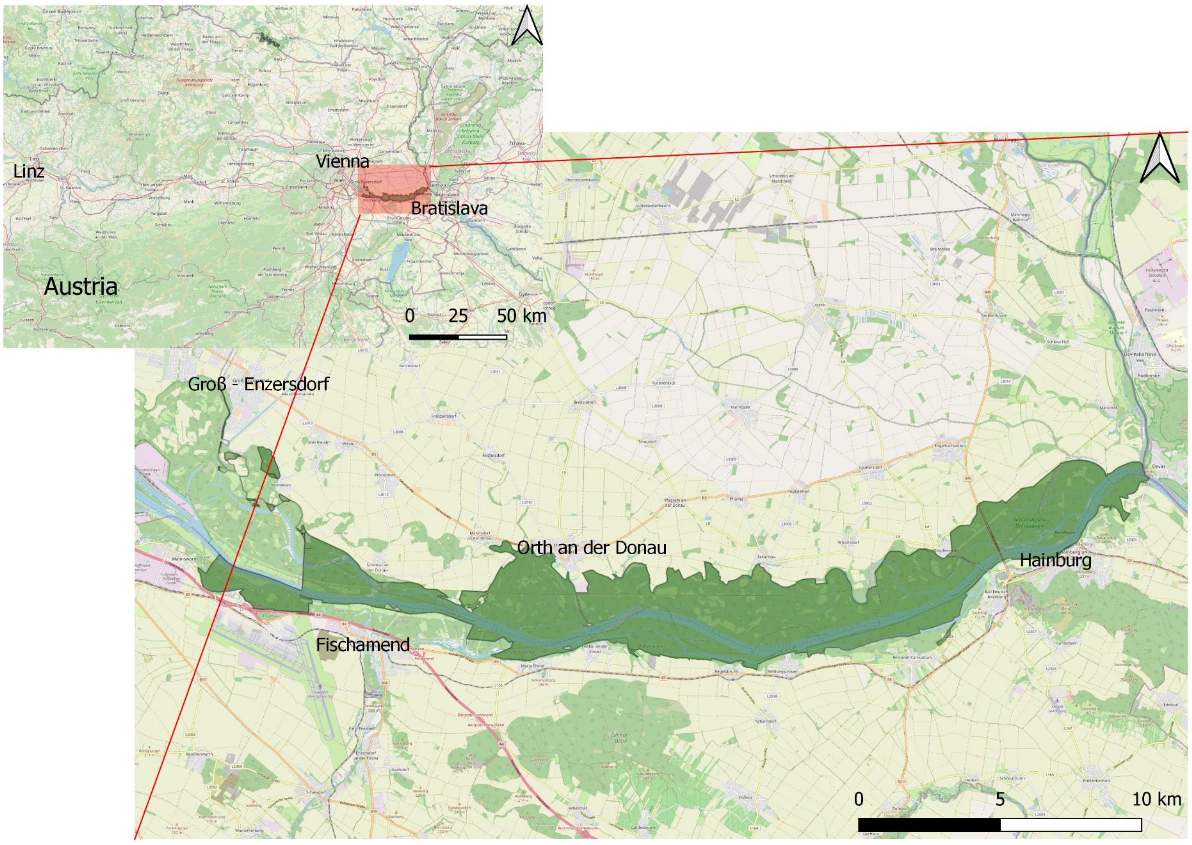

Fig. 1 *Borders of the Nationalpark Donau-Auen in Lower Austria (displayed in Open Street Maps 09/2022)*

The *Donau-Auen* are a floodplain national park located in Vienna and Lower Austria. For this study only the part in Lower Austria was sampled. It includes the major part of the protected area (Fig.1). The park forms a green band between the two cities Vienna and Bratislava. The total area of the park covers more than 9600 ha, whereof 65 % consist of floodplain forest, 15 % of meadows and 20 % are water areas (Donau-Auen, 2022). Since 1996 the Danube floodplain area, in the most eastern part of Austria, is declared as a national park. With water level fluctuations of up to seven meters the area gets flooded regularly and dynamic habitats are formed (Donau-Auen, 2022). In the core zone of the park no human interferences occur, while in the next outer zone conservation objectives like mowing are allowed and conducted. The *Nationalpark Donau-Auen* is divided by a dam which prevents the northern part to be flooded regularly. As floodplain forests only occur close to water areas the widest point of the park measures only four kilometres. The *Donau-Auen* are characterised by typical floodplain vegetation like Black poplar (*Popolus nigra*) and White willows (*Salix alba*) but also typical deciduous forest vegetation like Common oak (*Quercus robur*) can be found (Donau-Auen, 2022). Besides forest, water areas and meadows shape the appearance of the *Donau-Auen* (Fig. 2a, b). The latter ones are consciously preserved. Therefore they are mowed up to two times a year (Donau-Auen, 2022). In the park, the Danube and its sidearms are tried to be given back their natural morphological structure, to enable a regular flooding of the area, which is crucial to preserve the specific floodplain species composition (Donau-Auen, 2022). Data on bats in the Danube floodplains exist only sporadically. Nevertheless, an extensive monitoring was conducted in 2016 & 2017 by BÜRGER & PLANK in the national park and the surrounding villages (2017).

2.1.2 *Marchfeld*

Fig. 2 *Sampled habitat types in the Donau-Auen (a,b) and the Marchfeld (c,d). (a: Meadow south of the dam, b: Danube, c: Gravel pit, d: Woodland patch in between agricultural fields)*

The *Marchfeld* comprises an area of about 100.000 ha and is located in Vienna and to a major part in Lower Austria. It lies in a sedimentary basin and in one of the largest plains in Austria (Stadt Wien). It is shaped by little villages and agriculture. Despite the dry and hot summers, the region is the most important vegetable supplier for Vienna (Stadt Wien). In the *Marchfeld* a buffer zone around the *Nationalpark Donau-Auen* was sampled (Fig. 3). A clear cut between national park forest and the *Marchfeld,* with its huge agricultural fields is visible on the open street map image (Fig. 1). Little landscape elements however still exist and were used as sample points in the monitoring conducted for this thesis. Small woodland patches that are placed in between the agricultural fields, vegetated water creeks that are linked with the national park, Sutten (wet areas that occur in depressions at agricultural areas after snow melting) and gravel pits were sampled (Fig. 2c, d & 3). The latter ones are not used any more, filled with water and surrounded by vegetation.

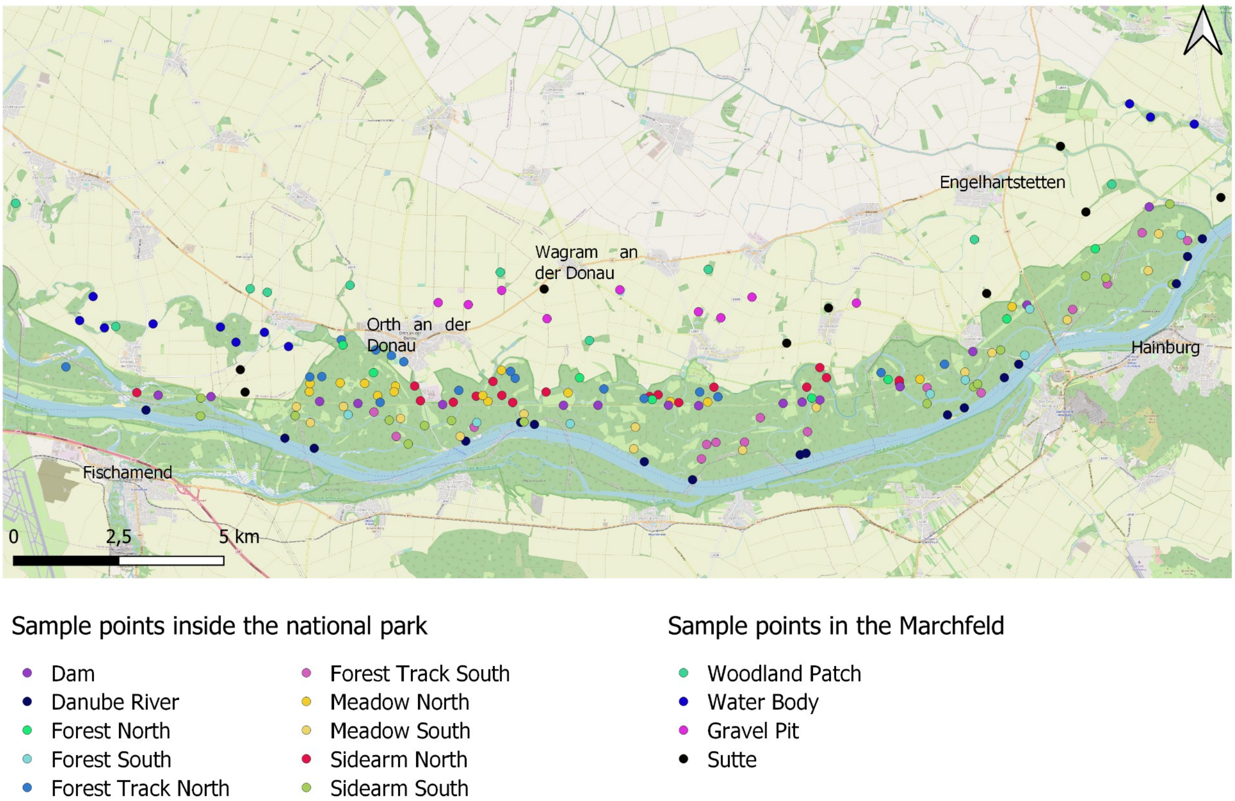

***Fig. 3** Map of the national park and its surrounding showing the sample points of the 14 different habitat types. (displayed in Open Street Map)*

2.2 Sampling design

From May to September 2021 a bioacoustic bat monitoring was carried out in the *Nationalpark Donau-Auen* and in a buffer zone of 2.5 km in the *Marchfeld*. 184 points were sampled twice – except for 16 points, which were only sampled once due to their insufficiently explanatory power – respectively for one night during the summer months. To record bat calls, special devices are necessary. These so-called batcorders digitally record ultrasonic signals in real time and use an online analysis tool to distinguish between bat calls and ultrasound signals from other acoustic sources, e.g. crickets (Plank et al., 2012). For this study six batcorders from *ecoObs Nürnberg* were used. Half of them were batcorder 2.0 while the other half were newer versions – batcorder 3.1. The devices were provided by the *Nationalpark Donau-Auen*, the University of Vienna and a landscape planning bureau (TB Raab). A calibration of each batcorder microphone was done before starting the monitoring and the settings were adapted accordingly. For the advanced settings the default values of the batcorders were used (Quality: 20, Threshold: -27db, Posttrigger: 400ms, Noise Filter: off). Only the frequency was changed (critical frequency: 14kHz) to record bat calls down to a frequency of 14 kHz.

Fig. 4 *Batcorder 3.1 set up on a telescope stick in 2 m height*

During the installation of the devices proximity to vegetation was avoided to reduce the amount of noise. Therefore the batcorders were placed at a pole in a height of 1.5 – 2 m and in a distance of 2 m to higher vegetation, as far as possible (Fig. 4). Recording time was set from one hour before sunset until one hour after sunrise. During the day the SD cards were changed and the sound- as well as the logfiles were saved.

2.2.1 Determination of sampling points

The study design of the bat monitoring is based on an unfinished master thesis (S. Flieth, 2014, unpublished). Back then 162 points out of ten habitat groups were sampled one night from May to October. Since the thesis was not finished, data were not sufficient to use them as a comparison for the monitoring of 2021. In the current monitoring 184 points were sampled. For the study the national park was divided into six different habitats. Four of them – forest, forest tracks, meadows and sidearms of the Danube – were respectively divided into north and south of the dam to examine if a flooding event influences bat activity in the national park (Table 1).

Table 1 *Sampled habitat types, their acronyms and number of sampled points. The habitats in italics are in the national park while the other ones lie outside the park.*

Habitat Type	**Acronym**	**No. of sample points**
Sidearm North	*SAN*	18
Sidearm South	*SAS*	16
Forest North	*FN*	8
Forest South	*FS*	8
Meadow North	*MN*	15
Meadow South	*MS*	15
Forest Track North	*FTN*	16
Forest Track South	*FTS*	16
Dam	*DA*	16
Danube River	*DR*	17
Water Body	WB	11
Woodland Patch	WP	10
Gravel Pit	GP	9
Sutte	SU	9

Most of the sampling points of the 2014 monitoring were used again in 2021, only some points had to be adapted, as a sidearm of the Danube was renaturated and some places were not accessible any more. Additionally to the ten habitat groups in the national park, four habitat groups outside the park were added (Table 1). In the *Donau-Auen* a total of 145 points was sampled, while 39 points were sampled outside the park (Table 1). The selection of sampling sites in the *Marchfeld* was based on satellite images from Google. Since the surroundings of the national park are used by agriculture, landscape elements were selected that were likely to be used by bats for foraging. Due to logistical reasons the sampled buffer zone in the *Marchfeld* was kept at a maximum distance of 2.5 km from the national park (NP).

2.2.2 Environmental parameters

Additionally to bat calls, environmental, respectively meteorological (temperature, wind, cloud cover, rain, moon illumination) and other parameters (distance to next village, light pollution, distance to next water body) were considered for each night or sample point (Table 2). Batcorder 3.1 measures the temperature automatically. Therefore the minimum and maximum temperature for each site could be specified. The older version, batcorder 2.0, does not have that feature yet, hence the minimum and maximum temperature data are only available for half of the recordings.

***Table 2** Parameters that were taken into account to explain bat activity levels and species richness in the sampled area*

Variable	**Description**	**Unit**
Wind	Average wind speed per night	km/h
Wind max.	Maximum wind speed per night	km/h
Wind min.	Minimum wind speed per night	km/h
Temperature	Average temperature per night	°C
Temperature max.	Maximum temperature per night	°C
Temperature min.	Minimum temperature per night	°C
Rain	Amount of rain for one night	mm
Habitat	14 different habitat types (10 inside and 4 outside the national park)	
Cloud cover	average cloud cover per night	%
Moon illumination	Percentage of the moon that is illuminated by the sun	%
Light level	Increase of natural lightning levels caused by anthropogenic sources of light	$mag/arcsec^2$
Distance to next village	Distance to the next village (beeline)	km
Distance to next water body	Distance to the next water body (beeline)	km

All other parameters were not measured single-handed but taken from a meteorological station. The mean temperature, wind speed (mean, maximum and minimum) as well as rainfall per night were taken from the website *meteostat.net*. The climate data from the web page, were all taken from the closest meteorological station 'Wien-Schwechat' and are provided by NOAA (National Oceanic and Atmospheric Administration), DWD (Deutscher Wetterdienst) and Environment Canada. Cloud cover data come from the same weather station and were found on *kachelmannwetter.com,* while moon illumination data were taken from *timeanddate.de*. Distance to the next village respectively water body were measured in beeline in QGIS 3.16.5. The light pollution data were taken from the light pollution map of J. STARE for each sample point.

2.3 Sampling

Sampling took place from 01/05/21 to 19/09/21. In this period every point from each habitat group was sampled for two nights, except for the groups Forest North and Forest South. Those points were only sampled once, as only very few calls could be detected in the partly dense vegetation. Moreover, no differing species composition was expected than in the habitat groups Forest Track North and Forest Track South. As this expectation proved true, the habitat 'Forest' was not included in sampling of the second round. The sampling order was random and based on the monitoring of 2014 by S. Flieth. Since most of the routes for setting up the measuring devices were covered by bicycle, some adjustments had to be made to the sampling order for logistical reasons. Also during the second sampling round, the route of the first round could not be completely repeated due to external circumstances, such as the Danube flooding in July.

Sampling nights were chosen due to weather conditions, mainly rainfall and minimum temperature. Only nights with a prediction of no or a low probability of rain and a minimum temperature of 8 °C were used for sampling. During the day the batcorders were installed at a pole, the timer was set to the respective recording hours and the next day the SD cards were changed and the devices were set up at a new sampling spot.

For the points inside the NP no permission for data collection was needed while the points outside the NP were mostly on private property or owned by the local communities. The *Nationalpark Donau-Auen* provided the land register entries and so every person and community was previously contacted and asked for permission to sample on their land.

2.4 Bat call determination and analysis

To determine bat calls and analyse the sampled sequences the corresponding software from *ecoObs Nürnberg* was used. First, the calls were structured with the database bcAdmin 4 and separated into single sessions for each sample point and night. BatIdent 1.5 automatically classifies calls into bat taxa or down to species level, depending on the call quality. Additionally it shows, with what probability the call is from the indicated species. In bcAnalyze 3 the sonagram of every call could be displayed and a manual species determination was possible.

As the amount of data was very huge not every call could be verified manually. For this reason, certain threshold rules (Table 4) were applied to select the most error-prone calls that were misclassified of batIdent 1.5 with a higher probability. These call files were then manually reviewed in bcAnalyze 3 and corrected if necessary. For species determination, published literature of SKIBA 2009, DIETZ AND KIEFER 2020 and the BAVARIAN LFU 2020 was used. Also habitat preferences were considered. For calls that were hard to discriminate an expert of the KFFÖ – K. Bürger – was consulted. As not every sound file could be reliably determined call groups were formed (Table 3).

If species-specific information were not of great importance, the reaction of functional groups was examined. Therefore bats can be grouped in so called echolocation guilds – the short-range echolocators (SRE), mid-range echolocators (MRE) and long- range echolocators (LRE) (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2022). The echolocation guild is closely linked to foraging behaviour of bats. While SRE prefer to hunt close to vegetation, LRE are usually found in open areas, whereas MRE preferably forage along vegetation edges. For this study the classification according to FREY-EHRENBOLD ET AL. was used (2013) (cf. Table 4).

For simplicity, actual species and acoustic call groups are both referred to as "species" hereafter, if a differentiation is not essential. To be able to compare bats in between the habitats it is necessary to set a comparative measurement. For this thesis bat activity was used, and defined as call seconds/ site/ recording hour. Besides bat activity, species richness (the number of occurring species) and diversity (the evenness of occurring species across the habitats) was used to compare bats in between habitats (Park, 2015).

Table 3 *Call groups of bat species. Species that can not be determined by their foraging calls with a high certainty are assigned to call groups.*

Species	**Call group**
Pipistrellus pygmaeus, Pipistrellus pipistrellus	*Phoch*
Pipistrellus nathusii, Pipistrellus kuhlii	*Pmid*
Pipistrellus nathusii, Pipistrellus kuhlii, Hypsugo savii	*Ptief*
Pipistrellus pygmaeus, Pipistrellus pipistrellus, Pipistrellus nathusii, Pipistrellus kuhlii, Hypsugo savii	*Pipistrelloid*
Myotis brandtii, Myotis mystacinus	*Mbart*
Myotis daubentonii, Myotis bechsteinii, Myotis brandtii, Myotis mystacinus	*Mkm*
all *Myotis* species	*Myotis sp.*
Nyctalus leisleri, Eptesicus serotinus, Vespertilio murinus	*Nycmi*
Nyctalus leisleri, Eptesicus serotinus, Vespertilio murinus, Eptesicus nilssonii, Nyctalus noctula	*Nyctaloid*
Plecotus auritus, Plecotus austriacus	*Plecotus sp.*

Table 4 *Threshold rules for manual bat call analysis after the automatic identification by batIdent. Calls were only determined up to a certainty level of more than 60 % otherwise the calls were assigned as Chiroptera. Probability values, up to which species calls determined by batIdent were accepted as true emerged from literature research (Dietz & Kiefer, 2020; Skiba, 2009; BLfU, 2020) and experience from test call analysis in batIdent (test calls were recorded in April 2021 in the Donau-Auen)*

Species	**Acronym**	**Guild**	**Threshold rules for bat call analysis**
Pipistrellus pygmaeus	*Ppyg*	MRE	accepted with a probability of >70%; otherwise checked manually if not *Ppyg* → *check for* ***Ppip*** → *if unsure* → ***Phoch***
Pipistrellus pipistrellus	*Ppip*	MRE	accepted with a probability of >70%; otherwise checked manually if not *Ppip* → check for ***Ppyg*** → if unsure → ***Phoch***
Pipistrellus nathusii	*Pnat*	MRE	always checked manually and changed to *Pmid*, not determinable by foraging calls (XX) if not *Pmid* → check for ***Hsav*** or ***Ppip*** → if unsure → ***Ptief*** or ***Pipistrelloid***
Pipistrellus kuhlii	*Pkuh*	MRE	always checked manually and changed to Pmid, not determinable by foraging calls (XX) if not *Pmid* → check for ***Hsav*** or ***Ppip*** → if unsure → ***Ptief*** or ***Pipistrelloid***
Hypsugo savii	*Hsav*	MRE	accepted with a probability of >80%; otherwise checked manually if not ***Hsav*** → check for ***Pmid*** or ***Ppip*** → if unsure → **Ptief** or ***Pipistrelloid***
Myotis daubentonii	*Mdau*	SRE	accepted with a probability of >85%; otherwise checked manually if not Mdau → check for ***Mbart***, ***Mbec*** or ***Mdas*** → often hard to determine and unsure → ***Mkm*** or ***Myotis sp.*** if call could have been from *Mdas*
Myotis brandtii	*Mbrandt*	SRE	always checked manually and changed to *Mbart*, not determinable by foraging calls (XX) if not *Mbart* → check for ***Mdau*** or ***Mbec*** → often hard to determine and unsure → ***Mkm*** → if unsure → ***Myotis sp.***
Myotis mystacinus	*Mmys*	SRE	always checked manually and changed to *Mbart*, not determinable by foraging calls (XX) if not *Mbart* → check for ***Mdau*** or ***Mbec*** → often hard to determine and unsure → ***Mkm*** → if unsure → ***Myotis sp.***
Myotis bechsteinii	*Mbec*	SRE	accepted with a probability of >85%; otherwise checked manually if not Mbec → check for ***Mbart*** or ***Mbec*** → often hard to determine and unsure → ***Mkm*** → if unsure → ***Myotis sp.***
Myotis alcathoe	*Malc*	SRE	accepted with a probability of 100%; otherwise checked manually easy to confound with ***Mkm*** or ***Mema*** → if unsure → ***Myotis sp.***
Myotis dasycneme	*Mdas*	SRE	accepted with a probability of >90%; otherwise checked manually easy to confound with ***Mkm*** → if unsure → ***Myotis sp.***

Myotis emarginatus	*Mema*	SRE	accepted with a probability of 100%; otherwise checked manually easy to confound with ***Malc*** → if unsure → ***Myotis sp.***
Myotis natteri	*Mnat*	SRE	accepted with a probability of 100%; otherwise checked manually relatively easy to identify → if still unsure → ***Myotis sp.***
Myotis myotis	*Mmyo*	SRE	accepted with a probability of >85%; otherwise checked manually if not *Mmyo* or unsure → ***Myotis sp***.
Nyctalus noctula	*Nnoc*	LRE	accepted with a probability of >85%; otherwise checked manually easy to confound with ***Nlei*** → if unsure → ***Nyctaloid***
Nyctalus leisleri	*Nlei*	LRE	accepted with a probability of >85%; otherwise checked manually easy to confound with ***Eser, Vmur*** or ***Nnoc*** → often hard to determine and unsure → ***Nycmi*** or ***Nyctaloid*** if call could have been from *Nnoc*
Eptesicus serotinus	*Eser*	LRE	accepted with a probability of >85%; otherwise checked manually easy to confound with ***Nlei, Vmur*** or ***Enil*** → often hard to determine and unsure → ***Nycmi*** or ***Nyctaloid*** if call could have been from *Enil*
Eptesicus nilssonii	*Enil*	LRE	accepted with a probability of >85%; otherwise checked manually easy to confound with ***Nycmi*** → if unsure → ***Nycmi*** or ***Nyctaloid***
Vespertilio murinus	*Vmur*	LRE	accepted with a probability of >85%; otherwise checked manually easy to confound with ***Nlei*** or ***Eser*** → often hard to determine and unsure → ***Nycmi*** → if unsure → ***Nyctaloid***
Barbastella barbastellus	*Bbar*	SRE	accepted with a probability of >70%; otherwise checked manually easy to identify
Rhinolophus ferrumequinum	*Rfer*		always checked manually; easy to identify
Plecotus auritus	*Plec*	SRE	always checked manually; automatically assigned to ***Plecotus sp.*** by batident as foraging calls of *P. auritus* and *P. austriacus* are hard to differentiate
Plecotus austriacus	*Plec*	SRE	always checked manually; automatically assigned to ***Plecotus sp.*** by batident as foraging calls of *P. auritus* and *P. austriacus* are hard to differentiate

2.5 Statistical data analysis

For data analysis and the final presentation of the data, the programs RStudio 2022.07.02, bcAnalyze 3 and LibreOfficeCalc were used. For map creation, display of sample points and distance measurements to the next water body respectively village, QGIS 3.16.5 was used. All boxplots and graphs in R were either created with ggplot (package: ggplot2) or the base R functions. In the following the main statistics used in R are shortly discussed. For all statistical tests, $p \leq 0.05$ was considered significant.

To find out which environmental parameters and variables had an influence on bat activity respectively species richness, generalized linear models (glm) were carried out. Each model was built up by stepwise variable selection. All explanatory variables that were considered can be found in Table 2. For choosing the best model the Akaike-Information-Criterion (AIC) was used. To make sure that no correlating variables are used in the same model the statistical correlation was tested with the Pearson test. Before application of the glm, the residuals of each model were controlled for normal distribution with the Shapiro-Wilk test. The model was only applied if the test was not significant. To analyse the results of the model an anova was used. To check for significant differences in between bat activity levels in the single habitats, the Welch t-test and Wilcoxon test were used. Besides p-values, for the Welch t-test, t-values were taken into account to show the magnitude of differences.

3 Results

In total a number of 90 654 passes of bats were recorded with a call duration of 90 845.98 s (seconds) which corresponds to 25.23 h (hours). During the first round of the monitoring 57 366 bat passes were registered with a call duration of 60 909.5 s while during the second round 33 288 bat passes with a duration of 29 936.48 s were recorded. It needs to be considered that during the second round fewer points were sampled as the forest sites north and south of the dam were respectively only sampled once. However the 16 forest sites only accounted for 484 passes respectively 39.54 s during the 1^{st} sampling round.

During the monitoring, 17 species could be identified by their foraging calls. Additionally ten call groups were assigned (Table 3). The most commonly recorded species during the bio acoustic monitoring was *P. pygmaeus*, with a call amount of almost 50 %. It is followed by *Nyctaloid* (11 %), *N. noctula* (10 %), *Phoch* (8.7 %) and *Pmid* (6 %). Fig. 5 gives a broad overview about the recorded species. The wider the bar, the more recordings of the species or call group were made. From the three main genera *Pipistrelloids* are the most recorded genus (64.1 %) followed by *Nyctaloids* (25.6 %), while the call amount of *Myotis* makes up for 8.7 %. *B. barbastellus* and to a lower extent *Plecotus sp.* were recorded during the monitoring as well. For *R. ferrumequinum* only one recorded call exists for the entire acoustic monitoring. 'Spec.' represents the calls that could not be assigned to a call group or species.

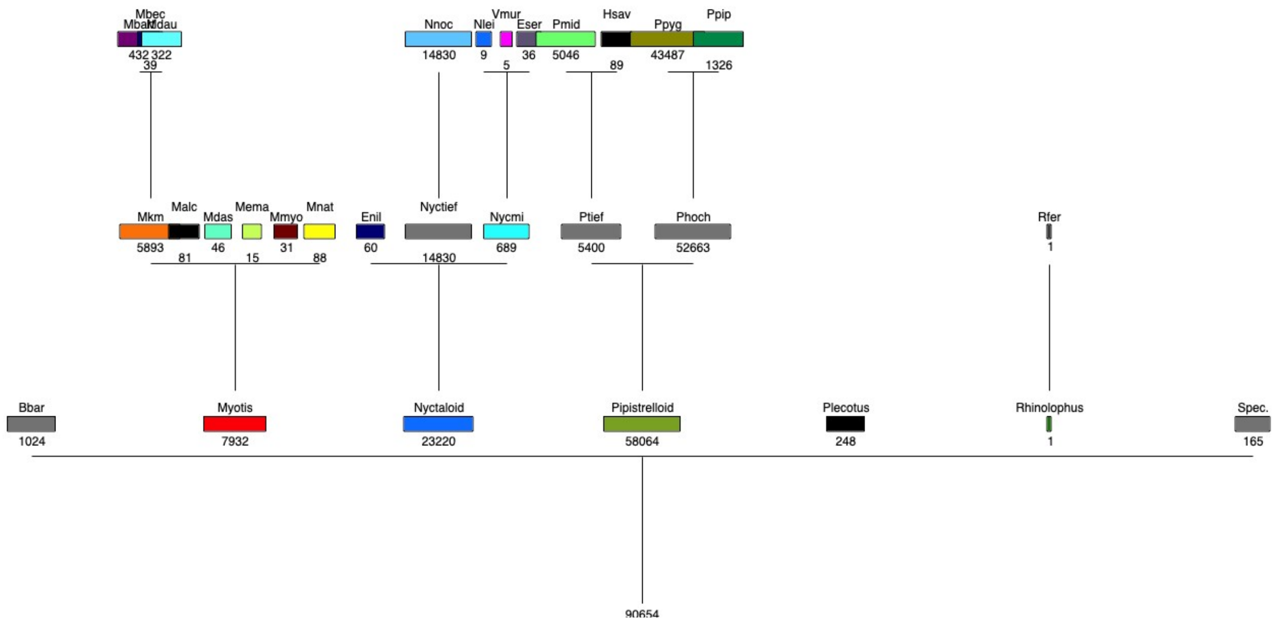

Fig. 5 *Species tree diagram. The numbers represent the recordings for each species and call group made during the entire monitoring.*

3.1 Bat activity and species richness in the habitats

Bats were recorded in all habitat types. During the two monitoring rounds a total of 352 points were sampled of which no bats were recorded at 22 points. These points are distributed over nearly all habitat types (except for meadows and forest tracks south of the dam) although it is noticeable that a large part (~ 25%) of them are located in woodland patches outside the national park. For two sample points (woodland patch and water body) respectively no recordings could be made in both sampling nights.

Fig. 6 shows that bat activity generally was higher in the ten habitats inside the national park, than in the four sampled ones outside the park. The mean activity of 2.36 (± sd: 1.35) in the Danube floodplains, compared to 1.44 (± sd: 1.46) in the *Marchfeld* confirms the assumption that bats prefer the Danube floodplains to the agricultural environment for foraging. The difference is significant according to the Wilcoxon test (p = 7.811e-08). A major part of bat calls for the *Marchfeld* habitats was recorded in the habitat 'Gravel Pit'. Less than 18 % of calls were recorded in the remaining three habitat types 'Woodland Patch', 'Water Body' and '*Sutten*'. For the habitats inside the Danube floodplains the distribution was more even, only the forest habitats show a significantly lower activity rate (Fig. 7 & 8).

Based on a one way anova bat activity (mean ± sd: 2.16 ± 1.43) differed significantly among some of the 14 habitat types (Figure 8). For habitats inside the national park, bat activity in forest sites was significantly lower than in all other habitat types, except for the dam where no significant difference could be found.

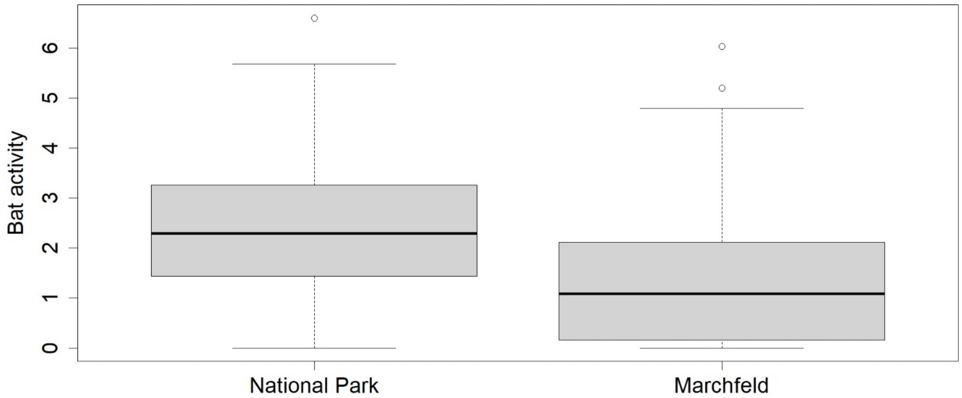

Fig. 6 *Mean bat activity rates for the 10 habitats inside the Nataionalpark Donau-Auen and for the four surrounding habitats in the Marchfeld*

While most habitats had similar bat activities DA and respectively SAS, FTN, FTS and DR showed significant differences in activity levels (Fig. 8). The same applies to MN and FTN. Habitats in the *Marchfeld* mostly have similar activity rates, only GP is differing significantly from the other three habitat types (Fig. 8).

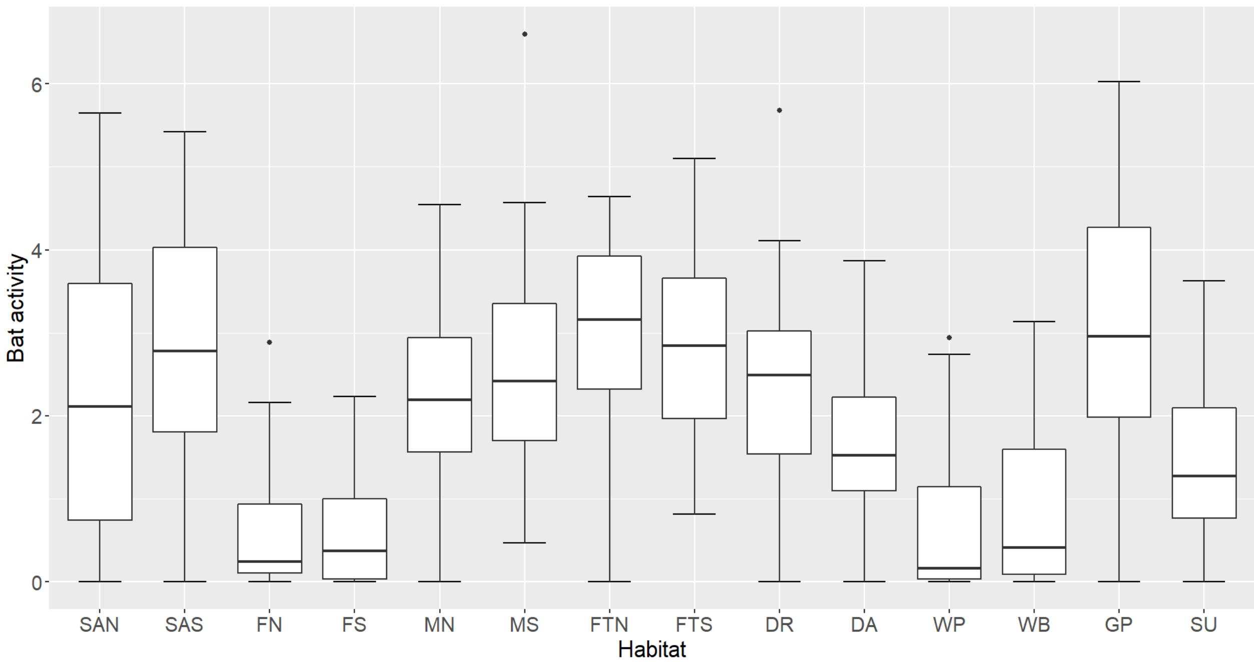

Fig. 7 *Boxplot showing the mean bat activity for all 10 habitat types inside the national park and the 4 in the Marchfeld in comparison to each other. DA = Dam, DR = Danube River, FN/FS = Forest North/South, FTN/FTS = Forest Track North/South, GP = Gravel Pit, MN/MS = Meadow North/South, SAN/SAS = Sidearm North/South, SU = Sutte, WB = Waterbody, WP = Woodland Patch*

As highlighted by Fig. 7, highest bat activity was found along forest tracks north of the dam (3.06 ± 1.12). It is followed by gravel pits (2.95 ± 1.72) – outside the national park – and sidearms south of the dam (2.78 ± 1.57). Lowest bat activities were registered in forest areas north (0.78 ± 1.11) and south (0.65 ± 0.8) of the dam, as well as in woodland patches (0.69 ± 0.94) and along water bodies (0.88 ± 1.01) in the *Marchfeld*.

	SAN	SAS	FN	FS	MN	MS	FTN	FTS	DR	DA	WB	WP	GP	SU
SAN		-1.503	3.1002	4.1355	-0.042426	-1.086	-2.6486	-1.7332	-0.45148	1.6081	4.0618	4.6813	-1.5505	2.2604
SAS	0.1378		4.1688	5.3536	1.5965	0.48505	-0.82424	-0.00989	1.2219	3.2104	5.4108	6.0043	0.7207	3.6713
FN	0.008193	0.000834		0.25298	-3.3	-3.935	-5.2054	-4.5139	-3.6065	-2.2218	-0.22156	0.19292	-3.8651	-1.4477
FS	0.000529	2.199E-05	0.8043		-4.5303	-5.1736	-6.9697	-6.0371	-4.9283	-3.2316	-0.62101	-0.10385	-4.6528	-2.1247
MN	0.9663	0.116	0.007081	0.000405		-1.1543	-2.9429	-1.8974	-0.46104	1.8904	4.5851	5.295	-1.6007	2.5454
MS	0.2816	0.6294	0.001682	5.49E-05	0.2533		-1.4608	0.5725	0.74859	2.8881	5.2556	5.8962	-0.75283	3.3913
FTN	0.01015	0.4133	0.000312	5.38E-06	0.004601	0.1496		0.96526	2.497	5.0835	7.4782	8.2467	0.22836	5.2655
FTS	0.08784	0.9921	0.0008204	1.95E-05	0.06267	0.5725	0.3382		1.4579	3.8805	6.3391	7.0629	-0.38091	4.2501
DR	0.6531	0.2268	0.004184	0.00019	0.6464	0.4572	0.01507	0.1499		2.4009	5.0596	5.7827	-1.3161	2.9826
DA	0.113	0.002274	0.05076	0.006685	0.0637	0.005611	3.632E-06	0.0002666	0.01931		3.0781	3.8146	-2.7841	0.9856
WB	0.000155	1.622E-06	0.8285	0.5435	3.325E-05	3.064E-06	1.326E-09	7.16E-08	6.28E-06	0.00357		0.61374	-4.5291	-1.7578
WP	2.011E-05	2.163E-07	0.8505	0.9187	3.412E-06	3.642E-07	1.318E-10	7.004E-09	5.85E-07	0.000443	0.5429		4.9647	2.3664
GP	0.1314	0.7207	0.0009388	0.000102	0.1217	0.4575	0.8212	0.7063	0.1999	0.01046	0.000113	3.8E-05		-3.2303
SU	0.02844	0.000615	0.1726	0.04877	0.01502	0.001486	5.552E-06	0.0001243	0.004892	0.3312	0.08714	0.02364	0.00321	

Fig. 8 *Results of the Welch two-sample t-test for differences in bat activity between the habitats. p- values are found in the lower part. Green fields indicate a significant difference. The upper part displays t-values to show how strongly the difference is.*

Regarding species richness the results differ slightly (Fig. 9). Here the habitat MS is the sampled area with most recorded species (8.5) – in the mean for all sampled nights – followed by SAS (8.5), DR (8.4) and GP (8.0). Lowest species richness was observed in the habitats WP (2.5), FN (2.1), and FS (2.0), so all completely forested areas. In the mean 6.5 species were recorded per habitat type. Highest species richness for one night was recorded on a sidearm south of the dam, with 16 different species respectively call groups observed in one night.

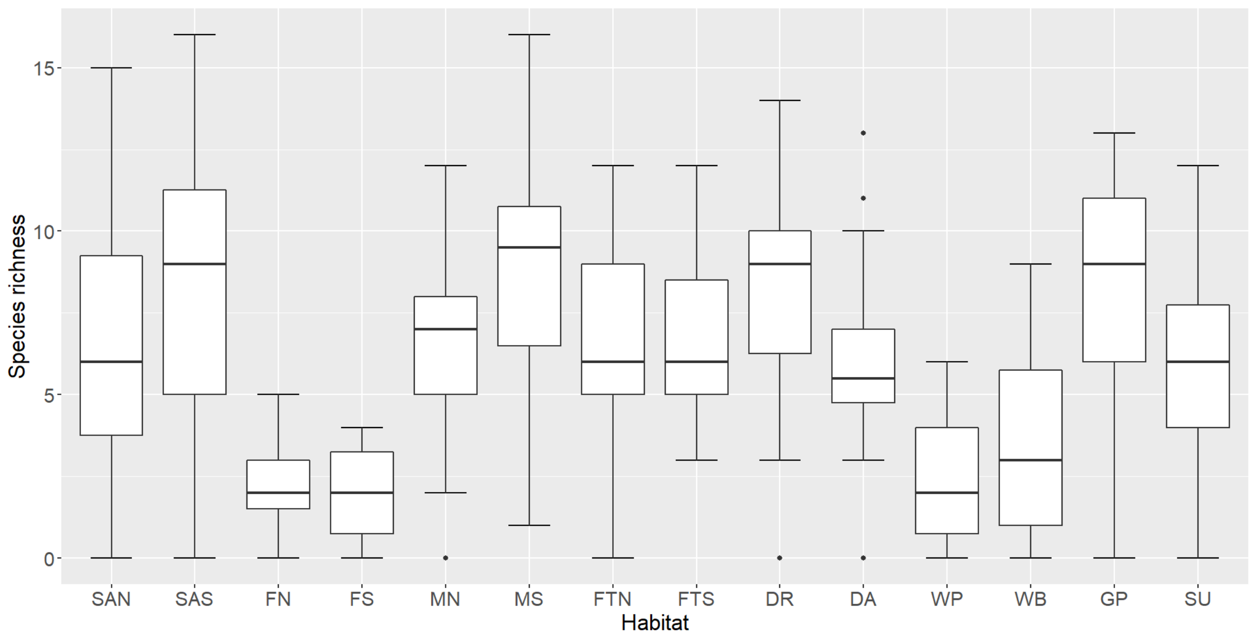

Fig. 9 *Boxplot showing the mean species richness for all 10 habitat types inside the national park and the 4 in the Marchfeld in comparison to each other.*

To analyse whether flooding events lead to an increased bat activity level, the data after the July 19, 2021 flood event along the Danube, were taken into account. During the following three weeks, the sampling sites south of the dam (the area is allowed to get flooded) were more difficult to access because large puddles of standing water were still present. Therefore, only data collected between 19th of July and 10th of August 2021 were compared for differences in activity levels north and south of the dam. North of the dam the habitats SAN, FN, MN and FTN were taken into account, while south of the dam, SAS, FS, MS, FTS and DR were analysed. Mean activity levels differed more for this three week period, than for the whole monitoring, but the differences were not significant (p = 0.2681).

3.2 Species composition in the habitats in the Danube floodplains

The Welch two sample t-test showed that neither species richness, nor bat activity levels in the habitats SAN and SAS, did differ significantly (p= 0.08957/ p = 0.1378). Hence the habitats were analysed for species composition combined. Still it is to mention that mean activity rates differed more (t = -1.503) than in between the other habitats that were divided into north and south of the dam (Fig. 8). For the sample points south of the dam a higher mean activity was registered. As visible in Fig. 10, five species are dominant in the habitat 'Sidearm'. Most abundant is *P. pygmaeus* (mean bat activity: 3.33 ± sd: 2.06) followed by *Mkm* (2.03 ± 1.68), *Nyctaloids* (2.02 ± 1.71), *N. noctula* (2.02 ± 2.05) and *Myotis sp.* (1.28 ± 1.18). *V. murinus* on the contrary, was not recorded at all along the sidearms of the Danube. A very low activity is likewise observed for *M. myotis* (0.01 ± 0.12), *M. emarginatus* (0.01 ± 0.08), *E. nilssonii* (0.01 ± 0.05) and *N. leisleri* (0.02 ± 0.11). A feature of the habitat 'Sidearm' is that the only recorded call of *R. ferrumequinum* was registered at a sample point south of the dam. This species is critically endangered (IUCN 2022) and its occurrence in the national park and surrounding could not be proved during the intensive monitoring conducted in 2016/17 by Bürger & Plank (2017). However, also in last years monitoring only one single call was recorded. Species richness along the sidearms is very high as only one of the 17 occurring species was not recorded.

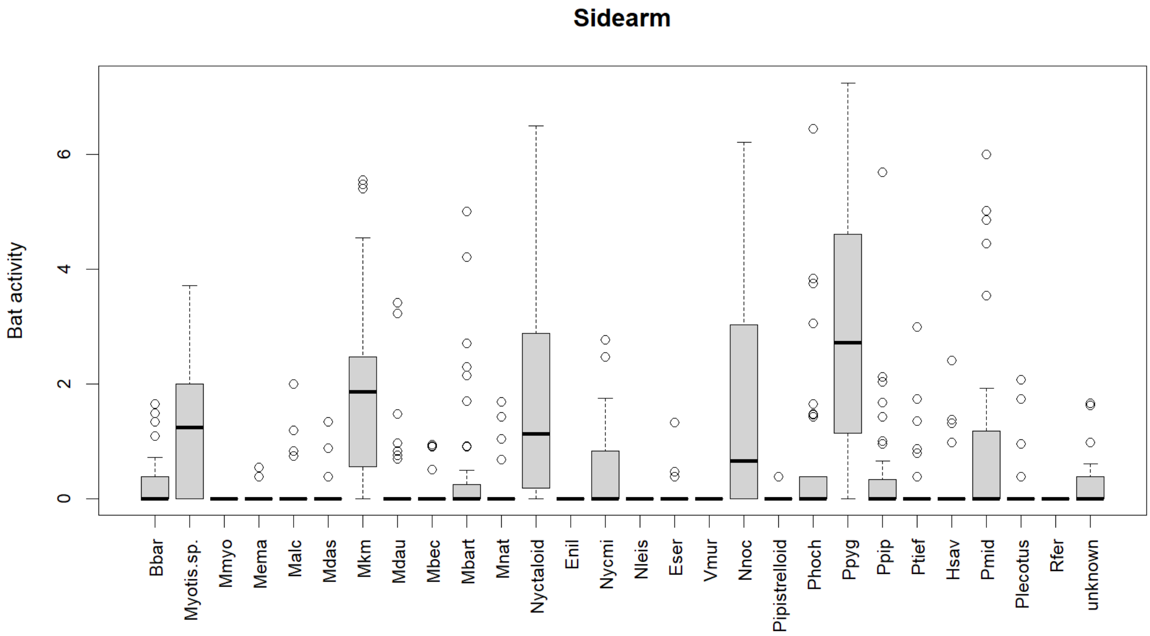

Fig. 10 *Mean activity rates for every species recorded in the habitat 'Sidearm' which includes sample points north and south of the dam*

As for SAN and SAS, no significant difference in species richness nor bat activity was found in forest sample points north and south of the dam (p = 0.8798/ p = 0.8043). Therefore the species-specific activity results were combined for all forest sample points (Fig. 11). Again *P. pygmaeus* (1.22 ± 1.70) was the dominating species. Besides, only *Mkm* (0.83 ± 1.18) and *Myotis sp.* (0.46 ± 0.55) show any mentionable activities. Species richness is low as 17 out of 27 species respectively call groups were not detected at forest sites. As Fig. 9 shows, species richness along forest tracks is higher than in the forest itself. All species that were recorded in the forest were detected along forest paths as well. Due to this outcome the points inside FS and FN were only sampled during the first monitoring round as no further knowledge about bat diversity could be gained by their sampling.

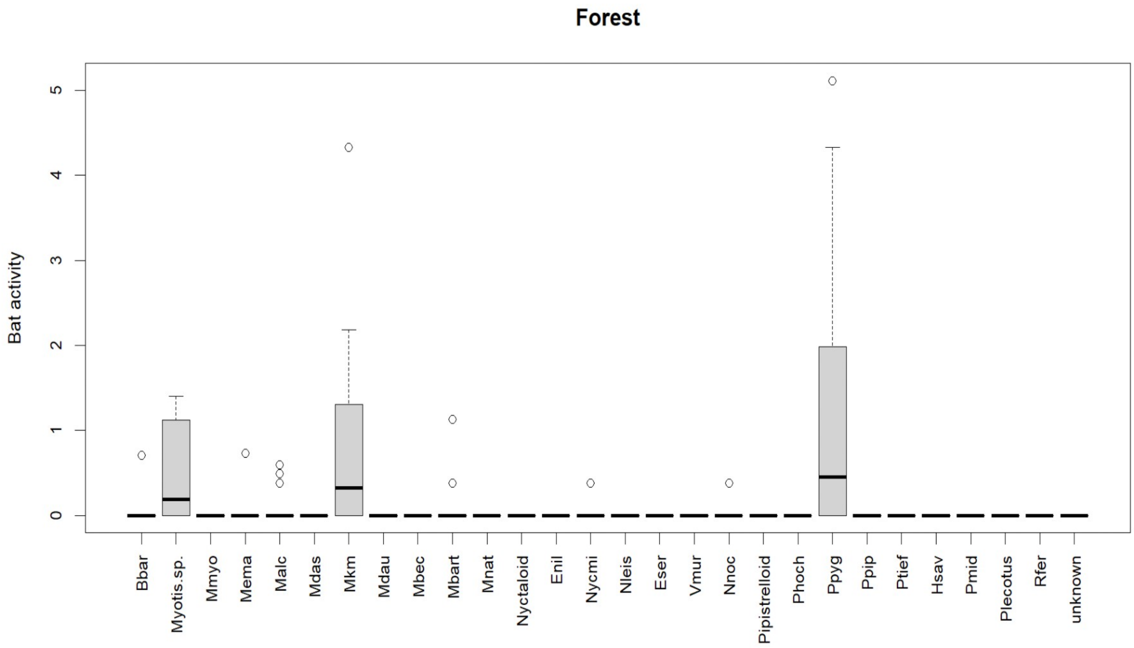

Fig. 11 *Mean activity rates for every species recorded in the habitat 'Forest' which includes sample points north and south of the dam*

The same species that were recorded in forest sites were detected along forest paths as well. Once more the sample points of FTS and FTN were combined as neither species-specific activity levels did differ significantly (p = 0.1501) nor species richness (p = 0.9392). Hence bat species composition was analysed for the habitat 'Forest Tracks'. The results are visible in Fig. 12. Again *P. pygmaeu*s (4.53 ± 1.58) was the species most recorded. Also animals of the call group *Mkm* (2.52 ± 1.52) and *Nyctaloids* (1.86 ± 1.79) were often abundant. Calls from *B. barbastellus* were recorded quite often with a mean activity of 1.29 (± 1.19). Also various bats from the genus *Myotis sp*. (1.36 ± 1.11) occurred along forest tracks but their calls could not be further classified. Besides *Mkm,* only the call group *Mbart* (0.84 ± 1.03) shows a noteworthy activity of the *Myotis* species. In general species richness for forest paths in the Danube floodplains was high. Only two species were not detected in the habitat at all, whereof one is *R. ferrumequinum*. The other one is *N.*

leisleri.. The activity of *M. bechsteinii* – a typical forest bat (Dietz & Kiefer, 2020) – is low with a mean activity of 0.15 (± 0.52).

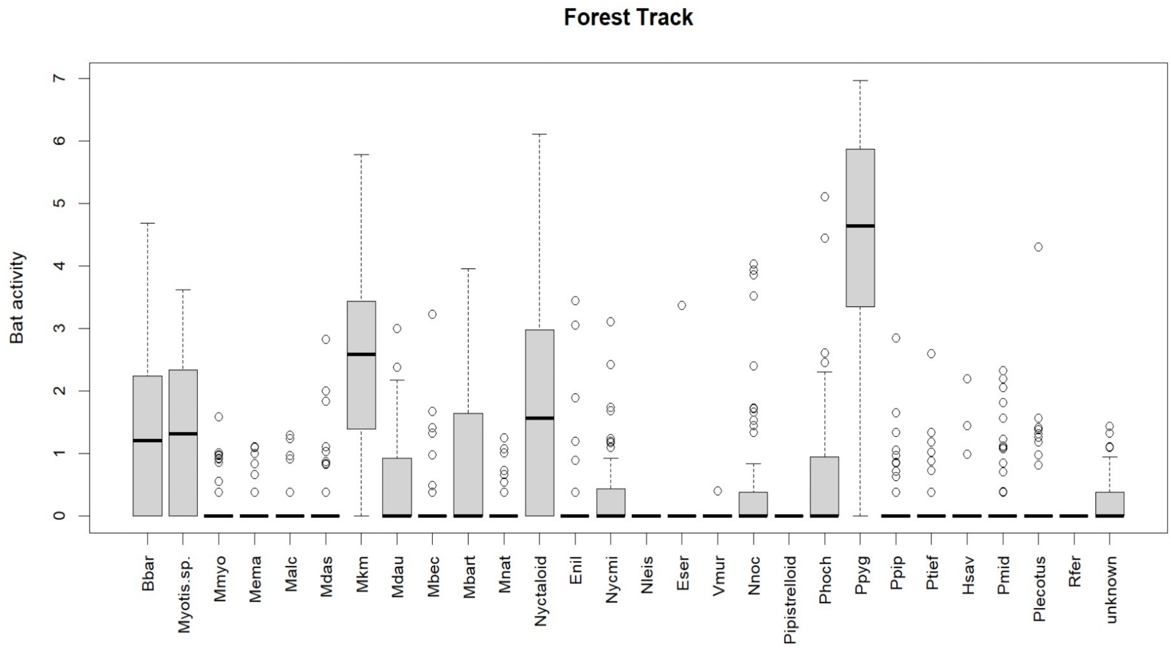

Fig. 12 *Mean activity rates for every species recorded in the habitat 'Forest Track' which includes sample points north and south of the dam*

For the habitat 'Meadow' the dam only had a negligible influence on bat activity (p = 0.2533) and also species richness shows no significant differences (p = 0.05016). Still, differences in species richness north and south of the dam are higher for meadows than for all other habitats. Four species were not detected in MN, that were found at sites of MS, while in reverse one species that did not occur in MS was recorded along sites of MN. Nevertheless results were examined for both meadow habitats combined. As displayed in Fig. 13, also here *P. pygmaeus* (3.58 ± 1.69) was the species most recorded. Animals of the genus *Nyctaloid* have high activity levels at meadow sites. *N. noctula* (2.57 ± 1.78) and also animals of the call group *Nycmi* (0.75 ± 1.08) were abundant. Calls that could not be further classified were generally assigned to the call group *Nyctaloid* (2.22 ± 1.60), which also indicates high bat activity for the meadow sample points. For *Pipistrelloids* the call group *Pmid* (0.85 ± 1.30) has mentionable activity rates. Also the group *Phoch* (1.13 ± 1.45) was recorded often. For *Myotis* species the call group *Mkm* (1.54 ± 1.22) shows the highest activity rates. Also some *B. barbastellus* (0.54 ± 0.84) calls were registered. Species richness for the habitat 'Meadow' is high. Only *R. ferrumequinum* was not detected.

In comparison to all other habitats analysed before *P. pygmaeus* (2.09 ± 1.19) is not the most abundant species along the dam sample points. Bats of the call groups *Nyctaloid* (2.37 ± 1.39) were most present in this habitat. While *N. noctula* (1.97 ± 1.83) likewise shows high activity levels, all other species of the call group *Nyctaloid* were not recorded often or at least could not be determined down to species level. Also the call groups *Pmid* (0.78 ± 0.91) and *Mkm* (0.69 ± 0.84) were quite abundant foraging along the dam.

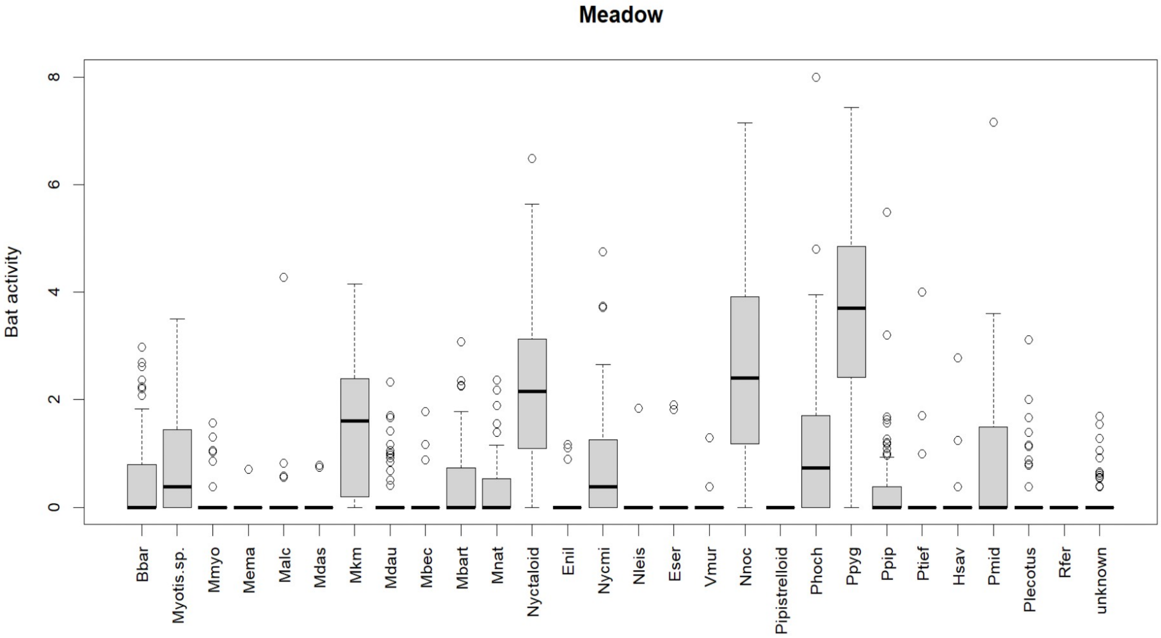

***Fig. 13** Mean activity rates for every species recorded in the habitat 'Meadow' which includes sample points north and south of the dam*

Species richness was lower in comparison to meadows, sidearms and forest tracks. In total seven species could not be detected. Besides *R. ferrumequinum,* four *Myotis* species did not use the dam for foraging (Fig. 14) and also *V. murinus* and *N. leisleri* were not recorded.

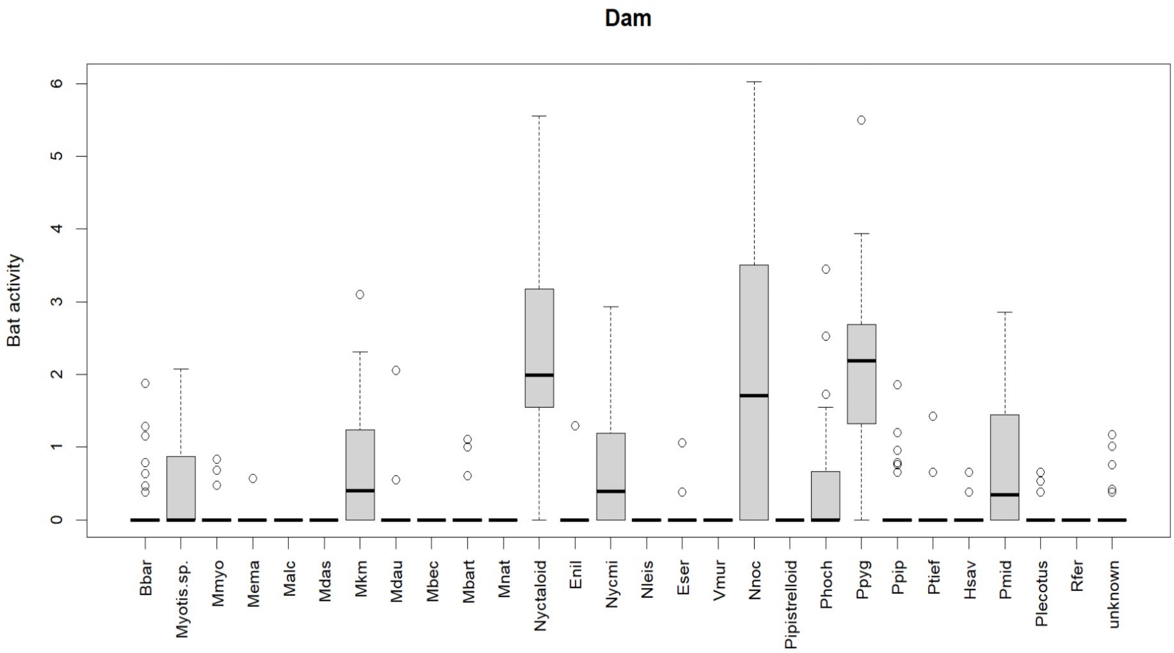

***Fig. 14** Mean activity rates for every species recorded in the habitat 'Dam'*

The last habitat inside the Danube floodplains national park is the river itself. Again *P. pygmaeus* (3.35 ± 1.52) was the species most abundant followed by *N. noctula* (2.16 ± 1.56) as displayed in Fig. 15. Besides these two species, highest activities were recorded for the call groups *Nyctaloid* (2.15 ± 1.72), *Mkm* (1.82 ± 1.15), *Pmid* (1.58 ± 1.53) and *Phoch* (1.58 ± 1.62). Species diversity is higher than at the dam. Four species were not recorded along any of the Danube sample sites. One of the species is again *R. ferrumequinum,* while the other three belong to the genus *Myotis.* Foraging calls of *M. emarginatus, M. bechsteinii* and *M. myotis* were not found along the river during last years monitoring.

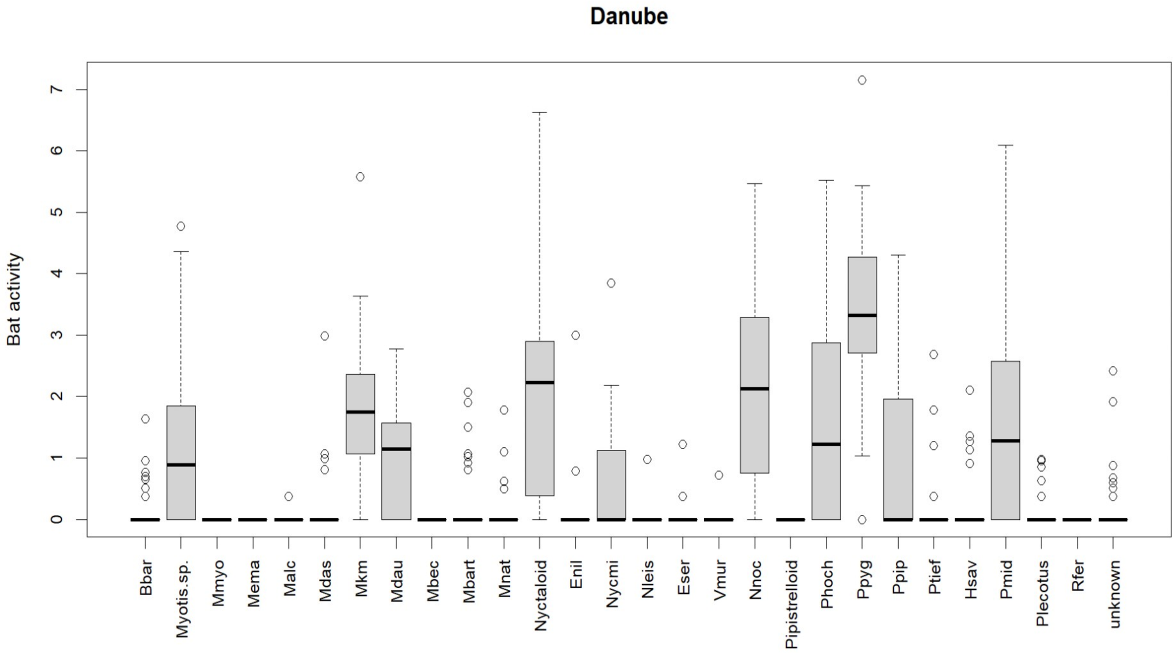

Fig. 15 *Mean activity rates for every species recorded in the habitat 'Danube'*

3.3 Species composition in the habitats in the *Marchfeld*

Fig. 16 displays species composition and activity rates for the habitat 'Woodland Patch'. As already shown before (Fig. 7) general activity rates in woodlands outside the national park are low. The main species that were detected, are *P. pygmaeus* (1.21 ± 1.57) and *N. noctula* (0.60 ± 1.19). Except those, only call groups – *Mkm* (0.48 ± 0.62) and *Myotis sp*. (0.22 ± 0.27) – show remarkable activity rates. While *Nyctaloids* (0.38 ± 1.17) have a comparably high mean activity rate, Fig. 16 shows that this can be attributed to a single sample point, where a large proportion of their calls were recorded. Species diversity in the habitat is very low. Besides the already mentioned, most abundant species, only two other ones – *M. natteri* and *B. barbastellus* – were recorded or rather could be determined down to species level. Regarding species composition, the habitat type 'Water Body' (Fig. 17) shows great similarities to 'Woodland Patch'. Also here *P. pygmaeus* (1.48 ± 1.76) and *N. noctula* (0.67 ± 1.23) are most abundant. Besides, the call groups *Nyctaloid* (0.66 ± 1.10), *Mkm* (0.62 ± 0.99), and *Pmid* (0.42 ± 0.76) display comparably high activity rates for this habitat. Species richness along the creeks in the *Marchfeld* is slightly higher than in woodland patches. Still the habitat use for foraging could not be proofed for nine species, whereof four belong to the genus *Myotis*. For the sample points next to creeks, *M. daubentonii*'s (0.22 ± 0.27) activity rates were highest in comparison to the other species of the genus.

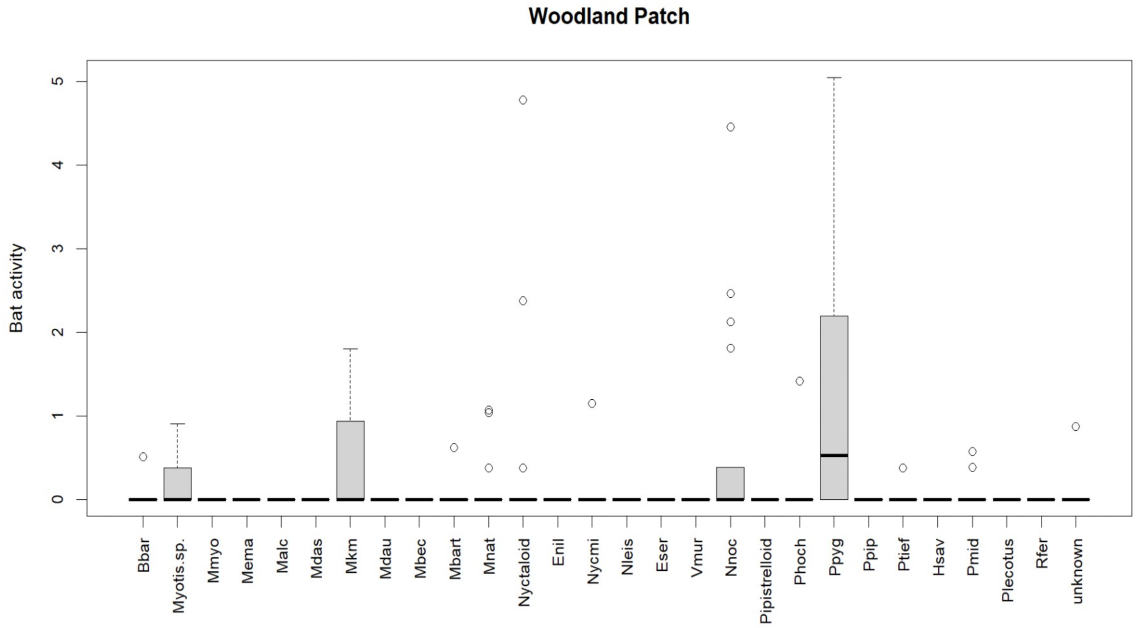

***Fig. 16** Mean activity rates for every species recorded in the habitat 'Woodland Patch'*

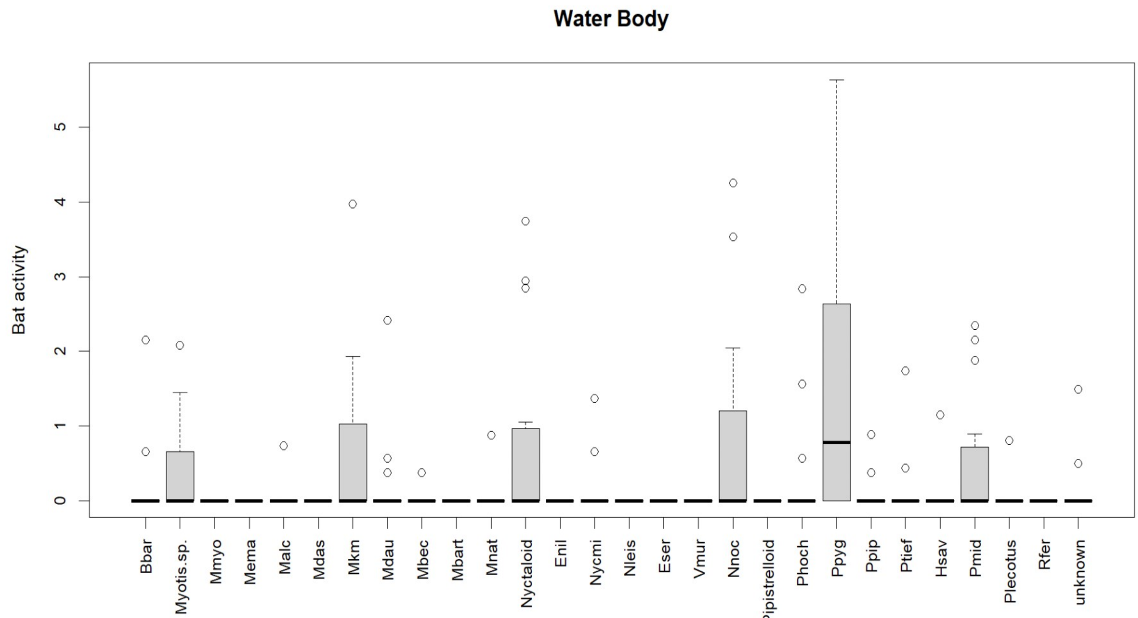

***Fig. 17** Mean activity rates for every species recorded in the habitat 'Water Body'*

On the contrary for the habitat type 'Gravel Pit', *M. daubentonii* (0.17 ± 0.40) shows very low activity rates (Fig. 18), despite the abundance of water areas that were also intensively used for foraging by other species. The dominant genus is *Pipistrelloid* with *P. pygmaeus* (4.59 ± 2.17) being most recorded once again. But also the call groups *Phoch* (2.43 ± 2.24) and *Pmid* (1.93 ± 1.80) were abundant around gravel pits. *P. pipistrellus* (1.20 ± 1.51) has high activity levels in comparison to all other habitat types. *Nyctaloids* (2.32 ± 1.65) and *N. noctula* (1.42 ± 1.57) were also abundant around the water-filled gravel pits. Activity levels for the genus *Myotis sp*. were relatively low only the call group *Mkm* (1.13 ± 1.09) showed elevated activity rates. Regarding the species composition five species were not present. Besides *R. ferrumequinum, M. alcathoe, M. bechsteinii, V. murinus* and *N. leisleri* did not use gravel pits in the *Marchfeld* for foraging.

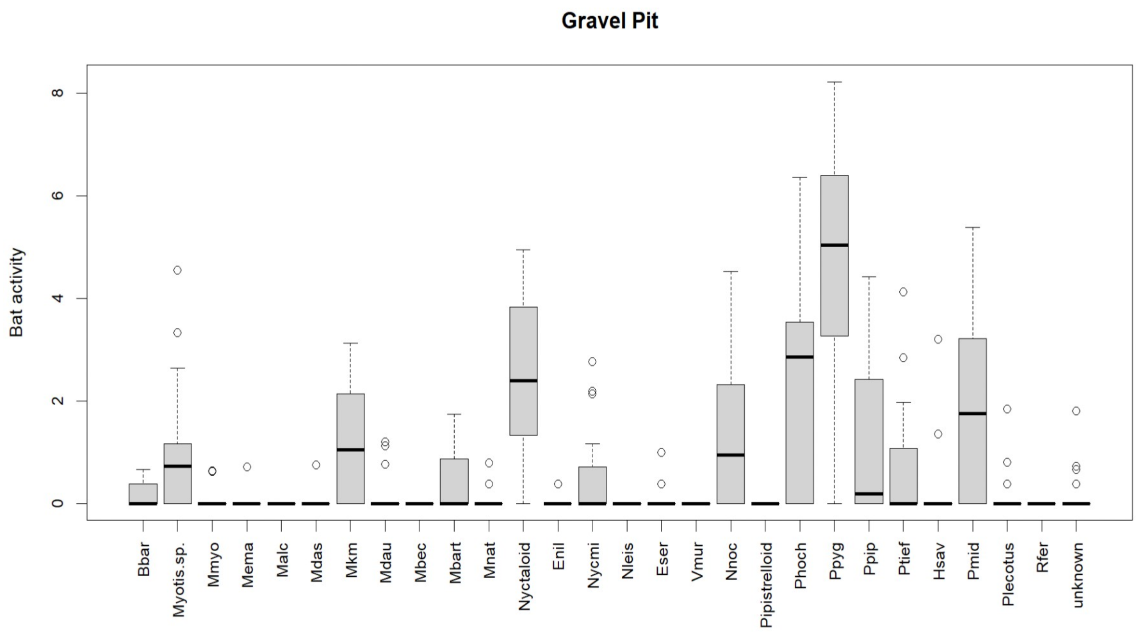

Fig. 18 *Mean activity rates for every species recorded in the habitat 'Gravel Pit'*

The last habitat type that needs to be studied for its species richness are '*Sutten*'. As visible in Fig. 19, again *P. pygmaeus* (2.17 ± 1.70) and *N. noctula* (1.52 ± 1.32) are the species most recorded in this habitat type. Third highest call activities are found for *Pmid* (1.36 ± 1.20). Abundance of *Myotis sp.* was again low, only the call group *Mkm* (0.87 ± 1.16) shows some mentionable activity levels. Species diversity for *Sutten* is the same as for water bodies. Nine species did not occur at all. Also the species composition of *Sutten* is similar to the one of water bodies. The only difference is that *M. alcathoe* and *M. bechsteinii* were not present along *Sutten,* while they rarely occurred along creeks in the *Marchfeld*. Therefore *M. myotis* and the call group *Mbart* were not detected in the habitat 'Water Body' (Fig. 17) but were recorded along *Sutten*.

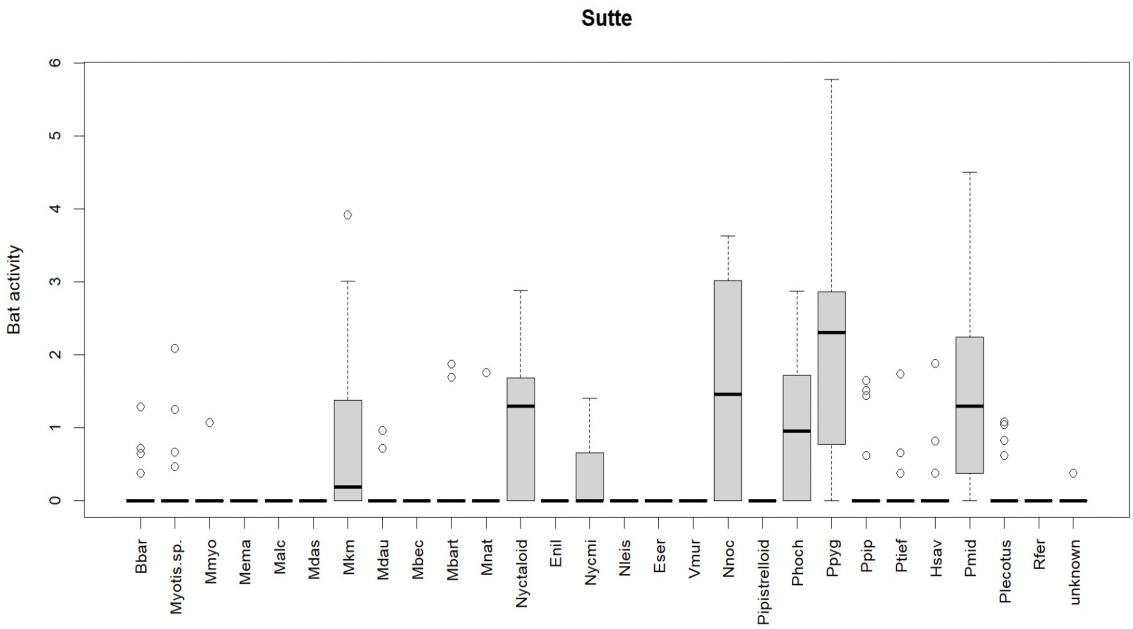

Fig. 19 *Mean activity rates for every species recorded in the habitat 'Sutte'*

3.4 Guild specific habitat use

Bat activity is differing significantly for echolocation guilds (p = 2.2e-16 [SRE & MRE]/ 0.001389 [SRE & LRE]/ 2.449e-10 [MRE & LRE]) and habitat-specific responses are visible (Fig. 20-22). Three guilds consisting of short- (SRE), mid- (MRE) and long-range echolocators (LRE) exist. Table 4 displays which species is assigned to which guild. In the monitoring conducted the MRE had the highest activity rates (mean ± sd: 1.61 ± 1.39) followed by the LRE (0.99 ± 1.12). Lowest activity was found in the guild of the SRE (0.75 ± 0.86). Highest foraging activities for short range echolocators were found along forest tracks north (1.65 ± 0.98) and south (1.01 ± 0.83) of the dam. Lowest activity was found in woodland patches (0.12 ± 0.15) in the *Marchfeld*. Also along water bodies (0.23 ± 0.44) outside the national park and forest sites south of the dam (0.19 ± 0.23) only little bat activity for the SRE guild was recorded (Fig. 20).

Most outliers are found for the habitat SAN, where three sample points had high mean activity levels for the respectively two sampled nights. For all three sample points the activity levels of the call group *Mkm* were highly increased in comparison to the other species of the guild, while for one site also *Mbart* was stronger represented.

MRE activity was highest around gravel pits (2.73 ± 1.79) in the *Marchfeld*, as evidenced by Fig. 21. Inside the national park the highest foraging activities were measured at sample points along forest tracks north (2.43 ± 1.27) and south (2.4 ± 1.29) of the dam. Lowest activities were recorded in forests points south of the dam (0.4 ± 1) and woodland patches (0.43 ± 0.75) outside the park. Mentionable are the outliers of the habitat types MS and DR. The one sample point on a meadow south of the dam had very high activity rates and was dominated by the species *P. pygmaeus* and the call group *Pmid*. For the point with highest activity rates in the habitat DR, as well *P. pygmaeus* was the species most recorded in the MRE guild.

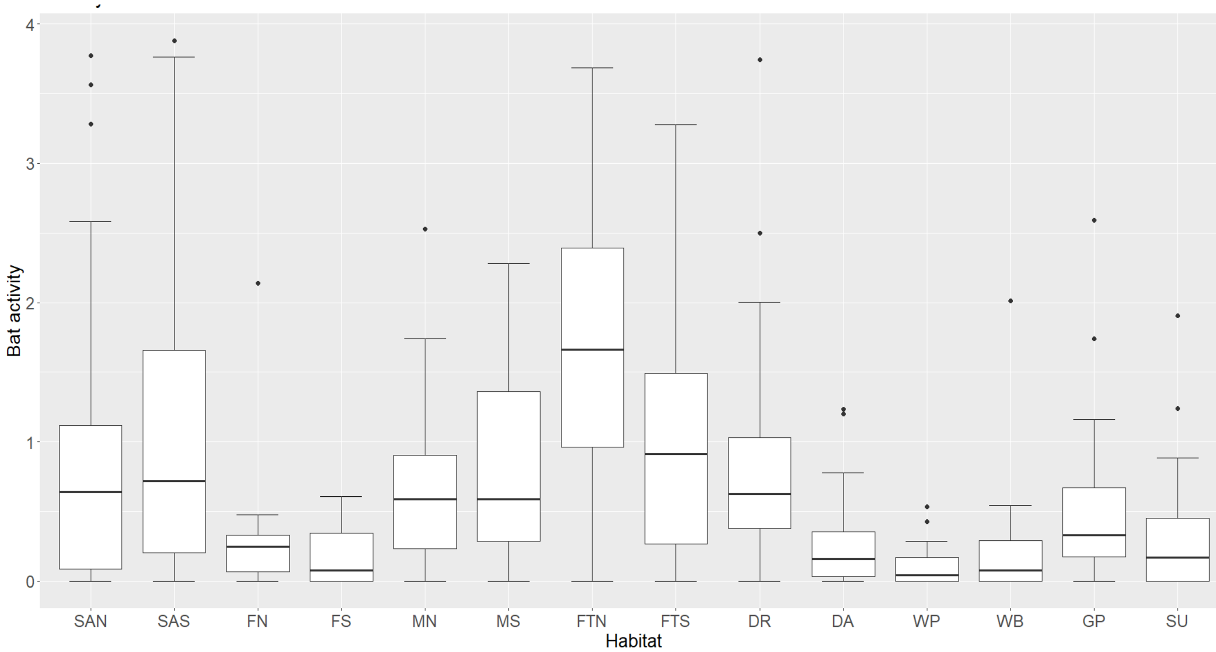

Fig. 20 *Bat activity in the 14 different habitats in- and outside the NP for short range echolocators.*

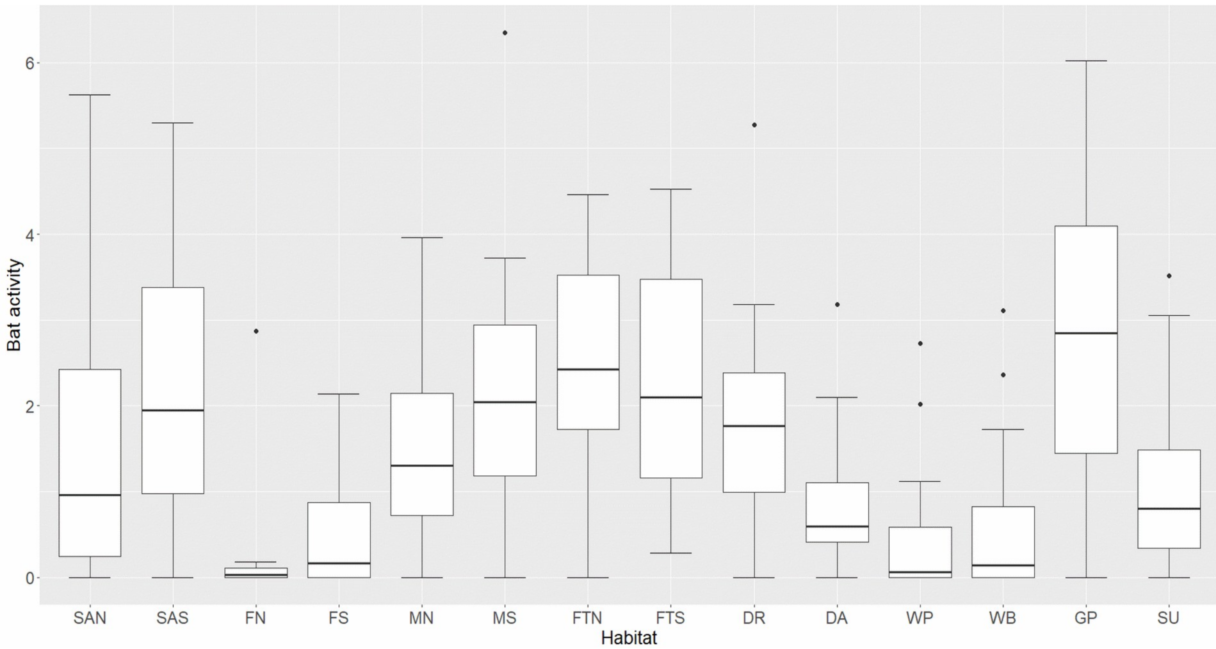

Fig. 21 *Bat activity in the 14 different habitats in- and outside the NP for mid range echolocators.*

For LRE highest activities are found along sidearms south of the dam (1.51 ± 1.32) (Fig. 22). Also meadow areas, both north (1.38 ± 1.06) and south (1.44 ± 1.34) of the dam were regularly frequented by species of the LRE guild. Other open areas like the Danube (1.24 ± 1.1) and the dam (1.32 ± 1.06) were preferred foraging grounds as well. Not used at all by LRE were forest areas north of the dam (Fig. 22). Only slightly higher activities were found in forests south of the dam (0.01 ± 0.02), woodland patches (0.25 ± 0.68) and along water bodies (0.32 ± 0.63) outside the *Donau-Auen*. Outliers for habitats SAN, DR and MN are all dominated by the call group *Nyctaloid*.

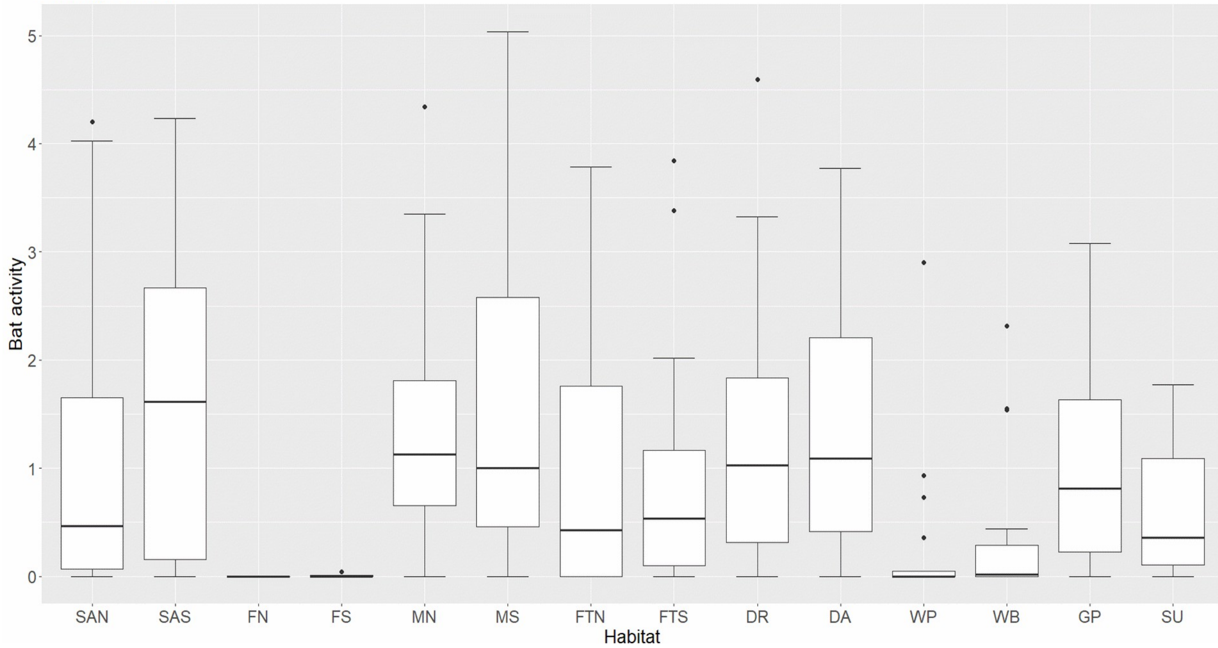

Fig. 22 *Bat activity in the 14 different habitats in- and outside the NP for long range echolocators*

3.5 Habitat preferences of threatened species in Austria

In the following the four species that show declining populations in Austria, according to IUCN, are examined (2022). One of these species is *B. barbastellus.* It is a typical forest dweller, which is shown in the results of the monitoring conducted for this study (Fig. 12). As displayed in Fig. 23 activity rates along forest tracks are significantly higher in comparison to all other habitat types except for MN and SAS (Appendix Fig. 30). *B. barbastellus* was most recorded along forest tracks north of the dam (0.82 ± 1.69), followed by the paths south of the dam (0.45 ± 0.78). Also the habitat MN was frequently used by the species and differs significantly from all other habitat types except for forest tracks and SAS (Appendix, Fig. 30). Activity levels in forest sites (north: 0.01 ± 0.03; south: 0) and in woodland patches (0 ± 0.01) in the *Marchfeld,* on the contrary, were low. Another species that was recorded during the monitoring and shows declining populations in Austria is *M. bechsteinii* (IUCN 2022). As *B. barbastellus,* it is known as a forest dwelling species, that also uses floodplain forests to forage and roost (Dietz & Kiefer, 2020). During this monitoring it was only recorded rarely, with a mean activity of 0.01 (± 0.12). Therefore it was not possible to look for habitat preferences, as the activity levels of the species do not differ significantly between any of the habitats.

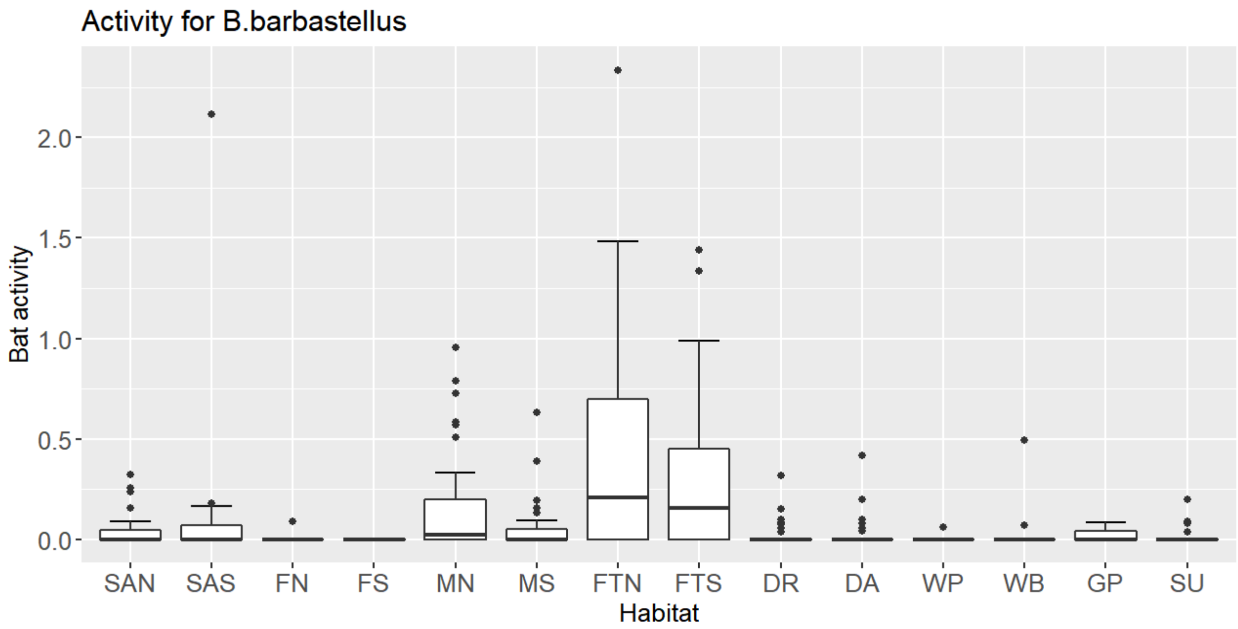

Fig. 23 *Mean activity levels of B. barbastellus for the 14 sampled habitats*

Also numbers of *Plecotus austriacus* are declining in Austria (IUCN 2022), hence the species was observed more closely for its habitat preferences. As their calls are hard to distinguish from the ones of *P. auritus,* the results for the call group *Plecotus sp.* are shown in Fig. 24. Also here, only few calls were recorded with a mean activity rate of 0.05 (± 0.42.) Only MS, FTS and DR differ significantly from the sites where no recordings of *Plecotus sp.* were made, so in both forest areas and in WP (Appendix Fig. 31). All other habitats show no significant differences in activity levels of *Plecotus sp*.

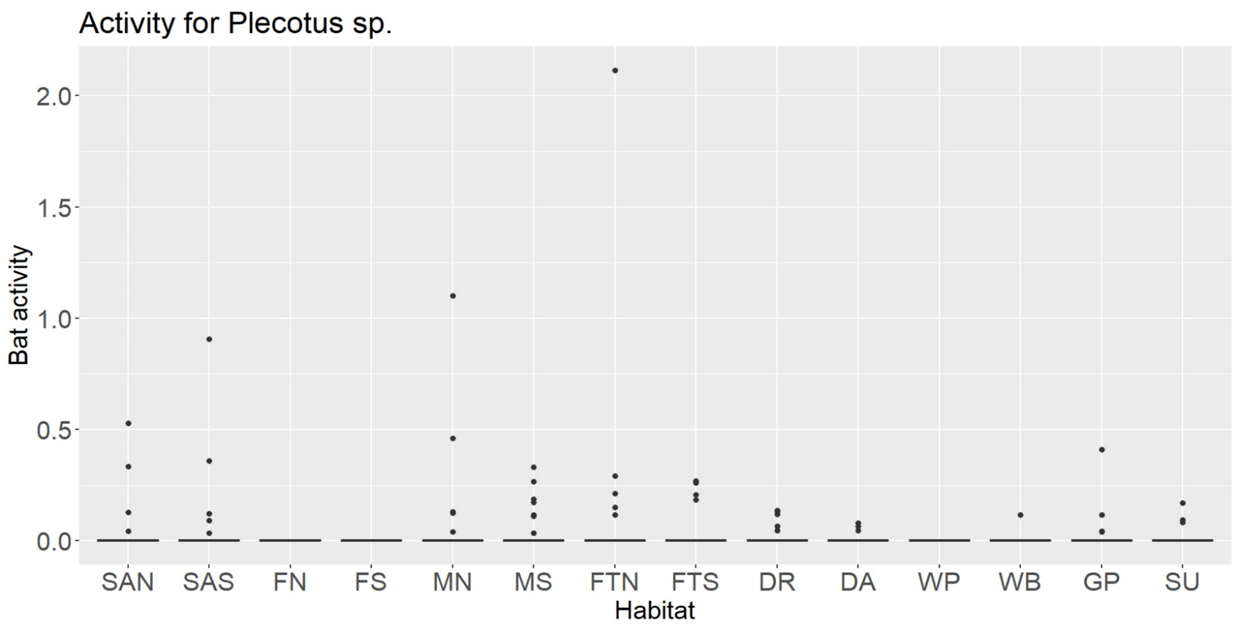

Fig. 24 *Mean activity levels for Plecotus sp. in the 14 sampled habitats*

The last occurring species, in the national park and its surrounding, with decreasing populations – according to the IUCN (2022) – is *R. ferrumequinum.* As only one single call was recorded during the entire monitoring no further statements about preferences of the species can be made.

3.6 Parameter influence on bat activity and species richness

To determine which parameters influenced bat activity or species richness the most, several glm were conducted. The first model was used to investigate the impact on bat activity. Activity data were log transformed and as family 'gaussian' was chosen because best results were achieved with this combination. Conducting an anova for every model revealed, that the habitat type and the distance to the next village have a significant explanatory power for bat activity (Fig. 25). The AIC was lowest when including only the parameters 'habitat', 'moon', 'distance to the next village' and 'wind' (AIC = 1093). Correlating variables were not included in the same model, hence not all variables can be found in Fig. 25. Including mean temperature, instead of wind, into the model led to an AIC of 1095.3, while the p-value was 0.6717, far from being significant. Habitat type and distance to the next village, influenced bat activity significantly. The latter one affects bat activity positively. The further a sample point is located from a village, the more bat activity was measured.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
habitat	13	196.3	15.100	10.040	<2e-16	***
moon	1	4.6	4.562	3.033	0.0826	.
distvillage	1	6.1	6.050	4.023	0.0457	*
wind	1	3.7	3.656	2.431	0.1200	
Residuals	314	472.3	1.504			

Fig. 25 *Results of the anova for a glm conducted to explain bat activity levels.*

The Pearson correlation test revealed that wind and temperature (r = 0.27) as well as wind and rain (r = 0.23) show a – however moderate – correlation. Also light and distance to the next village (r = 0.16) are correlating variables. The same applies for cloud cover and moon (r = 0.27). Using the interpretation of Cohen all these correlations are moderately (1988). Strong correlations are found for mean wind, with minimum (r = 0.71) respectively maximum (r = 0.91) wind speeds. Same applies to mean with minimum (r = 0.91) and maximum (r = 0.79) temperature.

Since activity rates are not the only criteria to provide information about bat species status in a region, another glm was carried out to see which parameters have influenced species richness (Fig. 26). Also here 'gaussian' was chosen as family function. The AIC for this model, including all parameters but no correlating ones, was 1785.107. The summary of the anova (Fig. 26) shows that three factors have a significant influence on the number of occurring species. Mean temperature, distance to the next water body and moon illumination affected how many different bat species were recorded per sample point. Rain shows a trend to affect bat activity levels.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
temperature	1	157	157.21	12.509	0.000464	***
distawater	1	155	154.64	12.304	0.000516	***
moon	1	58	57.98	4.613	0.032468	*
rain	1	36	35.96	2.861	0.091690	.
distvillage	1	9	9.01	0.717	0.397753	
Residuals	325	4085	12.57			

Fig. 26 *Results of the anova for a glm conducted to explain species richness.*

As displayed in Fig. 27 temperature influences species richness positively. The higher the mean temperature for a night the more species were recorded. For the distance to the next water body it is reversed (Fig. 28). The higher the distance to the next water area the fewer species were detected.

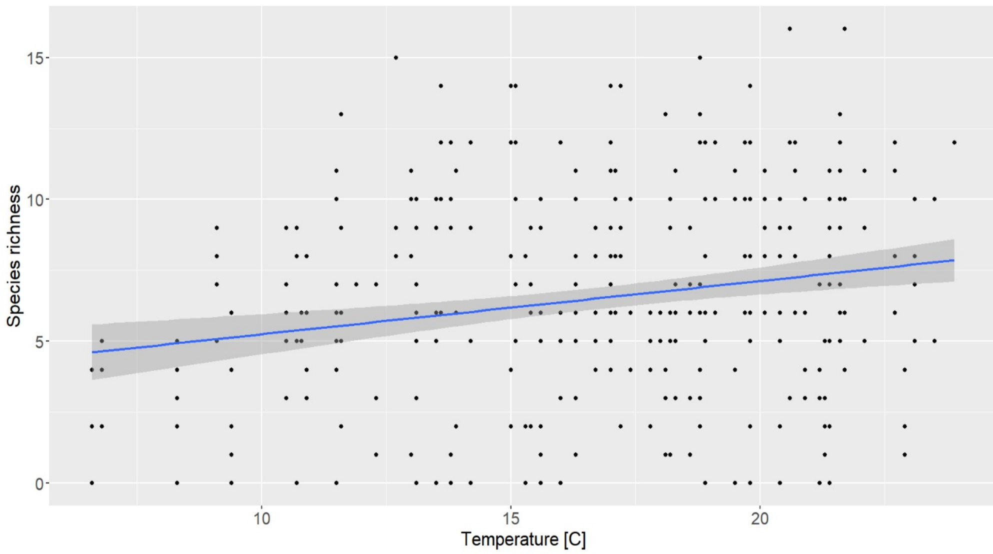

Fig. 27 *Visualization of glm result: species richness as a function of mean temperature (°C) per night*

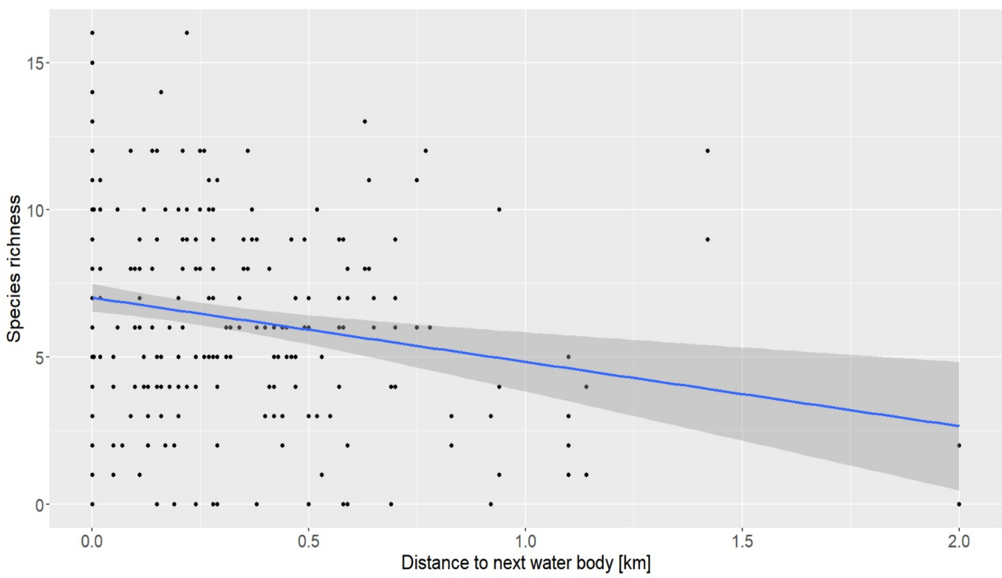

Fig. 28 *Visualization of glm result: species richness as a function of distance to next water body (km)*

Same applies to moon illumination, the more the moon was illuminated, the fewer species were found (Fig. 29). The effect of the moon is not as strong as temperature and the distance to the next water body though.

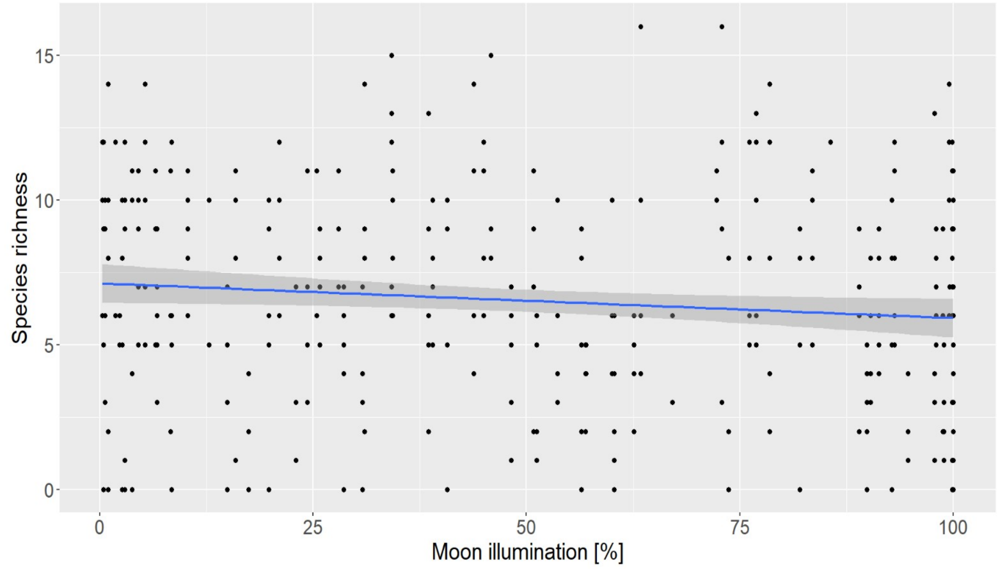

Fig. 29 *Visualization of glm result: species richness as a function of moon illumination (%)*

4 Discussion

4.1 Species richness, diversity and activity patterns in different habitats

Monitorings are usually conducted with an aim or the benefit to gain more general information about the studied species. On the one hand this study confirmed the higher bat species occurrence in a protected floodplain forest in comparison to the agriculturally used surroundings. Also it helped to understand which species preferably forages in which habitat. That makes decisions what areas are in need of protection, when focussing protection measurements on single species, easier. Therefore it is important to take a look at the species richness and in the next step at the species diversity. Merely because a habitat has a high species richness, does not automatically mean that it is worth implementing protection measures in this certain area. It can be of greater importance to check, in which habitats rare species occur that need further protection to prevent their populations from declining.

Hypothesis 1 has proven to be true (Fig. 6). The overall activity and also species richness in the national park was higher than in the *Marchfeld* (Fig. 7 & 9). FTN, SAS and FTS were the habitat types with highest activities. As mentioned in the results, only ‘Gravel Pit’ shows activity levels that are comparable to habitats inside the Danube floodplains, which confirms hypothesis 4. GP show significantly higher activity levels in comparison to WP, WB and SU (Fig. 8). The foraging conditions for this habitat were optimal, as the water filled pits were all surrounded by trees and shrub vegetation. A single disadvantage, why it might not be used by some species, e.g.

M. bechsteinii and *M. alcathoe* (Fig. 18), is the missing connection to the national park (which is the closest contiguous forest area) by landscape elements as hedgerows or vegetated creeks (cf. Fig. 4). The lack of bat activity and also species richness for WP, WB and SU are partly explainable with the nature of the habitats. While WP and WB were densely vegetated and WP were additionally small and not linked to the national park, SU sample points mostly were in open areas on, or around agricultural fields. Only little or no taller vegetation could be found in the vicinity. These areas are mainly used by species of the LRE (Fig. 22), like *N. noctula*. Nevertheless the habitat *Sutten* was used significantly less in comparison to open habitats inside the national park (Fig. 8), which is consistent with other studies that found lower bat activities and species richness in intensively used agricultural areas (Froidevaux et al., 2022; Wickramasinghe et al., 2003). Although the *Marchfeld* contains some landscape elements that might serve as corridors for animals, its quality for bats is much lower than protected meadows in the conservation area, that are surrounded by forests or lower vegetation. In densely vegetated areas, only highly manoeuvrable species can be found and the majority of bat species avoids those areas (Ciechanowski, 2015). For habitats inside the national park it is striking that neither bat activity in general (Fig. 7) nor species richness (Fig. 9) is high at the forest sample points. Due to the dense vegetation, forest tracks are obviously preferred flying paths for the mammals (Fig. 12).
Activity patterns after a flooding event were analysed by comparing sample points north and south of the dam three weeks after the Danube flooding in July 2021. No significant difference was found, although the temporary water areas south of the dam probably led to an increase in bat prey occurrence. As confirmed by other studies bat activity is strongly linked with prey availability (e.g. Ancillotto et al., 2015; Park, 2015) therefore the result was unexpected. The standing water puddles, after the flooding, provided an optimal habitat for insects to reproduce and so it was perceived during sampling. Around the newly emerged water bodies, insect density felt higher than in non-inundates areas. Still the results showed that no significant differences in bat activity could be verified, although activity levels north and south of the dam differed more during the three weeks time period than for the whole monitoring.

4.2 Guild and species-specific habitat preferences

The results of guild specific responses to habitat use are consistent with the findings of other studies (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2022) and confirm hypothesis 5, postulated in the introduction. Short range echolocators (SRE), were mainly recorded along forest tracks (Fig. 20). Also they have higher activity values in forest points in comparison to mid range echolocators (MRE) and especially low range echolocators (LRE) which was to expect, as many species of the SRE guild are forest dwellers like *B. barbastellus* and *M. bechsteinii* (Ancillotto et al., 2015; Dietz & Kiefer, 2020). All *Myotis* species – which make up for most of the SRE guild – call on high frequencies which makes their calls optimal for foraging close to vegetation why they are also known as narrow-space foragers (Frey-Ehrenbold et al., 2013). So it was unexpected that activity rates of the SRE were lowest in woodland patches in the *Marchfeld*. Despite the disadvantages of this habitat, it is interesting that activity rates for MRE and LRE in woodland patches were higher. This in turn could be explained by the already mentioned unequal detection of bat species. SRE are, with a higher probability, less often recorded because of their – as already displayed in their name – shorter call range (Frey-Ehrenbold et al., 2013). However, results show that even activity rates in SU were higher than in WP, for SRE. In comparison to *Sutten*, meadows were surrounded by forest or at least higher shrub vegetation, which explains the relatively high activity rates of SRE along the MN and MS sample points. Still, in comparison to MRE and LRE their activity rates are low for meadow sites.

Species from the MRE guild are usually known to forage along vegetation edges (Russo et al., 2016; Frey-Ehrenbold et al., 2013). Therefore, it is unusual that highest activity rates in the national park are found along forest tracks (Fig. 21). In the *Marchfeld* highest bat activity of MRE were found for the habitat GP. The combination of water areas and vegetation was very attractive for every echolocation guild, as they all preferred gravel pits over the other sampled landscape elements in the *Marchfeld*. Still MRE shows the highest activity rates for this habitat type. Surprising is, that meadow sites were not their most used foraging habitat in the national park. MS and MN would have been predestined areas to forage, as the batcorders were usually not placed in the middle of the meadow but several meters from the next vegetation edge. However, it must be mentioned that especially for MS, the MRE activity rates were quite high as well. As forest tracks, depending on their size, often function as vegetation edges themselves and bats use such tracks as transfer routes, e.g. from the roost to a foraging site, the high presence of MRE along these habitats can be explained as well.

The avoidance of densely forested areas as foraging habitat was even more evident for the species of LRE, than for MRE. Species of the LRE guild preferably forage in open areas (Frey-Ehrenbold et al., 2013) which is highlighted in Fig. 22. Sidearms south of the dam and both meadow habitats were the preferred foraging grounds for LRE in the Danube floodplains, while they mostly used gravel pits and *Sutten* outside the national park. Interestingly MRE foraged more in *Sutten* than species of the LRE, although the latter ones are specialized to forage in open areas. Anyhow, other open habitats that were not used much for foraging by the other guilds are the Danube and the dam itself. Both were regularly frequented by species of the LRE guild (Fig. 22).

4.2.1 Pipistrelloids

The dominant species in nearly every habitat in the *Donau-Auen* and the *Marchfeld* was *P. pygmaeus* which corresponds the findings of the monitoring by BÜRGER & PLANK (2017). Because the species is ubiquitous, it seems that no incentives need to be provided to increase population numbers in the sampled area. Especially gravel pits are important foraging habitats for *P. pygmaeus* although these landscape elements are not linked to the park at all. According to

BÜRGER & PLANK this species depends on standing waters for hunting, to a high degree, which is consistent with their high abundance in GP (2017).

P. pipistrellus on the contrary, was recorded much less frequently. Since both species were often occurring simultaneously in the foraging grounds, some calls of the species were also assigned to the call group *Phoch*. Also misidentifications between *P. pygmaeus* and *P. pipistrellus* are possible. The latter species was mostly recorded around gravel pits as well. Generally they preferably foraged around water bodies as the most frequented habitats were sidearms and the Danube itself (Fig. 10 & 15). In comparison to *P. pygmaeus,* it does not seem to be important for them, whether the water is standing or running. Only water bodies outside the national park were nearly not used at all by *P. pipistrellus*. This is not a peculiarity for the species but can be explained by the general low activity rates in this habitat (Fig. 17). Sample points of 'Water Body' in the *Marchfeld* were all linked with the national park and surrounded by vegetation which should provide perfect foraging conditions for most bat species. Besides the dense vegetation, water levels sometimes were very low or the streambed was completely dried out, which explains the lack of activity and species richness. The small streams may function as corridors, but outside the vegetation and thus not directly where the batcorders were placed.

The call group *Pmid* was mainly recorded in open areas, like the Danube, meadows and gravel pits. As *P. kuhlii* and *P*. *nathusii* are hardly distinguishable by their foraging calls, no statement can be made about a single species. According to BÜRGER & PLANK it is more likely to find the latter ones in the Danube floodplains as *P. kuhlii* tends to avoid forested areas (2017). However, during the monitoring most calls of *Pmid* were not made in forest habitats as it would be expected of *P. nathusii* but in open landscapes of the national park as well as in the *Marchfeld*. *P. kuhlii* on the contrary is known to be a synathropic species that can perfectly deal with anthropogenic shaped landscapes and is found in agricultural areas (Dietz & Kiefer, 2020). Therefore it is likely that call recordings in the habitat type '*Sutten*' are mainly from *P. kuhlii* (Fig. 19).

4.2.2 Nyctaloids

Another frequently recorded species during the monitoring was *N. noctula*. Typical for open space foragers, the species was mainly detected around meadow sites, the dam, the Danube and along sidearms – interestingly mainly south of the dam. Forest sites were avoided. All findings for *N. noctula* are according to other studies (Bürger & Plank, 2017; Ciechanowski, 2015). Although their populations for the sampled region seem to be stable, it is important to further monitor them as no information on their security status in Austria is available by the IUCN's red list. The same applies to *N. leisleri*. Unlike *N. noctula* it was detected very rarely during the monitoring. Only for the habitat type 'Meadow' it shows slightly higher activity levels (Fig. 13). According to DIETZ & KIEFER, *N. leisleri* actually is a typical forest dweller though it was not recorded in any forest habitat in this monitoring (Fig. 11, 12 & 16) (2020). It is probable that their calls are contained in the call groups *Nycmi* and *Nyctaloid*. Also calls of *V. murinus* and *E. serotinus* are hidden in those call groups as they are often hard to distinguish. Both species have generally low activity levels which is, on the one hand related to their calls, that are hard to discriminate and on the other hand they do not seem to be typical inhabitants of the region. Especially *V. murinus* was seldom detected in the 2016/17 monitoring as well (Bürger & Plank, 2017). With the little amount of recordings for most of the *Nyctaloid* call group*,* it is not possible to gain more reliable information on habitat preferences of single species.

4.2.3 Myotis

Regarding the *Myotis* species, it is more difficult to make general statements about their occurrence, as their calls are hard to determinate. As a consequence only fewer data on single species are available in comparison to *Nyctaloids* and *Pipistrelloids*. The call groups *Mkm* and *Myotis sp*. are dominating. Still it is interesting to take a closer look at some species.

M. daubentonii has stable populations in Austria (IUCN 2022) and is also present in the national park and its surrounding (Bürger & Plank, 2017). During the study the species was not detected often which may be due to the high risk of confusion with other species (mainly of the call group *Mkm)*. *M. daubentonii* is known to be at typical water bat. Therefore it is surprising, that it was only rarely detected around gravel pits (Fig. 18). In the national park the species was present along the Danube and its sidearms. The avoidance of gravel pits for foraging, despite offering optimal conditions, might be due to the agricultural surrounding, as *M. daubentonii* preferably uses linear structures to arrive at its foraging habitats (Dietz & Kiefer, 2020) and no sampled gravel pit is linked with the national park by landscape elements.

The detections of *M. dascyneme* must be regarded with caution. Their calls are easy to confuse with other *Myotis* species and were not clearly detected in the monitoring of BÜRGER & PLANK (2017). It is possible that the calls of the 2021 monitoring were confused with other *Myotis* calls during determination although best efforts were made. The Danube floodplain region would offer good foraging grounds and roosting sites for the species, as it mostly hunts in water-rich areas and uses, amongst others, attics and church towers as roost (Dietz & Kiefer, 2020). *M. dascyneme* prefers standing or slow running waters which are found in the habitats ‘Sidearm’, ‘Water Body’ and ‘Gravel Pit’. It was recorded in two of the three water-rich habitats, only around WB it was not found. Interestingly it shows comparably high abundances around forest tracks (Fig. 12) and also the Danube itself was used as foraging ground (Fig. 15).

M. alcathoe is considered a typical forest species which is partly reflected in the results (Fig. 11 & 12). It is one of the few species that were recorded inside the forest and not only along forest tracks. The species was found in every other habitat inside the national park – though to a small extent – except for the dam. In the *Marchfeld* on the contrary it was nearly not found at all, except for one detection next to a creek. Inside the forest *M. alcathoe* preferably forages in the canopy (Dietz & Kiefer, 2020) which explains why the species was detected in habitats with denser vegetation that was avoided by most other species.

Another of the *Myotis* species that is interesting to take a closer look at is *M. bechsteinii*. It belongs to the threatened species in Austria (cf. chapter 3.5). Due to the low occurrence during the monitoring it is hard to make any statements about its habitat preferences in the *Nationalpark Donau-Auen* and the *Marchfeld*. As a forest dweller, the species usually uses tree holes as roost and changes it every 2 – 3 days (Dietz & Kiefer, 2020). Actually the protected Danube floodplains would offer perfect living conditions for *M. bechsteinii*, with a high amount of older tree stands. One explanation for the small number of its recordings is the risk of confusion with other *Myotis* calls, e.g. of *M. daubentonii* or the call group *Mbart*. Hence some calls of the species might be hidden in the call group *Mkm*. Another factor that might have influenced the low occurrence in the studied area are the high habitat requirements of the species (Bürger & Plank, 2017) and its preference for old oak forests (Dietz & Kiefer, 2020), which can be found but are not the main tree species in the Danube floodplain forest.

4.2.4 *B. barbastellus, Plecotus sp.* and *R. ferrumequinum*

As mentioned in chapter 3.5, *B. barbastellus* belongs to the species with declining populations in Austria (IUCN 2022). In the national park it was mainly found along forest paths (Fig. 23), which was to expect as the species is a typical forest bat. Forest sites itself and also woodland patches outside the national park, were only rarely or not frequented at all – in case of FS – by *B. barbastellus*. As it uses floodplain forests not only for foraging but also as roost site (Bürger & Plank, 2017), the forested areas are an important habitat type for *B. barbastellus* in the region, especially as it was only rarely detected in the *Marchfeld*. It is possible that the species was more abundant but not always detected, because it preferably hunts in the canopy and its calls have a short range (Dietz & Kiefer, 2020). If no, or only strongly logged forest is available, *B. barbastellus* is able to adapt and uses alternative roosts. Instead of tree bark and tree holes it uses crevices of wall coverings or rocks and adapts to the existing landscape (Ancillotto et al., 2015). Still unmanaged forests increase the roosting availability for *B. barbastellus* and additionally seem to facilitate reproduction, as females preferably choose warmer roosts than males, which often is a given factor in deadwood trees on clearings (Russo et al., 2010). Therefore the *Nationalpark Donau-Auen* can be an important area for the species to increase its populations again.

As the foraging calls of *P. austriacus* and *P. auritus* are not distinguishable it was necessary to group them to *Plecotus sp.*. For the sampled region less information on these two species are available than on *B. barbastellus*. As *P. austriacus* shows declining populations in Austria, while *P. auritus* has stable ones (IUCN 2022), it would be necessary to use additional monitoring methods like net catches, photo traps and roost controls to gain a broader overview about their occurrence in the area. *P. austriacus* is known to be a typical synanthropic species that preferably roosts in villages. *P. auritus* on the contrary prefers foraging in forest areas, open meadow landscapes or parks (Dietz & Kiefer, 2020). During the monitoring conducted for this study, the most used habitats of *Plecotus sp.* were forest tracks north and south of the dam, meadows south of the dam, as well as the river and sidearms (Fig. 24). The occurrence of both species could be proofed during the monitoring of BÜRGER & PLANK (2017). As floodplain forests usually are no foraging area for the threatened species *P. austriacus,* it is possible that a major part of the calls are from *P. auritus,* while *P. austriacus* might have been more present in the *Marchfeld* – although to a low extent.

R. ferrumequinum is as well listed as threatened in Austria (IUCN 2022). As only one call was recorded during the entire monitoring no statements about the species can be made. It would be interesting to further monitor them in the Danube floodplain region. Actually the conditions would be optimal for the species, as they forage in floodplain forests and prefer mosaic landscapes with high structural diversity (Dietz & Kiefer, 2020). Why the species is only rarely present in the region is not clear. Again, their calls are more easily missed in comparison to other species due to their shorter call range but it does not explain their low occurrence during the monitoring. *R. ferrumequinum* is generally not often found in Lower Austria according to BÜRGER & PLANK (2017).

4.3 Limitations of the study and influencing variables on bat activity and species richness

When interpreting the results of the acoustic bat monitoring, some limitations of the study conducted must be discussed and considered.

One limitation is the acoustic monitoring with batcorders itself. Even if it has a lot of benefits, as a non-invasive study method with the possibility to take large-scale samples, also disadvantages need to be taken into account. The number of species revealed during a bioacoustic monitoring might be skewed, as not all species are equally well detected by the devices. Bats that call on higher frequencies and whose calls have shorter ranges can be overlooked by batcorders more easily (Russo & Voigt, 2016,). In this study, species that were at risk of being recorded to a lower amount are all *Myotis* species, as well as *Plecotus sp.* and *B. barbastellus*. Therefore, the recorded data were only used for comparing the different sampled habitats and look for habitat preferences of single species, as the recording conditions were equal at every sample point, as far as possible.

Another limitation of batcorder monitorings is the low amount of information about the recorded animals. The sex, age and other physical characteristics remain completely unknown (Russo & Voigt, 2016). Net catches would be needed to gain more information, e.g. on whether females reproduce in the area.

A further limitation of the conducted study becomes apparent in the weather data. Most meteorological parameters were not directly measured at each sample point, but regional data were considered (cf. Chapter 2.2.2). For mean temperature and mean, minimum and maximum wind speeds, weather data from the closest meteorological station were used. In particular, the wind speeds can only be regarded as guide values, since the speeds are different for an open meadow and a protected forest area. Since cloud cover and precipitation data also originate from the weather station, they similarly have the potential to deviate from the actual conditions, but the variability of these parameters is not expected to be as high as the wind speeds.

The results of the models conducted to find out which variables significantly influenced bat activity and species richness were partly surprising. The first model (Fig. 25) showed that habitats and the distance to the next village influence bat activity. The further a sample point was located from the next village, the higher were activity levels. This is reasonable, as the most detected species preferably forage inside forested areas and partly roost there (Dietz & Kiefer, 2020).

An influence of mean or minimum temperature and mean or maximum wind speeds on bat activity was expected, as it is mentioned in various papers (Froidevaux et al., 2022; Martin et al., 2017). An explanation for wind speed having no significant influence on bat activity in this study, are the generally low wind speeds. A paper of MARTIN ET AL. mentions that wind affects bat activity negatively, starting from speeds of 6 m/s (2017). This corresponds to 21.6 km/h which was only rarely reached during the monitoring. The same explanation is valid for wind speeds not influencing the number of occurring species (Fig. 26). As displayed in Fig. 27, mean temperature positively affects species richness. For mean temperature and bat activity this trend is not visible. For the second model conducted, that should display influencing variables on species richness, not only mean temperature but also distance to the next water body and moon illumination showed a significant effect (Fig. 28 & 29). Also rain shows a trend to negatively influence bat activity levels. All other variables taken into account did not affect species richness.

4.4 Mosaic landscape vs. continuous forest

Since the question was, whether it is beneficial for bats to keep open areas in otherwise contiguous forest areas, it is necessary to scrutinize the habitats 'Forest Track' and 'Meadow'. For bat activity levels only FTN and MN differ significantly but as the t- value shows not to a great extent (Fig. 8). Also both habitats show high species richness. For meadows it is slightly higher as only *R. ferrumequinum* was not detected, while along forest tracks additionally *N. leisleri* was not recorded (Fig. 12) but its calls probably hide in *Nycmi* or *Nyctaloid*. As not only species richness is of importance but also species diversity, it is necessary to look at the abundances of single species. Since species composition for the two habitats is quite similar, in forest tracks *B. barbastellus* was more abundant (Fig. 12), while meadows show higher activity levels of *N. noctula* and the call groups *Nycmi* and *Pmid* (Fig. 13). Along forest tracks, specialized species show higher activity levels, while on meadows more generalists (from the call group *Nyctaloid*) were abundant. According to ETHIER & FAHRIG, especially edge-foragers should benefit of mosaic landscapes, by increasing the amount of vegetation edges (2011). Species that belong, amongst others, to the edge-foragers are *P. pygmaeus* and *pipistrellus*. While the first one was more abundant in closed forest paths, the latter one and also the call group *Phoch* were more abundant around meadows. Also some *Myotis* species preferably forage along vegetation edges, as *M. daubentonii, M. myotis* and *Mbart* (Bürger & Plank, 2017). As their occurrence in MN and MS is lower in comparison to forest tracks, it is beneficial to look at other vegetation edges and open areas in the national park.

Also water areas like SAN and SAS fulfil these requirements. Both habitats show high activity levels and species richness (Fig. 7 & 9). All three edge *Myotis* foragers were abundant in the habitat and especially the call group *Mkm* shows high activity levels (Fig. 10).

In the *Marchfeld* the situation was different, as the habitat type 'Gravel Pit' shows significantly higher activity levels and species richness (Fig. 7, 8 & 9). Actually the *Marchfeld* area can not be described as a mosaic landscape, because landscape elements were really small in comparison to agricultural fields that are dominating the region (cf. Fig. 4). Still some vegetation edges exist. Due to the nature of the monitoring, the vegetation edges themselves were not sampled but the batcorders were installed inside the landscape elements – at least this is valid for WB and WP. Gravel pits on the contrary, are an important foraging ground in the *Marchfeld* for most bat species. *Sutten,* that were often located on field edges*,* were mainly used by open space foragers like *Nyctaloids* and also *Pmid.*

5 Conclusion

With all these information, it can again be confirmed that protecting nature as conservation areas is helpful for species diversity. For future bat monitorings in the area it would be interesting to additional monitor indicator species to see whether bats can be used as indicators for biodiversity themselves. As species-specific or at least guild specific habitat preferences were detected throughout the study, it is possible that only certain species or call groups are suitable as indicators for the region.

Keeping areas artificially open, as it is done with the meadows in the *Donau-Auen* and preserving respectively renaturating sidearms of the Danube in the national park area, can be considered beneficial for bats. The overall bat activity in the *Donau-Auen* is high and so is species richness. The national park is an important environment for bats, particularly as the region in between Vienna and Bratislava is shaped by agriculture or urban areas. Especially species that are specialized to live in a certain habitat and have high roost demands can profit of the park, as the well protected mosaic landscape offers various habitats that fulfil a diverse range of requirements. For future bat monitorings in the national park and its surrounding, the data of this monitoring can serve as basis of comparison.

IV Literature

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V Appendix

	SAN	SAS	FN	FS	MN	MS	FTN	FTS	DR	DA	WB	WP	GP	SU
SAN		-0.97855	1.6341	2.771	-2.5038	-0.79027	-2.5383	-2.8535	0.786	0.21927	0.23504	2.5338	1.4814	0.85399
SAS	0.3353		1.1095	1.1581	0.13246	0.85427	-1.3702	-0.61687	1.0432	0.99928	1.006	1.1458	1.0834	1.0528
FN	0.1116	0.2757		-1	2.9156	1.7322	2.644	3.0805	0.96071	1.2391	0.082857	-1.0205	-0.52992	-0.28557
FS	0.008887	0.2557	0.3506		-3.0891	-2.1844	-2.6839	-3.1705	-2.2661	-2.1125	-1.1207	-1	-2.7048	-7772
MN	0.01773	0.8953	0.006639	0.004397		2.0268	-1.8056	-1.2645	2.7134	2.5523	2.4722	3.0499	2.854	2.7326
MS	0.4338	0.3993	0.09219	0.03716	0.04964		2.4324	2.6023	-1.2624	-0.90642	0.082857	2.0855	1.6037	1.3045
FTN	0.01618	0.1757	0.01257	0.01143	0.07924	0.02063		1.0678	2.5908	2.5543	2.5551	2.6739	2.6234	2.5981
FTS	0.007675	0.5401	0.004362	0.003494	0.2123	0.01374	0.2913		2.9677	2.884	2.8606	3.1491	3.0416	2.9808
DR	0.4347	0.3049	0.3459	0.03013	0.01087	0.2147	0.01429	0.005799		-0.47594	-0.2193	1.9638	0.68797	0.1304
DA	0.8271	0.3253	0.2235	0.0428	0.01569	0.3695	0.01556	0.007087	0.636		0.082857	1.9204	1.038	0.5581
WB	0.8157	0.3219	0.9344	0.2751	0.01812	0.9344	0.01546	0.007304	0.828	0.9344		1.0205	0.52992	0.28557
WP	0.01559	0.2606	0.3189	0.3299	0.004846	0.04579	0.0117	0.003689	0.05713	0.06356	0.3189		-2.0625	-1.5333
GP	0.1453	0.287	0.6013	0.01502	0.007834	0.1188	0.01321	0.004841	0.4948	0.3057	0.6013	0.05033		0.45474
SU	0.3973	0.3005	0.772	0.09344	0.01031	0.1998	0.01403	0.005595	0.8969	0.5794	0.7772	0.1421	0.6533	

Fig. 30 *Results of the Welch two-sample t-test for differences between the habitats for bat activity of B. barbastellus. p- values are found in the lower part. Green fields indicate a significant difference. The upper part displays t-values to show how strongly the difference is.*

	SAN	SAS	FN	FS	MN	MS	FTN	FTS	DR	DA	WB	WP	GP	SU
SAN		-0.59577	1.6427	1.6427	-0.85618	-0.33888	-0.95032	0.08702	0.72566	1.342	1.3614	1.6427	-0.095797	0.17671
SAS	0.5544		1.4298	1.4298	-0.38624	0.41892	-0.78871	0.67042	1.0057	1.2932	1.3007	1.4298	0.50017	0.72243
FN	0.1094	0.1628		NA	-1.4017	-2.4828	-1.1283	-2.0922	-2.5258	-1.7202	-1	NA	-1.395	-2.0896
FS	0.1094	0.1628	NA		-1.4017	-2.4828	-1.1283	-2.0922	-2.5258	-1.7202	-1	NA	-1.395	-2.0896
MN	0.3978	0.7009	0.1707	0.1707		0.73486	-0.6165	0.90658	1.1275	1.3155	1.326	1.4047	0.78746	0.94165
MS	0.7358	0.6775	0.01907	0.01907	0.4676		-0.90551	0.49364	1.3325	2.1062	2.1088	2.4828	0.18597	0.6063
FTN	0.3489	0.4356	0.2676	0.2676	0.5411	0.3719		0.96404	1.0356	1.0984	1.1025	1.1283	0.9306	0.97555
FTS	0.9309	0.5067	0.04498	0.04498	0.3714	0.6234	0.3422		0.81363	1.6655	1.6735	-2.0922	-0.17811	0.10584
DR	0.472	0.3219	0.01652	0.01652	0.2686	0.1905	0.3081	0.4203		1.5443	1.4975	-2.5258	-0.69216	-0.72271
DA	0.1878	0.2054	0.09536	0.09536	0.1986	0.04332	0.2802	0.1053	0.1292		0.13914	1.7202	-1.1663	-1.6296
WB	0.1812	0.2003	0.3287	0.3287	0.1951	0.04247	0.2785	0.1028	0.1402	0.8901		1	-1.1866	-1.6361
WP	0.1094	0.1628	NA	NA	0.1707	0.01907	0.2676	0.04498	0.01652	0.09536	0.3287		-1.395	-2.0896
GP	0.9242	0.6193	0.181	0.181	0.436	0.8537	0.3588	0.8599	0.497	0.2591	0.2507	0.181		0.25375
SU	0.8604	0.4746	0.05199	0.05199	0.3535	0.5473	0.3365	0.9162	0.4763	0.1197	0.1165	0.05199	0.8017	

Fig. 31 *Results of the Welch two-sample t-test for differences between the habitats for bat activity of Plecotus sp.. p-values are found in the lower part. Green fields indicate a significant difference. The upper part displays t-values to show how strongly the difference is.*