Fly me a river – bat activity along regulated rivers in Northern Sweden

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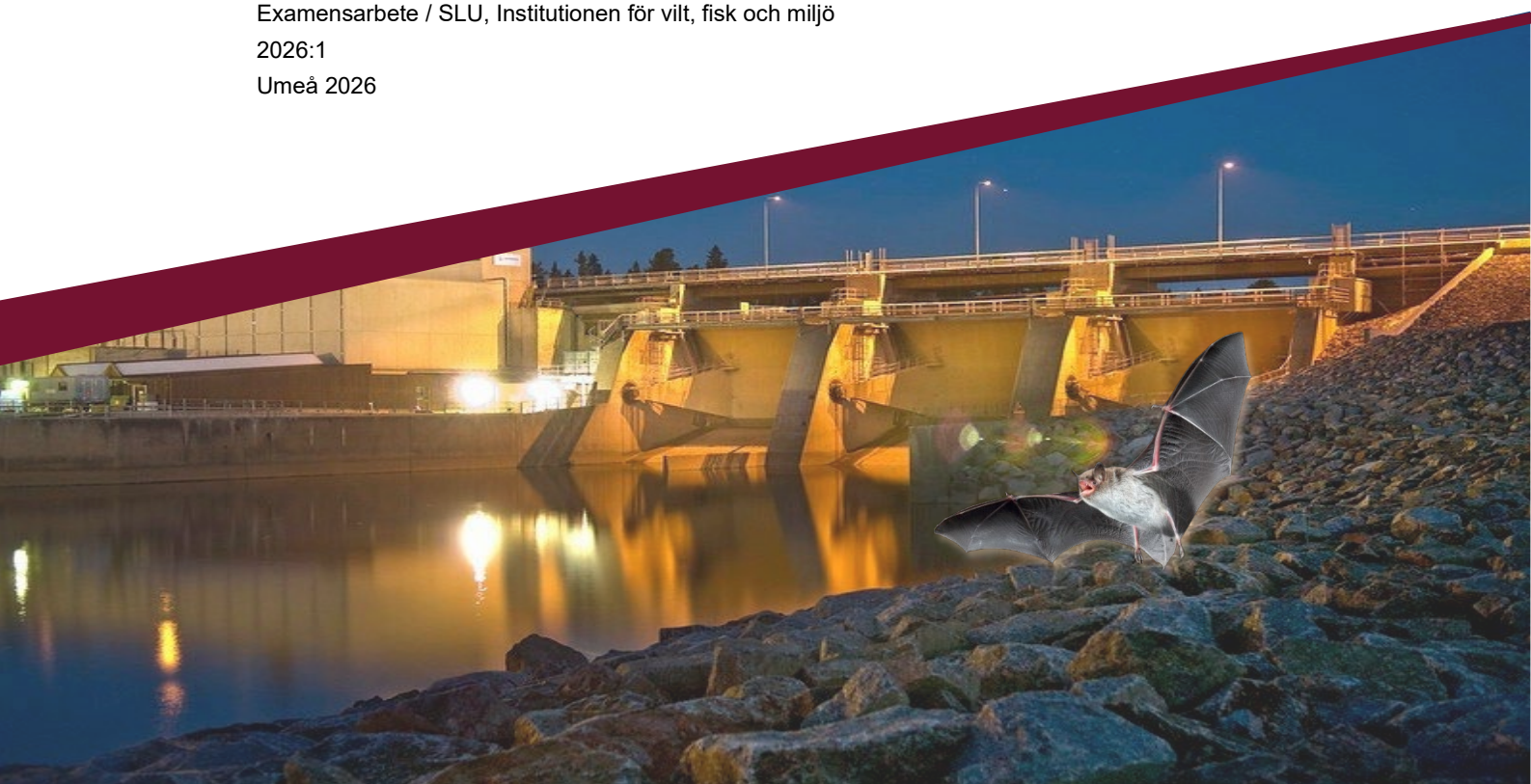

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Abstract

In Northern Fennoscandia, the installation of hydropower plants has influenced the hydrological and ecological condition of almost all riverine and riparian ecosystems. River regulation can have negative effects on ecosystems through lowered species diversity, declining populations as well as densities. Bats are important indicator species in riparian ecosystems and negative impacts of hydropower on invertebrate food species for bats may be visible through changes in bat diversity, activity and population abundance. As the main bat species in this region, Northern bat *Eptesicus nilssonii*, heavily depends on insects. However, there is little knowledge on how river regulation by hydropower affects bat activity.

In this study, I compared the activity of *E. nilssonii* and other detected species across a gradient of river regulation in 31 sites widely distributed throughout northern Sweden. Bats can be easily detected using audio recorders. Specifically, the project aims to evaluate in the northern rivers:

- Occurrence and timing of bat detections, especially of *E.nilssonii*

- Variation of bat activity over time, regulation, and riverbank habitat parameters - habitat heterogeneity (represented through variability of slope and NDVI)

I found a strong seasonality of bat detections with a strong peak 07th to 13th August, likely due to the bright summer nights prior to that. Surprisingly, I identified bats of the genus *Myotis* as often as *E. nilssonii*, even at the northernmost locations. My results show that in this region, latitude is the strongest factor controlling bat activity, as we approach the limit of the distribution range. Through modelling I further found river regulation, represented by the amount of zero-flow hours, to be a major negative influence. I therefore attest an effect of hydropower operations on bat activity in Northern Sweden. This highlights the strength of this indicator for steering and monitoring restoration efforts. However, behavioural patterns and drivers for bat activity across the landscape need to be solidified by further research.

Keywords: Bat activity, habitat index, riparian zones, river regulation, hydropower

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Abbreviations

a	Year
AIC	Akaike information criterion
Enil	*Eptesicus nilssonii*
ha	Hectare
m asl	Meters above sea level
MQ	Mean annual flow/discharge
Ms	Millisecond
m^3/s	Cubic meters per second
n; N	Number
NDVI	Normalized difference vegetation index
RBF	Richard-Baker flashiness index
ur	Unregulated

1. Introduction

1.1 Hydropower in Sweden

Humans have modified rivers for many different purposes. These include measures for supplying water for irrigation and drinking water, timber floating and accessibility for boats as well as power generation (Poff et al. 1997). Today, Sweden operates about 2100 hydropower plants that cover about 40 % of the country's electricity production. A significant amount of these is located along the large rivers in the northern part of the country. Investments during the 20th century led to the development of a tight net of hydropower plants (Xylia et al. 2024). Hydropower dams utilize the natural fall height of a stream, which depends on the geomorphology of the catchment. Typically for this region, multiple hydropower plants are lined up and form cascades of reservoirs (Renöfält et al. 2010). Because of that, these regulated systems seem more like chains of lakes than large rivers. Most hydropower dams in Sweden were built without fish migration pathways and without a minimum discharge value, posing a threat to fish and other environmental factors (Renöfält et al. 2010; Xylia et al. 2024). Accordingly, ecological concerns are rising and questioning the sustainability of hydropower plants (Renöfält et al. 2010). At the same time, climate change and the increasing demand for renewable energy sources fuel the expansion of hydropower production (Renöfält et al. 2010; Xylia et al. 2024).

1.2 Flow alterations by dams

By building dams we significantly alter stream flow, which is considered as "master variable" determining the ecological status, i.e. species occurrence, prevalence and distributions, of the rivers (Poff et al. 1997). Not just the river itself, but also the associated aquatic ecosystems are influenced by river exploitation, including groundwater, soil water, wetlands and riparian areas.

The flow regime of a river consists mainly of the amount of discharge on different temporal scales: minutes to hours, days to months, seasons to years and decades (Zimmerman et al. 2010). Together with the base flow, floods of varying intensity and frequency shape the morphology and determine the species composition of the river and the riparian zone. In natural systems, this is highly dependent on the regional climate and topography of the catchment (Poff et al. 1997). In a tight feedback interaction with the landscape, rivers also shape their own environment. This means, based on their physical properties, rivers distribute sediments and nutrients and control the water availability and microclimate of associated habitats (Poff et al. 1997; Renöfält et al. 2010). Accordingly, the aquatic and riparian species composition typically reflects the stream flow pattern

(Poff et al. 1997). With the building of dams for hydropower plants, the stream flow undergoes significant changes. Besides holding back sediments, dams replace natural variations in flow intensity with an artificial discharge pattern to ensure power generation according to the needs of the market (Poff et al. 1997; Renöfält et al. 2010). Upstream of hydropower plants, the reservoir likely develops lentic, i.e. stagnant, water body properties as substantial amounts of water are held back. Downstream of the dams, the stream flow directly depends on the outlet and typically becomes narrow and eroded (Poff et al. 1997). Often, installing hydropower plants also involves mechanical modifications to the streambed and riparian zone downstream of the plants. This includes channeling the stream and relocating extracted sediments into the riparian zone. Knobloch (2024) found a decrease in biodiversity on a heavily modified site as compared to less or non-modified sites in Northern Sweden.

1.3 Ecological implications

A natural river ecosystem in the boreal is characterized by typical lotic habitats and species compositions both in the river and in a pronounced riparian zone. All biota inhabiting these spaces are adapted to flow fluctuations in varying magnitude and frequency (Poff et al. 1997). However, hydropower dams alter these fluctuations beyond a natural level, where zero-flow events are common in regulated Swedish rivers. In these extreme scenarios, no water is released from the upstream reservoir (zero-flow), potentially turning the downstream channel into a lentic habitat or even having it dry out (Widén et al. 2021). This would lead to a devastating loss of all aquatic biota that are not mobile or adapted to it, including algae, plants and several species of macroinvertebrates.

Past studies have shown riparian vegetation cover and diversity to be lower on regulated than on free-flowing rivers in Northern Sweden (Jansson et al. 2000). By losing natural flow variability we likely also lose heterogeneity within the riparian zone, as the typical zonation is highly dependent on seasonal floods (Ström et al. 2012). This leads to a decrease in habitat heterogeneity and, therefore, biodiversity (Stein et al. 2014).

Arheimer & Lindström (2014) reported that 19 % of the discharge in Sweden's rivers is manipulated by river regulation. This is mainly because spring floods are being held back while discharge is increased during the winter (Renöfält et al. 2010). In Sweden, hydrological models showed that the intensity of spring floods decreased by 15 % due to regulation (Arheimer & Lindström 2014). The Richards-Baker flashiness index (RBF) was introduced as a measure for the fluctuations of discharge in a stream. It is based on changes in daily flow in relation to the total daily flow. By comparing natural patterns from unregulated rivers to those of regulated ones we can quantify the degree of regulation or disturbance a river experiences (Baker et al. 2004; Zimmerman et al. 2010).

When a stream is regulated by a hydropower plant, former fast-flowing rivers slow down and lose their flow variability (Poff et al. 1997). Some insect species in the boreal region like filter-feeding blackflies (*Simuliidae*) are dependent on fast flowing water and sensitive to sedimentation (Poff et al. 1997; Malmqvist et al. 2004). Accordingly, Jonsson (2013) found significantly lower biomasses of emerged aquatic insects in regulated rivers compared to free flowing rivers in the boreal region. Englund and Malmqvist (1996) showed a decreased diversity and abundance in macroinvertebrates in regulated streams in Northern Sweden and explained these results with heavily altered flow patterns. These and other insect groups also act as important food sources for predators like bats and birds and therefore connect aquatic and terrestrial ecosystems. Along regulated rivers, Strasevicius (2013) found that the Pied Flycatcher *Ficedula hypoleuca* had a lower breeding success than along unregulated rivers in Northern Sweden. This bird only feeds on insects and is therefore negatively impacted by river regulation and the associated decrease in insect populations. This can apply to both insects emerging from the water and insects that feed on riparian vegetation (Murakami & Nakano 2002). Jonsson, Strasevicius and Malmqvist (2012) also found higher cumulative densities of insect dependent bird species along unregulated rivers compared to regulated streams and suggest differences in the aquatic insect availability as a reason for this result.

1.4 Bats as indicator species

Bats represent another species group in the boreal forest that heavily depends on insects as a food source. As predators on a high trophic level, insectivorous bats tend to be sensitive to changes in the food web. Additionally, bats have a long life span and low fertility rates (Tuttle & Stevenson 1982), making population sizes responsive to environmental impacts. For these reasons, bats have been proposed as suitable bioindicators for rivers and forests (Jones et al. 2009; De Conno et al. 2018; Russo et al. 2021). Fukui et al. (2006) found a tight link between aquatic insect availability and bat activity in riparian zones. At the same time, Patriquin and Barclay (2003) report species dependent impacts of silvicultural methods on bats foraging in boreal forests. One major advantage of using bats is that they can easily be monitored using a passive acoustic approach with audio detectors.

The diversity, distribution and population dynamics of bats can be used as measures for the ecological quality/value of a landscape. A change of these parameters can indicate a changing environment (Jones et al. 2009; Russo et al. 2021). On a smaller scale, bat activity on a specific site represents the habitat quality. Assessing their dynamics is valuable for evaluating the impact of hydropower dams on the ecology of rivers and connected environments. We can use this information to steer and control mitigation and restoration measures.

The Northern bat, also referred to as Northern serotine, is considered the most common bat species in northern Scandinavia with its distribution ranging beyond the Arctic Circle (Rydell et al. 1994; Speakman et al. 2000; Wilson & Mittermeier 2019; Russ 2021). Its scientific name was recently updated to *Cnephaeus nilssonii* (Cláudio et al. 2023). For simplicity, I will stick with the commonly known former name *Eptesicus nilssonii* (*E. nilssonii* or *Enil)* in this paper. Because of its fast flight, *E. nilssonii* typically forage in open areas such as open forests, forest edges, lakes, rivers and pastures (Rydell 1986; Wilson & Mittermeier 2019). Associated with water bodies in Sweden, these insectivorous bats preferably hunt dipterans, moths and flies, between 3 and 30 mm in size (Rydell 1986). The IUCN presents this insectivorous bat species as of least concern (Coroiu 2016). In recent years, however, Rydell (2020) has reported declining numbers of *E. nilssonii* populations. At the same time, based on the Habitats Directive (EU) and the EUROBATS Agreement (UNEP), all bats are strictly protected species in Sweden and beyond. Combined monitoring as an indicator species could thus serve two purposes at the same time: protecting valuable species while also assessing human impacts on habitats and landscapes (De Conno et al. 2018).

1.5 Aim of the study

This study had two main aims:

- To assess the extent of bat activity across space and time in regulated vs unregulated sites
- To test the correlation between bat activity and the ecological status and extent of regulation at the study sites

The above aims were addressed by conducting field and remote assessments, bioacoustic monitoring of bat activity at these sites using sound recorders. Furthermore, I evaluated information on the riverbank ecology such as the naturalness of the riparian buffer, natural values of the surrounding forests as well as the extent of river regulation. In the context of this study, I expect a correlation between the bat activity and river regulation. I **hypothesize** that a stronger impact on stream flow parameters would lead to lower quality conditions for insects in the open water and in the riparian. Therefore, the food source available for bats would be reduced as compared to a free-flowing river, resulting in lower bat activity along regulated streams. I also expect the habitat quality of the riparian zone and the adjacent forest to be a major driver for bat activity as these habitats produce insects as food and roosting sites. This is especially true for forest dwelling species of the genus *Myotis* (Wilson & Mittermeier 2019). In this context, I determine habitat heterogeneity in terms of slope (microtopography) and horizontal heterogeneity in biomass (NDVI) as well as the structure of the riparian zone and riverbed (Stein et al. 2014; Heidrich et al. 2020).

2. Material and Methods

2.1 Study area

The studied river basins are located in Northern Sweden, stretching over the landscapes of Lappland, Västerbotten and Norrbotten. All sites are located above 63° latitude. At these latitudes, the nights during the sampling period from the beginning of July to mid-August are bright and have extended twilight hours. Some study sites are located above the arctic circle (66.5° latitude) and therefore experience midnight sun for at least the first week of the recording period (beginning of July, SMHI 2025a).

The climate in these regions is characterized by harsh winters and short but sunny summers. Average temperatures during the summer months range between 10 and 16°C (reference period 1991-2020). Most of the 300 – 2000 mm annual precipitation is registered during the summer. However, great variations are present depending on the altitude. Close to the coast, gentle hills reach up to 600 m, while the mountains of Lappland are up to 2100 m high. Here, great amounts of rain and snow feed the basins of the studied rivers (SMHI 2025b). I acquired weather data for the sampling period from the open data portal at SMHI, Sweden's meteorological and hydrological institute (SMHI 2025c).

Coniferous forest dominates the landscape. Above the tree line at around 600 m asl (meters above sea level), tundra vegetation with dwarf shrubs and herbs takes over (SMHI 2025d). The study sites show riparian zones of varying width followed by typical upland forest consisting of Scots pine (*Pinus sylvestris*), Norway spruce (*Pica abies*) and birch trees (*Betula pendula* and *Betula pubescens*). Being close to hydropower plants, buildings, roads and other infrastructure is present around the sites, which are important for bat roosting sites (Wilson & Mittermeier 2019; Merlet 2024).

The studied streams all have their origin in the Scandinavian mountain range and empty into the Bothnian Sea (Figure 1). They represent big Swedish rivers and vary in length, catchment size and mean flow (Table 1). Of the eight rivers, four are regulated by hydropower plants along the stream. This includes the rivers Ångermanälven, Umeälven, Skellefteälven and Luleälven. The sites at the remaining four rivers are considered unregulated and count as natural reference sites. These are along Vindelälven, Piteälven, Kalixälven and Torneälven. Besides hydropower dams, all of the studied rivers have been subjected to river regulation measures for timber floatation between the 19th and 20th century (Törnlund & Östlund 2006).

Table 1. Catchment area, river length and mean flow of the studied rivers (SMHI n.d.)

River	Catchment area	River length	Mean flow (1991-2020)	Number of sites
	km^2	km	m^3/s	
Ångerman	31865	460	524	5
Kalix	28123	472	316	2
Lule	25262	470	521	7
Pite	12278	410	184	1
Skellefte	11711	423	169	5
Torne	39782	545	448	2
Ume	26782	477	445	8
Vindel	12629	467	195	1

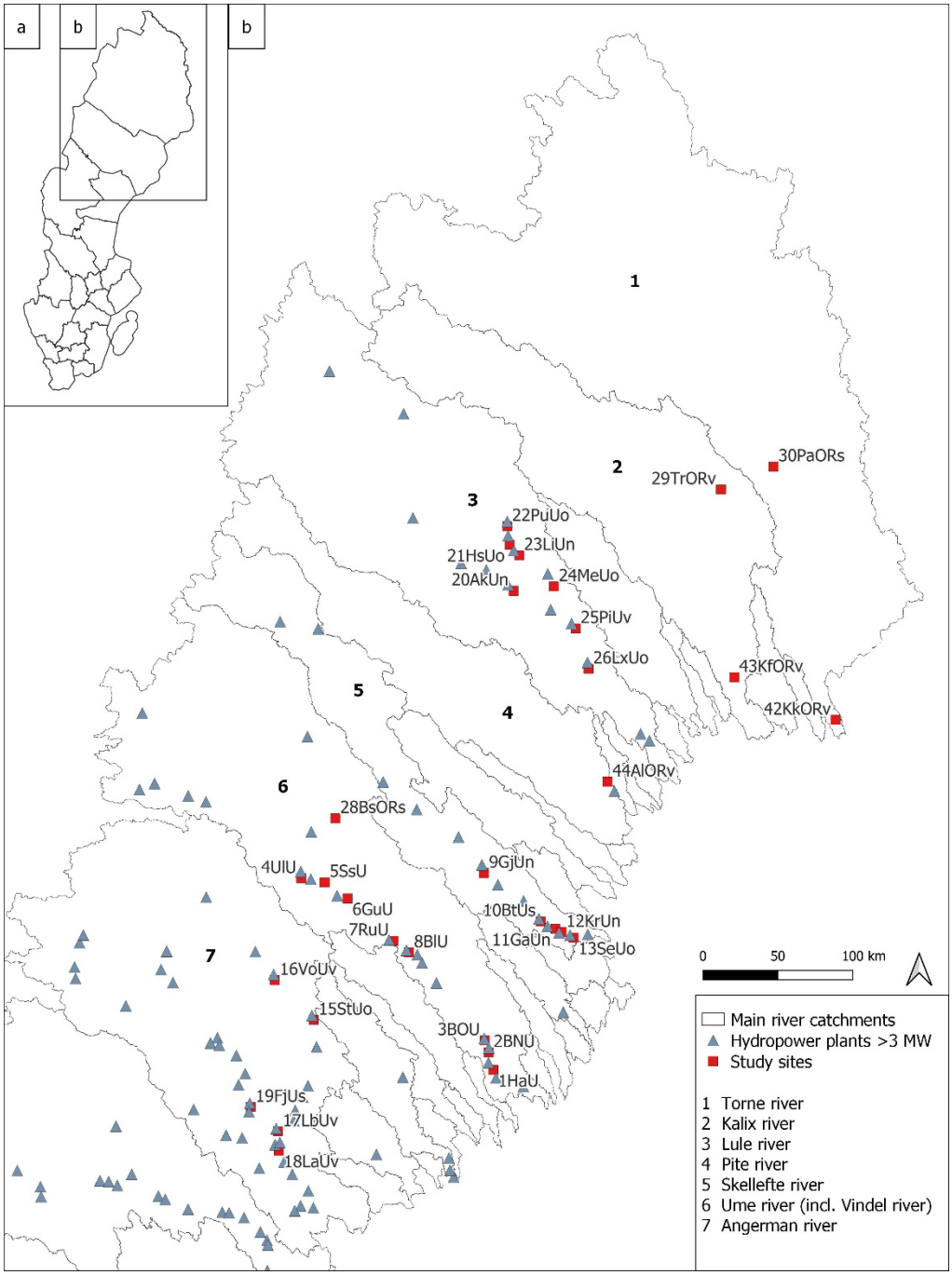

Figure 1. Overview of the study sites within Sweden (a) and within the respective catchments (b). Red squares mark the location of study sites, blue triangles represent hydropower plants producing more than 3 MW (SMHI, adjusted from eurofresh.se)

2.2 Study design

I collected data from 31 audio recorders of the type AudioMoth (© Open Acoustic Devices). These acoustic loggers record full-spectrum audio files and can be used for different ecological surveys (Hill et al. 2018; 2019). Due to their easy

handling, minimal invasive installation and passive recording, AudioMoth represents a convenient monitoring technology (Pronk 2022).

Because of varying numbers of hydropower plants present and to represent different reservoir sizes and regulation efforts, the rivers had different amounts of detectors, ranging from five to eight. The unregulated streams were equipped with one or two detectors each. This way, I collected data from 25 detectors on regulated and 6 detectors on unregulated streams. Along regulated streams, they were placed within the reservoirs but fairly close to the upstream outlet. This way, I expect 70-100% of the water flow here to originate from the outlet and not from tributaries. The chosen sampling site names consist of a unique number, an abbreviation for the name of the upstream outlet, U or O highlights the position inside the reservoir and a small letter represents the cardinal direction of the sampled riverbank: e.g. “23LiUn” for the site downstream of the Ligga outlet, upstream within the reservoir, at the northern riverbank. “OR” in the name marks unregulated sites. The recorders were placed in spots with potentially residual riverine habitats, meaning where the streams are narrow, show a vertical drop and permanent flow. The AudioMoth devices were mounted within the IPX waterproof case (Figure 2) in 1.8-2 m height on trees close to and facing towards the river (Hill et al. 2019).

Figure 2. Left-to-right: AudioMoth device, mounted in waterproof case (©2025 Open Acoustic Devices) and deployed at site 30PaOR

The recorders were set up at the beginning of July 2024 and operated until the beginning of September 2024. However, due to different battery lifetimes, I retrieved data from all devices for the first 5 weeks, spanning from 5th July to 14th August. They were programmed to record during a total of four hours every day in two recording periods: from 2:00 to 4:00 and from 22:00 to 24:00, respectively. This aimed for twilight conditions which are the favored foraging conditions by *E. nilssonii* (Wilson & Mittermeier 2019; Speakman et al. 2000). Following Hughes and Laux (2025a) these settings were used for the recordings: sample rate 192 000, trigger 63.0 kHz, window length 16 samples, medium gain, minimum trigger duration 2 s, recording duration 25 s, sleep duration 5 s. The full configuration parameters can be found in Table 6 (Appendix I).

2.3 Data analysis

Data on **flow parameters** of the rivers originated from the hydropower plant operators. These consist of hourly discharge (m^3/s) data for the period 2008-2020. Based on that, the annual amount of hours with zero discharge for a hydrologically normal year (2010) was calculated. The latter is defined as a year with average amounts of discharge as compared to wet and dry years, which differ greatly in discharge amounts. Since I assume perennial flow for unregulated rivers, this acts as a quantitative measure for flow alteration by dams (Widén et al. 2021).

Zimmermann *et al.* (2010) identified alterations in sub daily flow fluctuations (flashiness) as another main factor for describing the flow patterns of a river. Accordingly, daily values for the Richards-Baker flashiness index (RBF) and a flashiness threshold based on the unregulated river data were calculated. This then led to the number of days with RBF values above this threshold for a hydrologically normal year at the regulated sites. This acts as another way to quantify the level of flow disturbance by dams (Baker et al. 2004; Zimmerman et al. 2010).

Additionally, I assessed the normalized difference vegetation index (NDVI) for 1 ha of the adjacent riparian and upland forest by analyzing satellite data taken during the summer of 2024 (01.06. - 31.08.2024; Copernicus Sentinel data 2024). The NDVI, ranging from -1 to 1, is a common measure for quantifying the productivity of a vegetation cover (Pettorelli et al. 2005; Gessesse & Melesse 2019) and represents the horizontal biomass cover in my sampling sites. I calculated the mean value, as well as the standard deviation (SD). With those two values, I found the **coefficient of variation** (CV) as a measure for heterogeneity as CV = SD/Mean (Pélabon et al. 2020). The CV ranges between 0 and 1 with low values representing low variability while high values indicate high variability within a site.

Another parameter for **habitat heterogeneity** of the sites is the variability of the terrain, also called microtopography (Heidrich et al. 2020). I express this with the coefficient of variation of the slope within the site area. I used data from the digital elevation model (DEM) with a resolution of 2+ m as input for these calculations (Lantmäteriet). For this, I created site polygons of about 1 ha stretching along 200 m of the riverbank and covering both shallow water and the riparian zone or adjacent forest. With the help of high-resolution drone images, I further quantified ecologically valuable parameters of these sites (see Figure 3). This includes the area of the riparian zone, as well as the proportion of the visible riverbed beneath shallow water, which represents an aquatic habitat suitable for plant growth and therefore supports insect populations. Further, I counted the

number of boulders and deadwood (> 1m). These are **habitat structures** that can be adjusted by riparian restoration and forest management.

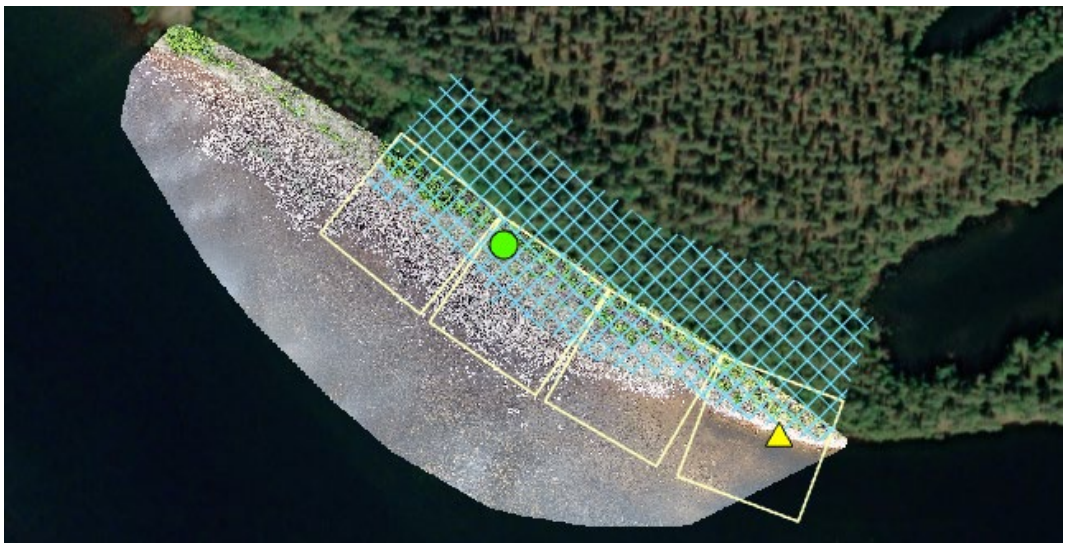

Figure 3. Analysis of the drone (bright area) and satellite images (dark area) at the site 23LiUn. Yellow squares (0.25 ha each) were used for quantifying riparian zone and habitat features. Blue marked area was used for the calculation of slope and NDVI. Green dot marks location of audio recorder.

I analyzed the audio files with the BatExplorer 2.2 software (*BatExplorer* 2023). Here, I manually separated noise from **bat calls** by comparing the spectra. Generally, I did not consider files with less than 10 % recording quality for future evaluation. Bat calls resemble distinct slashes in the spectrum and have species specific ranges in frequency. *Eptesicus nilssonii* calls have a unique shape and frequency range making them easily identifiable among European species (Russ 2021). In the spectrum (Figure 4) they appear as hockey-stick shapes with frequencies between 25 and 45 kHz and a frequency of maximum energy at about 30 kHz (Marckmann & Pfeiffer 2020; Russ 2021). Each call lasts for around 12.6 ms (millisecond) with a varying repetition interval, depending on the surroundings, but averaging around 200 ms (Russ 2021). Sometimes the detectors record feeding buzzes, which are visible in the spectrum by a decrease in both interval length and frequency, often followed by a significant pause (Figure 4). This occurs when a bat approaches its prey and needs a finer resolution of its echolocation to successfully catch it.

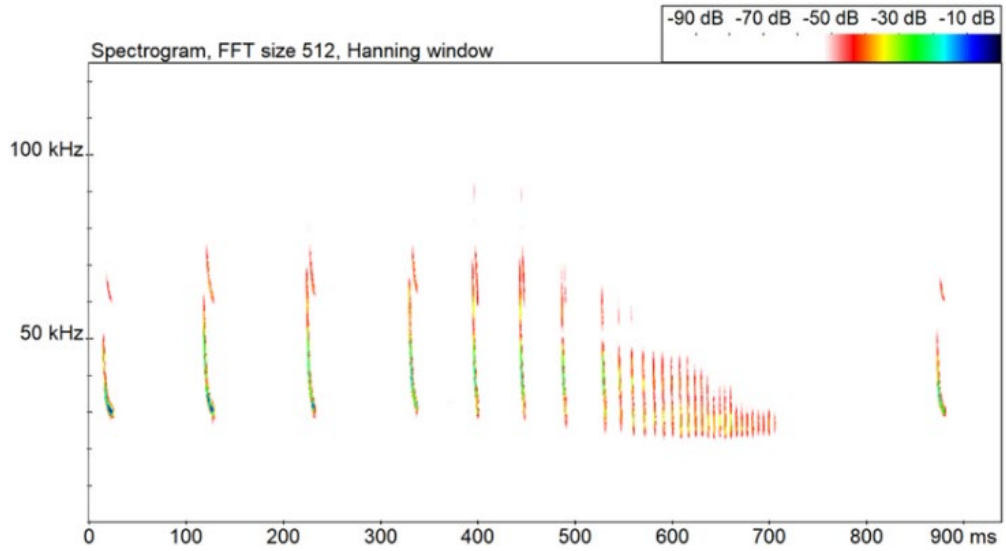

Figure 4. Spectogram of Eptesicus nilssonii calls progressing into a feeding buzz (Russ 2021)

According to Russ (2021), *E. nilssonii* is the most common bat species in the studied region. However, other species have been found at least up to 63° latitude. In the county Västerbotten, for example, a total of 11 species have been reported (Schneider 2024). Bat research in these regions is scarce, and I might find some of them on my recordings. These include Parti-coloured bat *Vespertilio murinus*, Nathusius's pipistrelle *Pipistrellus nathusii*, Brown long-eared bat *Plecotus auritus*, Brandt's bat *Myotis brandtii*, Daubenton's bat *Myotis daubentoniid,* Whiskered bat *Myotis mystacinus* and possibly Common noctule *Nyctalus noctula*.

All of these can be distinguished from *Eptesicus nilssonii* when comparing the respective spectra based on differences in shape, frequencies, duration and harmonics. Figure 5 shows spectrograms of typical calls of the above-mentioned species. However, bats can produce a variety of different calls and in some cases these are difficult to assign to a single species (Marckmann & Pfeiffer 2020). I therefore only used recordings in my analyses that I was able to identify with high confidence. A limitation for species identification are the bats of the genus *Myotis*. Based on audio recordings, Brandt's bat cannot be differentiated from Daubenton's bat or Whiskered bat (Figure 5). Therefore, I will classify these calls as *Myotis spp*.

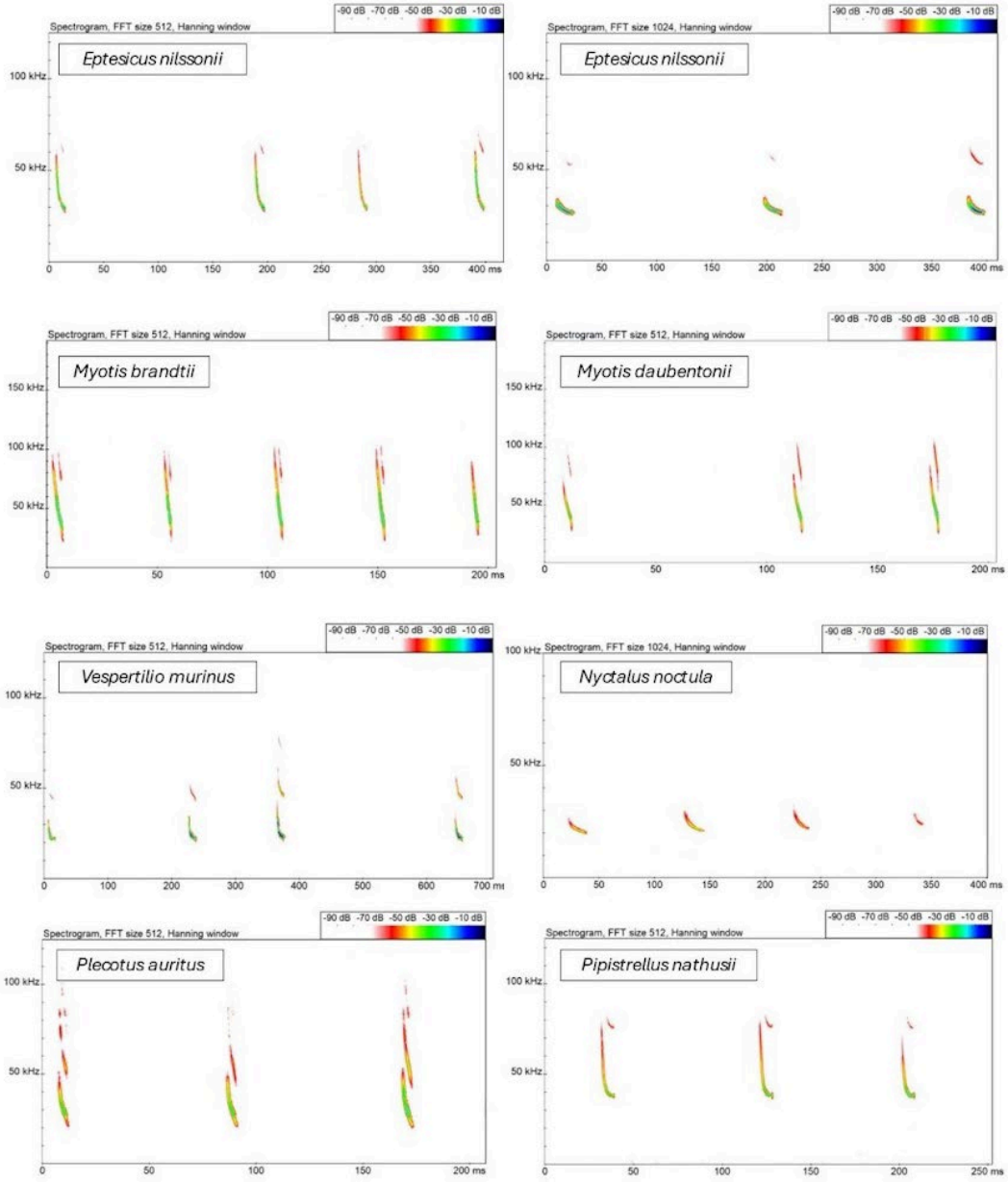

Figure 5. Typical echolocation calls of different bat species that could potentially be recorded in the study area (Russ 2021)

Each audio file also delivered a value for the air temperature at the recording time. I supplemented these with temperature data from the nearest weather stations to each site (SMHI, open data). I chose the daily minimum temperature as representative of the nighttime temperature. This allowed me to evaluate a potential relationship between the temperature and bat activity.

I analyzed the amount of bat detections further using RStudio. Adding up all the detections I assigned each site with a total number of bat detections and feeding buzzes as well as species specific counts. My data did not follow a normal distribution, so I used Spearman Rank **correlations** to test the relationship between bat detections and location, flow parameters and habitat heterogeneity

factors. With Wilcoxon rank-sum tests I also determined the statistical difference of habitat features and bat detections between “regulated” and “unregulated” streams. Because I found significant overdispersion and zero values in my data, I then used Negative Binomial **Generalized Linear Models** (GLM) to describe bat detections with a combination of the above mentioned factors (Salinas Ruíz et al. 2023). This shows the relative importance of each factor and can hint towards a causal relationship. Total as well as species-specific detections were the response variables. I used the Akaike information criterion (AIC) to select between competing models. This relates the strength of the model fit to the amount of predictors used to find the best models explaining the variation in the data (Symonds & Moussalli 2011).

3. Results

3.1 Site characteristics

3.1.1 Location

The sites cover a latitudinal range from 63.5 to 67.2°N, with a mean at 65.3° (SD = 1,1) (Table 7 in Appendix II). In East-West expansion, the sites cover longitudes between 16.4 and 24.1°E, averaging around 19.5° (SD = 2.0). Along the way from the headwaters to the Bothnian Sea, the elevation of the sites naturally decreases. The highest site is located 331 m asl (28BsORs at Vindel river), the lowest 4 m asl (42KkORv at Torne river). The average site elevation is 167 m asl (SD = 101). The histogram in Figure 6 shows that the sites cover the elevation classes somewhat evenly while also having an elevational gradient.

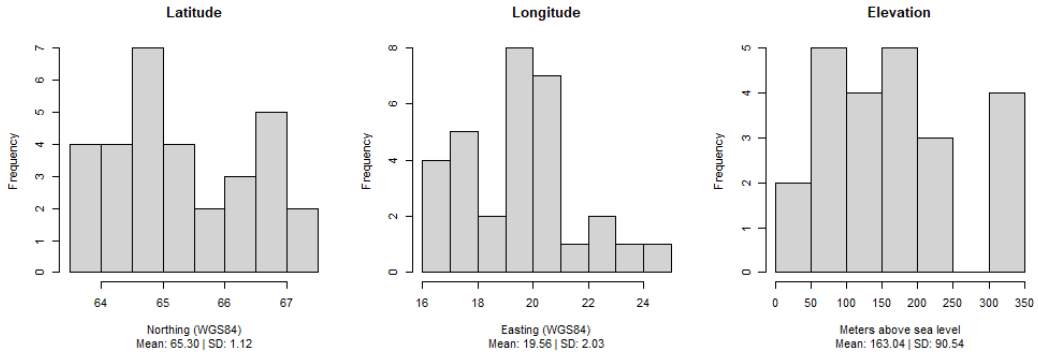

Figure 6. Histograms of latitude, longitude and site elevation (N = 31, left to right)

3.1.2 Flow parameters

The studied rivers showed mean annual flows between 123 (19FjUs at Ångerman river) and 495 m^3/s (26LxUo at Lule river) at the sites. The mean value is 228 m^3/s with a standard deviation of 97 m^3/s. Most sites have a mean annual flow < 200 m^3/s, as shown in the histograms in Figure 7 (bottom). The sites along the Lule river have the highest values (mean = 328 m^3/s). Figure 7 (top) shows the mean annual flow of the sites within the study area. It highlights the different sizes of the rivers as well as the increase of discharge as they progress towards the Bothnian Sea.

Table 2. Comparison of catchments regarding flow parameters

Catchment	**MQ (m^3/s)**			**Reservoir area (ha)**			**Zero flow hours (per a)**			**RBF (per a)**		
	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n
Angerman	158.2	29.7	5	1030	1301	5	1872	749	5	181	45	5
Kalix (ur)	251.0	80.6	2	-	-	0	0	0	2	0	0	2
Lule	328.5	115.8	7	1316	932	7	1523	1297	7	164	42	7

Pite (ur)	168.0	-	1	-	-	0	0	-	1	0	-	1
Skellefte	157.0	17.9	5	280	260	5	714	1158	5	188	50	5
Torne (ur)	302.0	206.4	2	-	-	0	0	0	2	0	0	2
Ume	221.7	25.9	8	1148	1716	8	1010	261	8	212	42	8
Vindel (ur)	148.0	NA	1	-	-	0	0	-	1	0	-	1

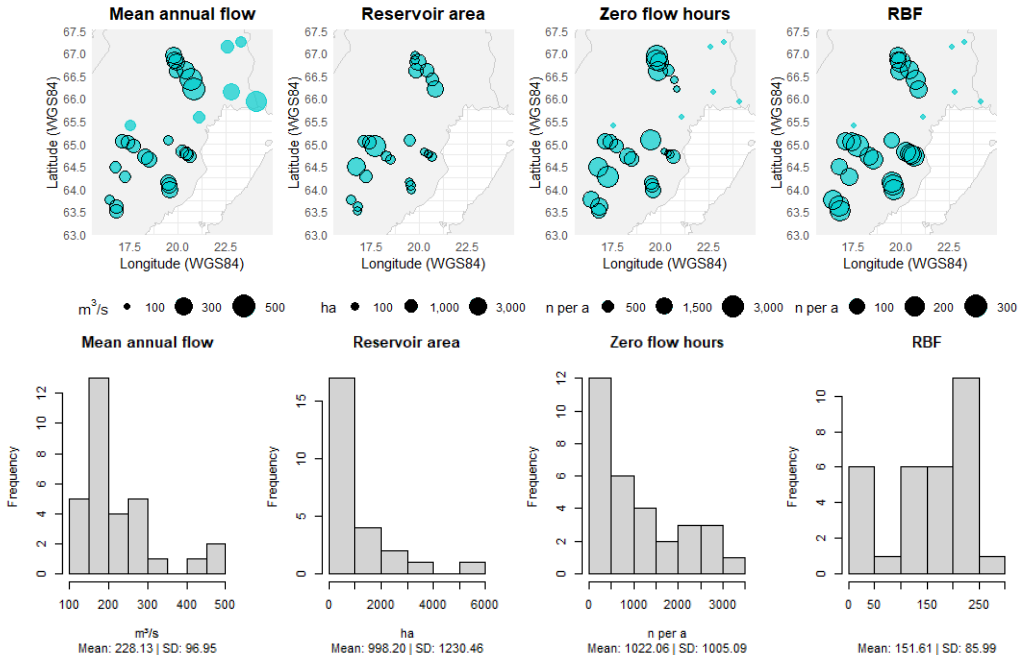

Figure 7. Top: Flow parameters at the studied sites visualized by point size. Points without outline represent unregulated sites (ur). Bottom: Histograms of mean annual flow (N = 31), reservoir area (N = 25), zero flow hours and RBF (N = 31). Abbreviations: MQ = mean annual flow, ha = hectare, n per a = number per year, RBF = Richards-Baker flashiness index.

The reservoirs ranged in size from 104 ha to 5264 ha. With an average of about 1000 ha (SD = 1230), most of the reservoirs were rather small, while only four were bigger than 2000 ha (23LiUn, 26LxUo at Lule, 16VoUv at Ångerman and 6GuU at Ume river). Each catchment showed a variety of reservoir sizes (Table 2). Noticeably the Skellefte river had the smallest reservoirs. The biggest individual reservoirs were located in Ångerman river (16 VoUv with 3284 ha) and Ume river (6GuU, 5264 ha), while the Lule river sites had the highest mean size. Note that only sites along regulated rivers can be assigned a reservoir area.

The amount of zero-flow hours at the reservoir outlets ranged from 3 (10BtUs and 11GaUn along Skellefte river) to 3043 (22PuUo at Lule river) for the regulated streams. I assigned the unregulated rivers zero values, assuming perennial flow. Accordingly, the histogram in Figure 7 shows a right-skewed distribution. This results in an average value of 1022 (SD = 1005), which equals 42 days per year. Five regulated sites along the Skellefte and Lule river had less than 500 zero-flow hours and eight showed average amounts (i.e. 7 of the sites at

Ume river and one at each of the other rivers). The remaining nine sites (4 of these at Lule, 3 at Ångerman, 1 at Ume and 1 at Skellefte river) had over 1500 zero-flow hours. On a catchment scale, sites at Skellefte river had the lowest amount of zero flow hours on average, Ångerman river the most (Table 2). Further, the amount of zero-flow hours positively correlates with site elevation ($\rho = 0.69$, $p = 0.0001$), suggesting stronger river regulation effects closer to the river head. This is visible in the map in Figure 7 for the rivers Lule, Skellefte and Ångerman.

The values for the days above the flashiness threshold (RBF) ranged between 115 (22PuUo at Lule river) and 285 (6GuU at Ume river) for the sites at regulated streams. Table 2 shows that the mean at the regulated catchments is higher than 160. For the unregulated streams, I assigned zero values. Therefore, the mean across all sites is lower (151, SD = 86). Besides the unregulated streams, the histogram in Figure 7 shows that just one other site (9GjUn, Skellefte river) had less than 100 days above threshold, twelve had less than 200 and the remaining twelve more than 200 days. The latter contains sites of each of the studied catchments. Generally, the variability in RBF between sites and catchments is low (Table 2, Figure 7). Furthermore, I found a significant negative correlation between RBF and zero-flow hours for the regulated sites ($\rho = -0{,}51$, $p = 0{,}009$).

3.1.3 Habitat features

The heterogeneity of the terrain at each sampling site is expressed through the variability within the slope. The sites varied in slopes ranging from 3 % (23LiUn, Lule river) to 42 % (1HaU, Ume river) with a mean of 17 % (SD = 10 %). Table 3 shows that all catchments showed a variety of mean slopes. Noticeably, the Skellefte catchment had the steepest slopes on average with three sites (13SeUo, 10BtUs, 11GaUn) having more than 30 % in mean slope. The histogram in Figure 8 suggests that most sites have mean gentler slopes. Comparing the coefficient of variation shows that there are sites with little variation (e.g. 22PuUO at Lule with 0.35), however most sites have a quite high CV (mean = 0.7, SD = 0.19). The site with the highest slope variability was 17LbUv at Ångerman river (slope CV = 1.1).

Representing the vegetation cover, the value for the mean NDVI for the sites ranges between 0.4 (18 LaUv at Ångerman river) and 0.9 (42 KkORv at unregulated Torne river) with an average of 0.68 (SD = 0.1). The histogram suggests an evenly distribution of NDVI between the sites (Figure 8). Additionally, there is little variation between and within catchments (Table 3).

Remarkably, most of the sites have a low coefficient of variation for NDVI with an average of 0.1 and standard deviation of 0.05. I found the lowest values (< 0.05) at sites 4UlU (Ume river) and 42KkORv (Torne river) and the highest

values (> 0.2) at 28BsORs (Vindel river) and 21HsUo (Lule river). I could not find a spatial trend in the distribution of NDVI variables.

Table 3. Comparison of the catchments regarding slope and NDVI

Catchment	Slope mean (%)			Slope CV			NDVI mean			NDVI CV		
	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n
Angerman	16.0	7.2	5	0.8	0.2	5	0.63	0.16	5	0.09	0.03	5
Kalix (ur)	11.0	2.3	2	0.9	0.1	2	0.72	0.02	2	0.07	0.00	2
Lule	16.1	10.4	7	0.7	0.2	7	0.67	0.10	7	0.13	0.07	7
Pite (ur)	22.2	-	1	0.6	-	1	0.57	-	1	0.05	-	1
Skellefte	26.1	13.2	5	0.7	0.2	5	0.74	0.12	5	0.08	0.03	5
Torne (ur)	9.0	2.0	2	0.7	0.2	2	0.80	0.08	2	0.11	0.09	2
Ume	14.6	11.8	8	0.7	0.2	8	0.65	0.07	8	0.08	0.03	8
Vindel (ur)	18.4	-	1	0.6	-	1	0.63	-	1	0.22	-	1

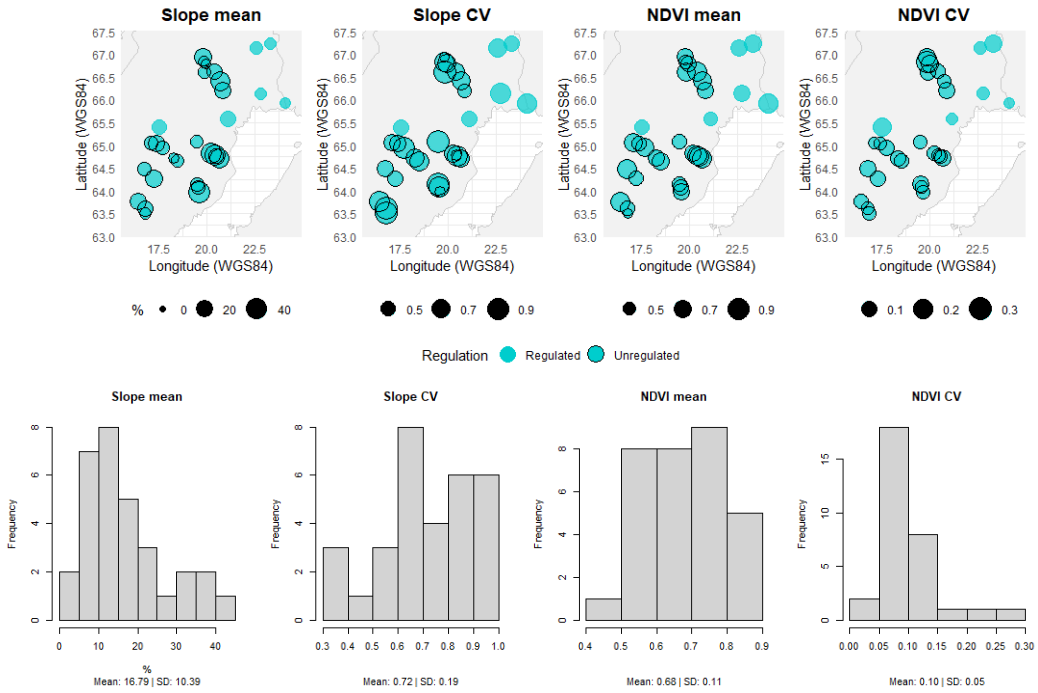

Figure 8. Top: Slope and Normalized difference vegetation index (NDVI) at the studied sites visualized by point size. Points without outline represent unregulated sites (ur). Bottom: Histogram of slope and NDVI of the sites (N = 31) expressed by mean values and the coefficient of variation (CV).

The following photographs (Figure 9) were taken at two visibly different study sites. Note the steep terrain in the picture on the left (25PiUv at the regulated Lule river) compared to the broad intact riparian zone in the picture on the left (30PaORs at the unregulated Torne river). The images in the second row show the aerial view (drone footage) of the respective sites. Observe the difference in visible riverbed (shallow water) and the amount of boulders.

Figure 9. Photographs taken at two different sites (top) and the corresponding drone images (bottom). Left: Site 25PiUv at the regulated Lule river. Right: Site 30PaORs at the unregulated Torne river.

The following histograms (Figure 10) show to which extent the studied sites are equipped with certain habitat structures: the size of the riparian zone, the proportion of visible riverbed and the amount of boulders and deadwood per ha. The maps show specific values at the studied sites. While the riparian zone extent ranges from 0 to 0.46 (23LiUn, Lule river), most sites (N = 21) had little to no riparian zone (mean = 0.1, SD = 0.14). All of these represent regulated sites. Five sites had values between 0.1 and 0.3, of which two are regulated (16VoUv, Ångerman river and 7RuU Ume river). Four of the five sites with values > 0.3 are unregulated. I found a significant negative correlation between the size of the riparian zone and the mean slope at the sites ($\rho = -0.44$, $p = 0.01$)

Visible riverbeds and therefore the proportion of shallow water close to the riverbank ranged between 0.08 (11GaUn, Skellefte river) and 0.73 (44AlORv, Pite river) with a mean of 0.37 (SD = 0.2). Eight sites, all of which regulated, had low values below 0.2, thirteen about average values and ten sites had values above 0.5. Six out of these were regulated. Comparing the river catchments shows higher values for unregulated catchments, except for Lule river catchment (Tab.X). Further, I found a significant positive correlation between latitude and riverbed visibility ($\rho = 0.56$, $p = 0.001$), suggesting more northern rivers to be shallower. This is also shown in the map in Figure 10.

The amount of boulders per ha varies between the sites from 0 (19FjUs, Ångerman river and 10BtUs, Skellefte river) to 271 (24MeUo, Lule river) with a mean of 93 (SD = 88). Out of the 31 sites, 13 had less than 40 boulders per ha, one of them was unregulated (44AlORv at Pite river). 14 more sites had about

average amounts and four regulated sites (17LbUv at Ångerman, 4UlU and 8BlU at Ume, 24MeUo at Lule river) had more than 200 boulders per ha.

Noticeably, the amount of deadwood in the riparian zone was little (< 10) at most (N = 23) of the sites (Figure 10). It ranges from 0, at seven regulated (2BNU, 3BOU at Ume; 18LaUv, 19FjUs at Ångerman; 9 GjUn at Skellefte; 20AkUn, 23LiUn at Lule river) and one unregulated sites (28BsORs at Vindel river), to 50 at site 15StUo (Ångerman river). The mean for deadwood per ha is 8 with a standard deviation of around 12.

Table 4. Comparison of catchments regarding habitat features

Catchment	Riparian zone (ha/ha)			Visible riverbed (ha/ha)			Boulders per ha			Deadwood per ha		
	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n
Angerman	0.05	0.04	5	0.22	0.13	5	77	107	5	12	22	5
Kalix (ur)	0.25	0.07	2	0.54	0.04	2	128	61	2	2	1	2
Lule	0.11	0.18	7	0.45	0.15	7	113	95	7	9	10	7
Pite (ur)	0.27	-	1	0.73	-	1	33	-	1	12	-	1
Skellefte	0.01	0.02	5	0.20	0.19	5	13	15	5	3	3	5
Torne (ur)	0.37	0.05	2	0.56	0.16	2	127	93	2	6	6	2
Ume	0.05	0.10	8	0.38	0.17	8	121	100	8	10	13	8
Vindel (ur)	0.34	-	1	0.40	-	1	134	-	1	0	-	1

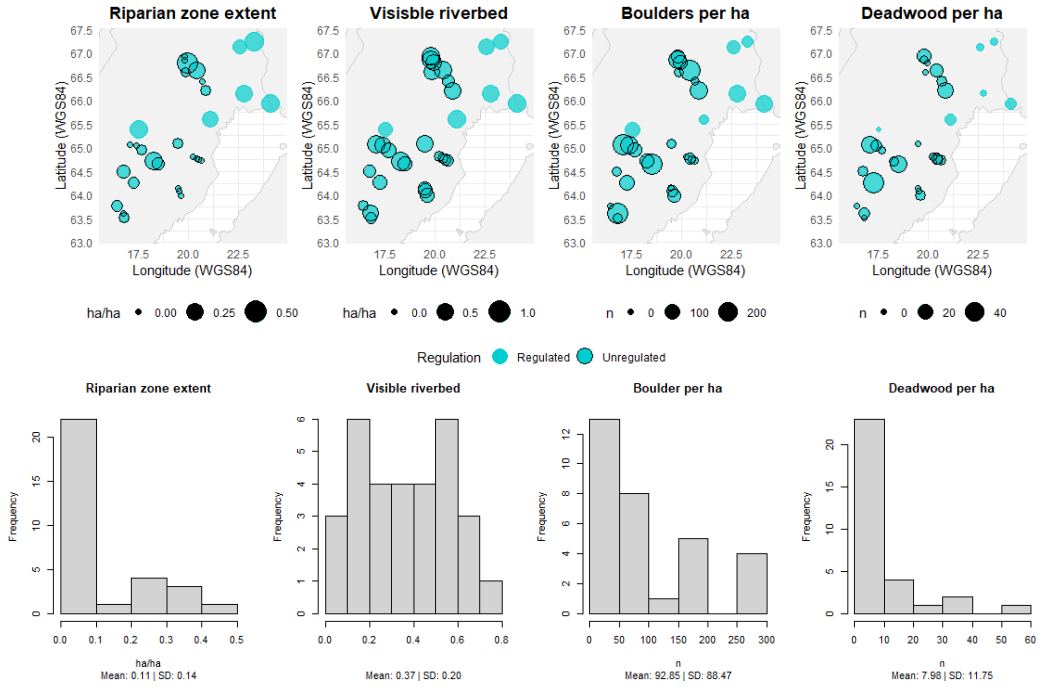

Figure 10. Top: Habitat features at the studied sites visualized by point size. Points without outline represent unregulated sites (ur). Bottom: Histograms of habitat features: riparian zone extent, visible riverbed, boulders and deadwood (left to right, N = 31, ha = hectare)

Since these factors might be influenced by river modification for hydropower plants, I tested for correlations regarding regulation. The following boxplots (Figure 11) show how these habitat features differ between regulated and unregulated sites. Wilcoxon rank-sum tests proof significance ($p < 0.05$) in the higher values at unregulated sites for the riparian zone area and the proportion of visible riverbed and thus, shallow water.

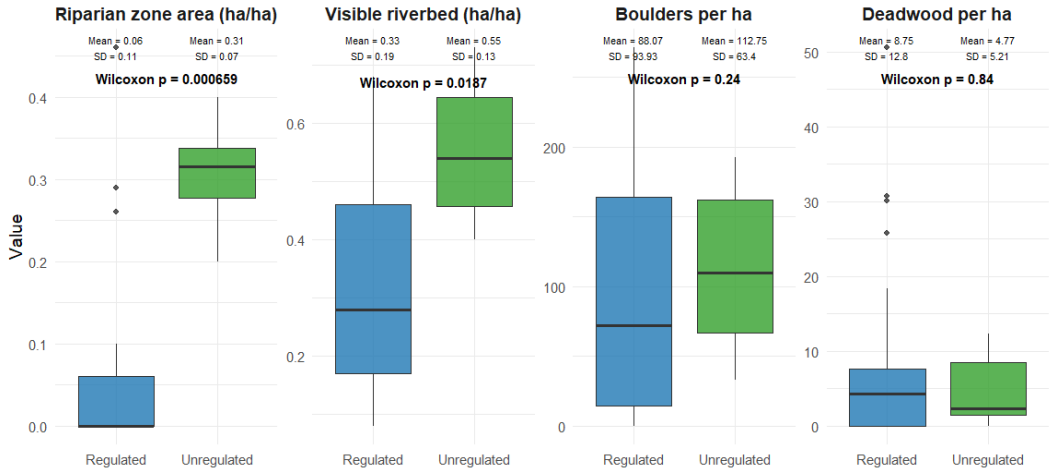

Figure 11. Boxplots for habitat features (left-to-right: riparian zone area, visible riverbed, amount of boulders and deadwood; ha = hectare), grouped by regulation (regulated = blue, N = 25; unregulated = green, N = 6). Mean, standard deviation are displayed above the results of Wilcoxon Rank Sum Tests between regulated and unregulated for each variable. These are significant ($p < 0.05$) for riparian zone area and visible riverbed.

3.2 Bat detections

3.2.1 Timing and location

The 31 devices recorded for 41 nights, equaling a total of 1217 nights. More than half of these (N = 885) showed no bat detections. I detected bats a total of 6540 times, and about half (N = 3185) were identified as *E. nilssonii* and the remaining 3355 belonged to the *Myotis* genus. There is no significant difference in the number of detections per site by species (*E. nilssonii*: mean = 102, SD = 162, *Myotis spp.*: mean = 108, SD = 150; p = 0.64). Four detectors did not record any bats (Table 8 in Appendix III). Two of them were installed along the Lule river (22PuUo and 23LiUn), one at Ume river (3BOU) and one at the unregulated Kalix river (29TrORv), which is one of the northernmost sites. Three devices recorded *E. nilssonii* but no *Myotis*: 21HsUo and 24MeUo at Lule river, 30PaORs at unregulated Torne river. Another two detectors at unregulated sites had recordings with *Myotis spp.* calls but none of *Eptesicus nilssonii*: 43KfORv at Kalix and 44AlORv at Pite river. The average amount of total bat detections per site is 210 (SD = 265, Figure 12). The highest counts at a single detector were

1120 in total (6GuU at Ume river), 707 for *E. nilssonii* (6GuU at Ume river) and 536 for *Myotis spp*. (17LbUv at Ångerman river).

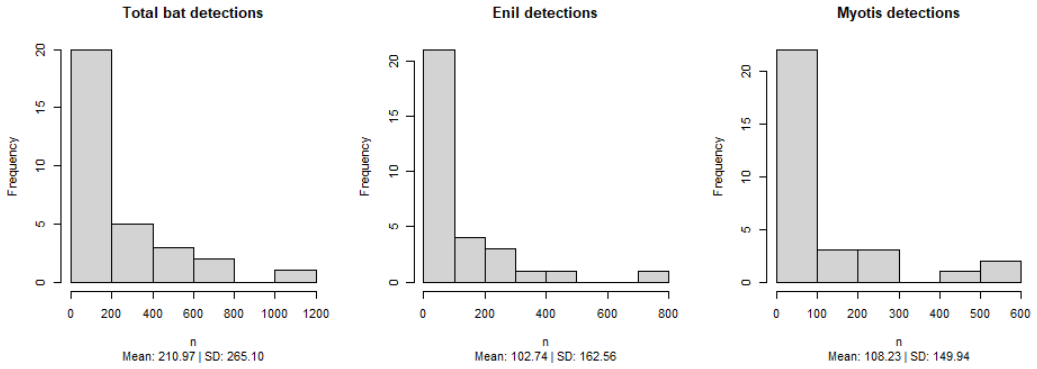

Figure 12. Histograms showing the amount of bat detections at the sites (N = 31), total counts and species specific for Eptesicus nilssonii (Enil) and Myotis spp. (Myotis) (left to right).

Within these recordings I found 1292 feeding buzzes, of which 735 came from *E. nilssonii* and 557 from *Myotis* species. On average, the devices recorded 41 feeding buzzes (SD = 63, Figure 13), 23 of those would be from *Eptesicus nilssonii* (SD = 42) and 18 from *Myotis spp.* (SD = 28). The amount of feeding buzzes per site is strongly positive correlated with the amount of bat detections ($\rho > 0.9$, $p << 0{,}05$ for total and species-specific counts, respectively). Two detectors that had bat calls did not record feeding buzzes (20AkUn at Lule river and 30PaORs at Torne river). Both sites had only two and one bat call in total, occurring towards the end of the sampling period. Highest amounts per site were recorded at the site with the most total bat calls, 6GuU at Ume river: 272 in total, 160 and 112 for *Eptesicus nilssonii* and *Myotis spp.*, respectively.

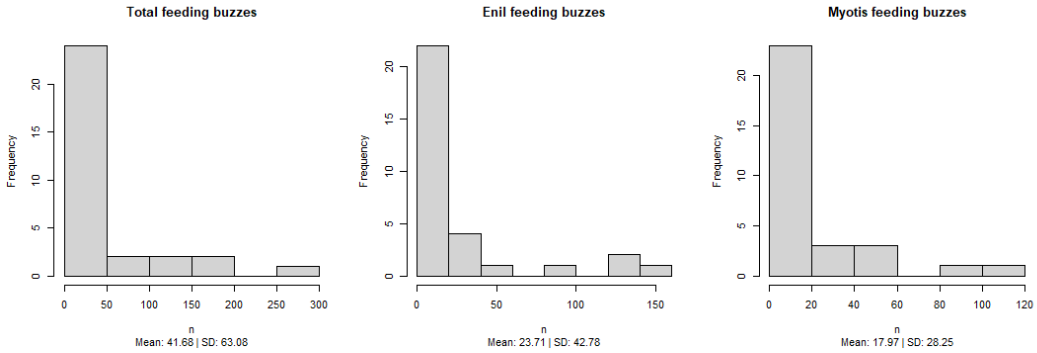

Figure 13. Histograms of the amount of feeding buzzes recorded at the sites (N = 31). Left to right: total, Eptesicus nilssonii and Myotis spp..

Figure 14 shows the development of detection counts over the sampling period. Four nights in early July had zero detections across all recorders. Most detections took place in the last recording week (9th - 14th August). The orange line in Figure 14 represents the median of the nightly temperatures of all sites. During

the last two weeks (2nd - 14th August) I found a significant positive correlation between bat detections and temperature ($\rho = 0.23$, $p = 0.02$). This indicates higher bat activity during warmer nights.

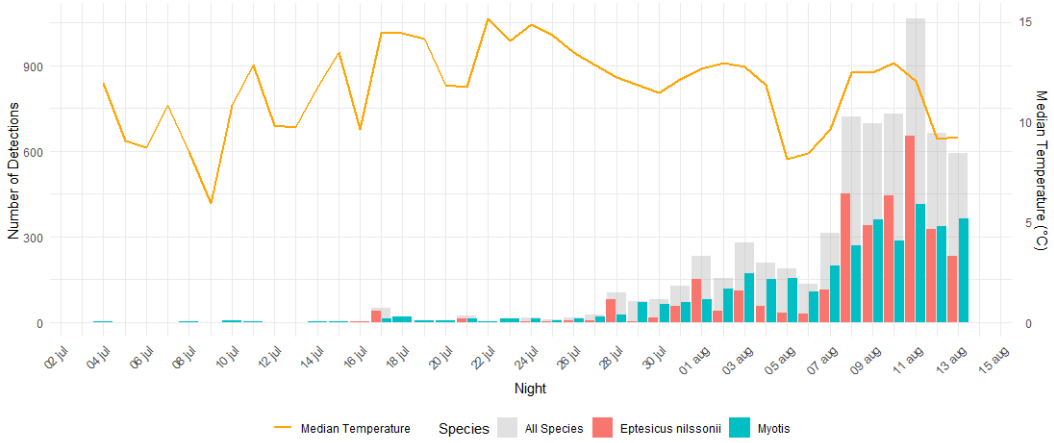

Figure 14. Number of bat detections across all 31 sites by species and date for the whole sampling period. Red bars represent Eptesicus nilssonii, blue represent Myotis spp. and the grey bars in the background show the total number of detections. The orange line shows the median of the nightly temperature (°C) measured at weather stations close to the sites.

The late emergence of bat detections (Figure 14) did not occur simultaneously at all sites. Figure 15 shows the amounts of detected bat calls distributed over the studied sites over the whole sampling period.

Overall, most bat detections were recorded at around 65° latitude (Figure 17). At around 66°, noticeably more recordings were made of *Myotis* species than of *Eptesicus nilssonii*. Latitude showed a significant negative correlation with the number of bat detections in Spearman rank correlations. This applies to the total number of detections per site ($\rho = -0.54$, $p = 0.002$), as well as to the number of *E. nilssonii* detections ($\rho = -0.54$, $p = 0.002$) and the number of *Myotis spp.* detections ($\rho = -0.57$, $p = 0.001$) per site (see Figure 16). Correlation with longitude was only significant ($\rho = -0.48$, $p = 0.0007$) for *E. nilssonii* detections (Figure 16).

Spearman rank correlation tests using the number of bat detections with site elevation showed no significant correlation (Figure 21 in Appendix III). The same result was found for the distance of the site from the dam.

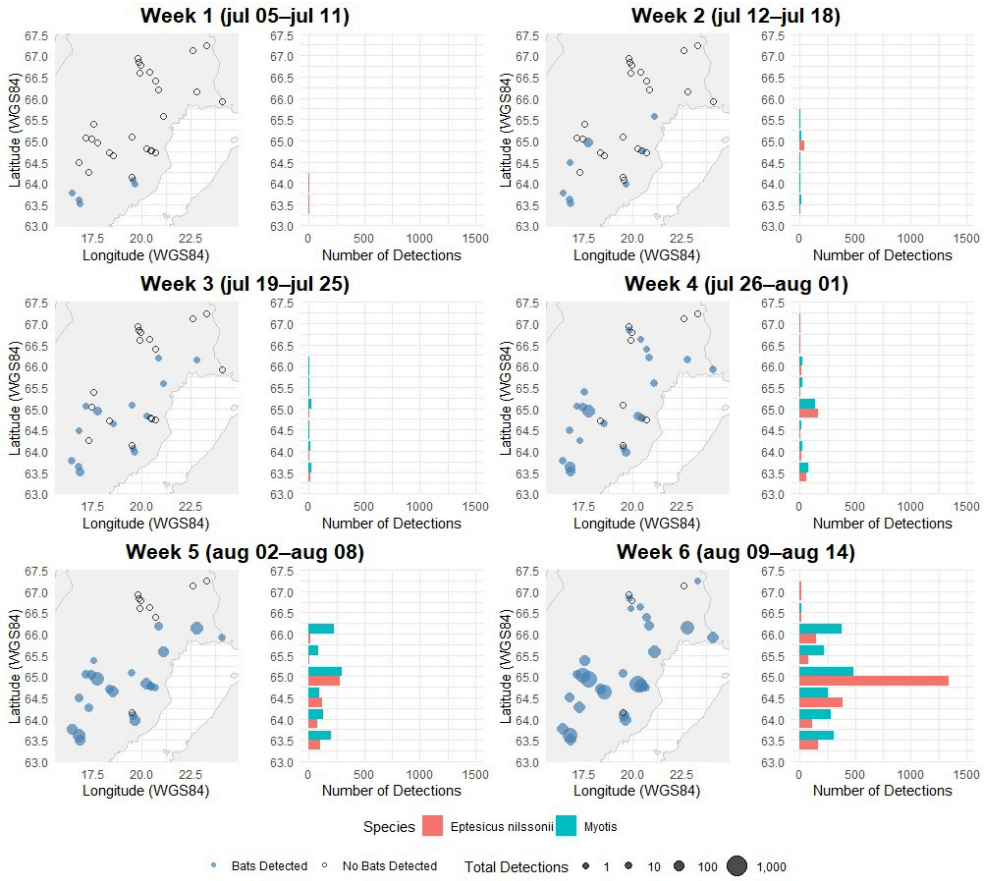

Figure 15. Progress of bat detections over time and location, divided into weekly periods. Total amounts of detections are represented by dot size in the maps. Species specific counts depending on latitude are represented in the respective bar plots.

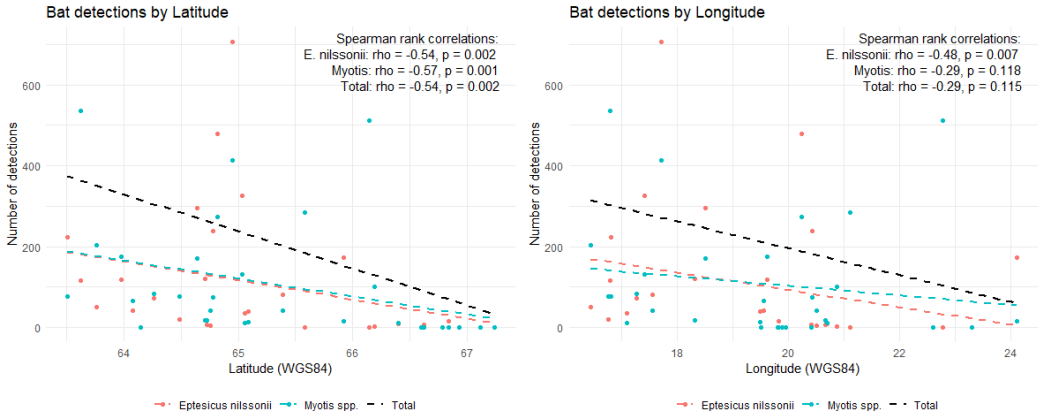

Figure 16. Relationship between bat detections and the latitude (left) and longitude (right) based on a linear regression (dashed lines). Red dotted lines represent E. nilssonii, blue - Myotis and black - the total amount of bat detections. Correlations are not significant. The negative correlations with latitude are significant ($p < 0.05$). Regarding longitude, only E. nilssonii correlates significantly.

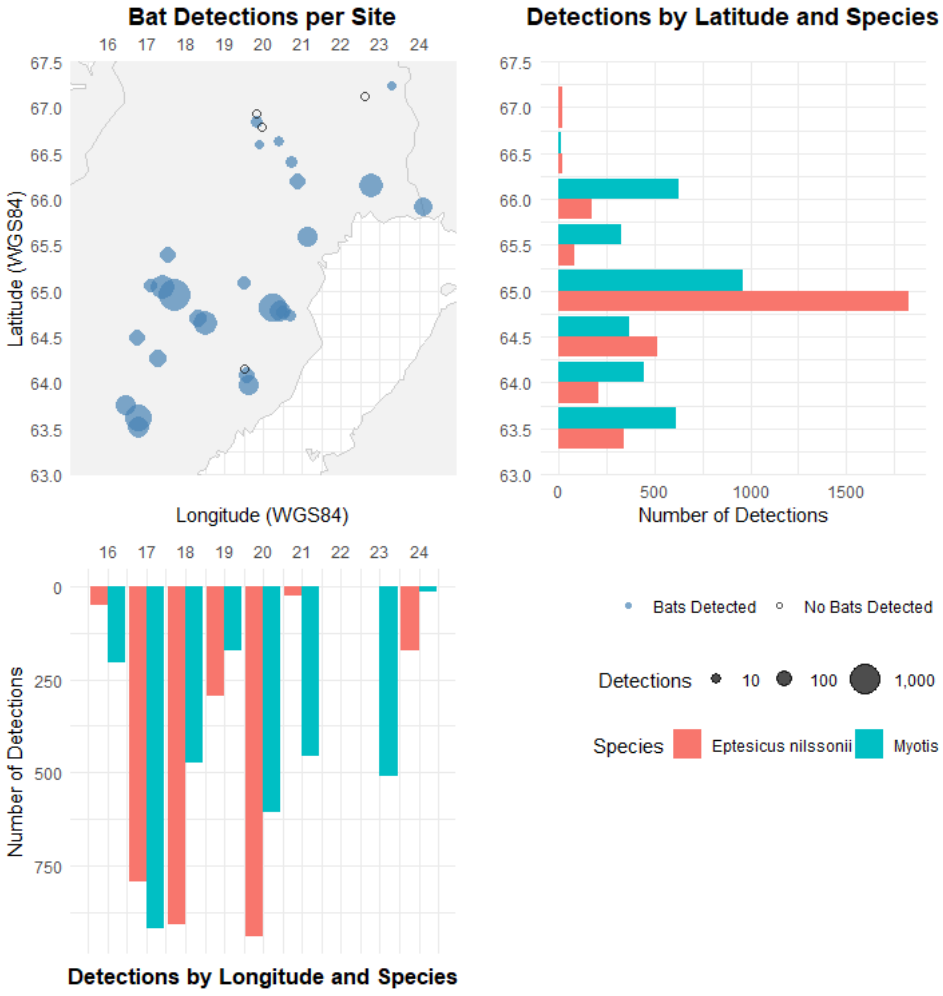

Figure 17. Distribution of all bat detections across sites, latitude and longitude. Blue dots (top left) mark sites with bat detections, empty dots mark sites where no bats were recorded. The dot size represents the total amount of bat detections. Bars display the amount of bat detections grouped by latitude and species.

3.2.2 Flow parameters

Wilcoxon rank-sum tests did not show a significant difference between bat detections at regulated and unregulated river sites (Figure 18).

I could not find significant correlations between bat detections and mean annual flow or reservoir area (Figure 21, Table 9 in Appendix III). Note that the tests for reservoir area only include regulated sites. Further, there were no significant correlations between the annual amount of zero-flow hours and the number of bat detections. I found similar results when testing the correlations with the number of days above RBF threshold (Figure 21, Table 9 in Appendix III).

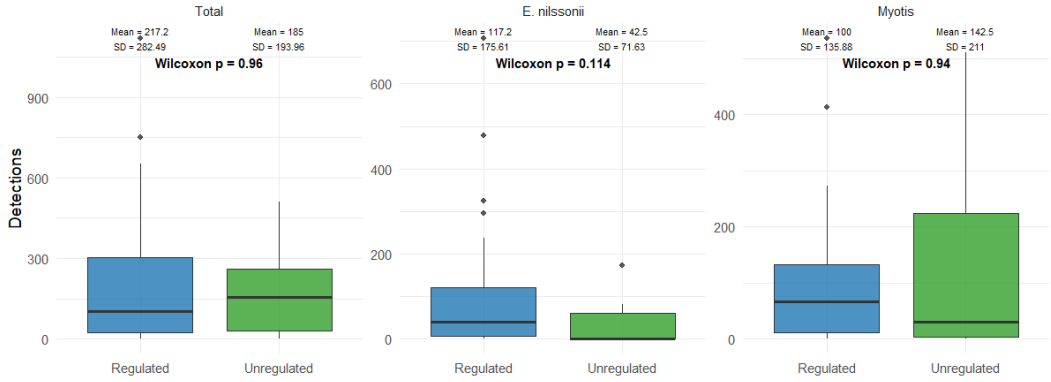

Figure 18. Boxplots comparing regulated to unregulated sites regarding bat detections (left to right: total detections, E. nilssonii detections, Myotis detections). P-values between plots represent results of Wilcoxon Rank-Sum Tests between respective groups. No tests showed significance.

3.2.3 Habitat features

The amount of bat detections does not correlate with the mean slope nor the variability of the slope of the studied sites (Figure 21, Table 9 in Appendix III). Regarding the NDVI I found significant correlations between total bat detections and *Myotis spp.* detections with the coefficient of variation of NDVI (Figure 19), but none with the mean NDVI.

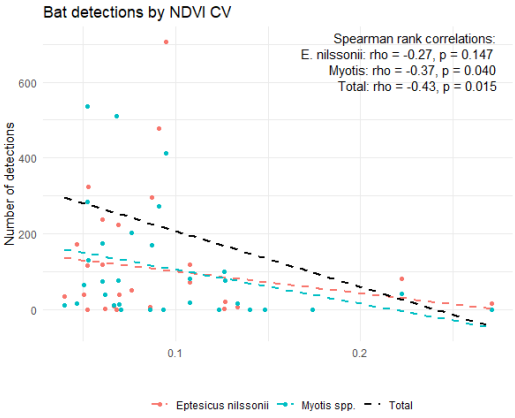

Figure 19. Relationship between bat detections and the coefficient of variation of NDVI based on a linear regression (dashed lines). Red dotted lines represent E. nilssonii, blue - Myotis and black - the total amount of bat detections. Only significant correlations are between NDVI CV and Myotis and total detections, respectively.

The relationship between bat detections and the extent of the riparian zone and of shallow water seem to be of negative nature, however none are significant, as Figure 21 shows (Appendix III). I could not find a significant correlation between the amount of bat detections and the amount of boulders and deadwood in the water.

3.3 Modelling

In the negative binomial GLMs I avoided using correlated predictor variables (Symonds & Moussalli 2011). A correlation matrix for all variables can be found in Figure 20 (Appendix II). To start the model comparison, I used the following variables as predictors: latitude, site elevation, average nightly temperature, mean annual flow, regulation (y/n), zero-flow hours, (reservoir area), NDVI CV, slope CV, riparian zone area, boulders and deadwood per ha.

I tested models for the total amount of bat detections as well as species-specific detections as response variables. First evaluations with the AIC showed great importance of the latitude for each response. I then split the dataset in two regions to decrease this influence: above (16 sites) and below 65.5 degrees (15 sites). With another subset I modelled the bat detections that were made only on regulated sites (N=25). This allowed testing of the impact of the reservoir area and an unbiased evaluation of the amount of zero-flow hours. Overall, I used four subsets of my data: the full dataset, a northern subset, a southern subset, a regulated subset.

For each subset-response pairing I chose the three best models according to the AIC based model selection, as long their scores did not differ in more than two units. A full overview of these 36 models with the respective AIC scores, predictors and p-values can be found in Table 10 (Appendix III). The following table (Table 5) shows all the predictors of the above-mentioned models and summarizes how many times they were part of the models as well as the magnitudes of their coefficients. Noticeably, latitude was the most important factor in most of the models. In the north subset, latitude was still highly relevant for every response variable, while it was occurring only in one model in the southern subset. In the latter, it showed a positive coefficient. Apart from that, the coefficient was always negative, meaning less bat detections with increasing latitude. With the effect of the latitude accounted for, the amount of zero-flow hours turned out to be an important factor improving 19 of the 36 models. This occurred especially in all models of the “regulated” subset, but also in the full dataset models. The coefficient was consistently negative, connecting a higher number of zero-flow hours with a decrease in bat detections. One third of the models had site elevation as a significant predictor. Noticeably, this was the case in models of the northern subset, where coefficients were negative and in the regulated subset, where coefficients were positive. The CV of NDVI was a predictor in 7 of the 36 models, with coefficients ranging from -0.87 to 0.92. With presence in 6 models and positive coefficients throughout, the amount of boulders seems to have a positive effect on bat detections. The reservoir area was important in 4 of the 9 regulated models, with only positive coefficients, suggesting higher

bat activity on bigger reservoirs. Other predictors, including the amount of deadwood and the riparian zone area occurred two or less times in the models.

Table 5. Overview of predictors in the models describing bat detections best.

Predictor variable	**Occurrence in the models (out of 36)**	**Coefficient range**	**Mean coefficient (SD)**
Latitude	28	-3,70 … 0,35	-1,82 (0,80)
Zero-flow hours	19	-1,26 … -0,24	-0,88 (0,27)
Site elevation	13	-2,45 … 1,10	-0,37 (1,29)
NDVI CV	7	-0,87 … 0,92	0,05 (0,63)
Boulders per ha	6	0,12 … 0,89	0,58 (0,19)
Reservoir area	4	0,65 … 0,69	0,59 (0,13)
Avg Temperature	2	-0,46 … 0,35	-0,06 (0,40)
Deadwood per ha	2	-0,78 … 0,35	-0,22 (0,57)
Regulation (ur)	2	1,39 … 1,93	1,66 (0,27)
MQ	2	0,54 … 0,67	0,65 (0,06)
Riparian zone area	1	-0,34	-
Slope CV	1	0,29	-

4. Discussion

4.1 Timing and location of bat detections

The studied sites cover a wide latitudinal range in Northern Sweden. This comes with implications for species communities. At these high latitudes (63 to 67°), north-south gradients can be found and strongly pronounced regarding temperature and brightness. Generally, temperatures are lower in the north and the summers are short. This leaves only 2-3 months for the bats to give birth and raise their young before hibernation (Frafjord 2021). Merlet (2024) showed that the foraging behavior of *E. nilssonii* in Västerbottens mountain region is heavily influenced by the weather. I also found a higher bat activity during warmer nights when bats were present.

At the same time, bats are nocturnal and are therefore influenced greatly by the brightness at nighttime. Frafjord (2021) observed emergence and entry at *E. nilssonii* roosts in northern and southern Norway. They concluded that the bats in the North tolerate brighter light conditions to forage while still preferring to hunt in darker hours when possible. During my sampling period from early July to mid-August, the northern parts of the study area experience significantly more daylight than the southern parts. This is especially interesting considering that the sites above the arctic circle experience midnight sun in the beginning of the sampling period.

In my dataset, it becomes evident that the latitude plays a major role in predicting bat detections. It correlates with total and species-specific detections and shows to be the most important predictor in most of the models. Even when split into two regions, latitude still determines bat activity in the northernmost part. This is likely because the study area is located on the northern limits of the distribution range of bats. Rydell (1992) found *E. nilssonii* population densities in northern Sweden to be five times lower than in the southern part of the country, highlighting the bats sensitivity to the change in temperature, light and food availability along the latitudinal gradient.

This relevance becomes clear as my results show a strong seasonality of bat activity. Most of the sampling period (June-July) seems to cover a time in which the bats are not present in the study area or avoid rivers. Bat activity in both *E. nilssonii* and *Myotis spp*. peaks in the middle of August. However, the sampling period, which was covered by all detectors, ends on the 14th of August. Reports on bat activity in Kvarken, the archipelago between Umeå and Vaasa, show high detection rates until mid-September (Fritzén 2014; 2015; Schneider & Fritzén 2020). I therefore advise extending the recording season further into autumn, possibly by exchanging the batteries. Alternatively, it could be worth

shifting the sampling period to a later start date to reliably cover the decrease in bat activity.

Earlier research from Northern Sweden and Finland report similar activity patterns (Nyholm 1965; Rydell 1992; Fritzén 2014; Schneider & Fritzén 2020; Vasko et al. 2020; Kotila et al. 2023; Hughes & Laux 2025b). Based on these, it is likely a combination of migration (Wilson & Mittermeier 2019), the emergence of young bats (Kotila et al. 2023) and the avoidance of open habitats (Nyholm 1965; Vasko et al. 2020) that lead to the strong activity peak I found in the later stages of my sampling period. I suggest the latter to be the main reason for this trend: bats, especially *Myotis* species, at northern latitudes avoid foraging in open habitats during the brightest nights in the summer. As this is independent from the insect availability, it is likely an adaptation to avoid diurnal predation or competition (Nyholm 1965; Speakman et al. 2000). When nights become darker, bats then shift their foraging towards more open spaces, including younger forests, riparian zones and water bodies. To prove this further, I suggest future research focusing on different foraging habitat types in the boreal zone.

Interestingly, I recorded *Myotis* species quite often at latitudes above 65°. Earlier studies (Rydell 1992) declare *E. nilssonii* as the only bat species to thrive that far in the north. However, a warming climate shifts the distribution range of these species further up (Rebelo et al. 2010). Especially close to rivers and cities, which provide advantageous properties regarding food and temperature, I expect more species to show up in the future.

The northern Swedish landscape is characterized by mountain ranges in the west and gentler slopes towards the Bothnian Sea in the east with the rivers following this topographic gradient naturally. This reflects well in the elevation of my sites along the longitudinal gradient. The only correlation with bat detections I found was between longitude and *E. nilssonii* detections, with less detections at locations further towards the east. Since longitude and elevation strongly correlate, this is likely connected to the site elevation being an important predictor in some of the models. The drivers for this trend remain unclear and encourage further research.

4.2 Bat detections as habitat index

Most of my study sites (25 of 31) are influenced by river regulation in the form of dams for hydropower plants. I expected to see a difference between regulated and unregulated sites, like Strasevicius (2013) did for an insectivorous bird. However, I could not find a significant difference in the amount of bat calls. This might be due to the small sampling size (only 6 unregulated sites) or the fact that most unregulated sites are located far in the North.

The study sites represent a wide range of discharge rates, and therefore, river sizes. According to my correlations and modelling approaches, this is not related to the amount of bat detections that I found. The regulated rivers show further variation in the magnitude of regulation impact, represented by RBF ranging from 115 to 285 and the amount of zero-flow hours ranging from 3 to more than 3000. Most reservoirs are small and the size seems not to play a big role regarding bat activity. However, in a few models the reservoir area did have a positive coefficient. This means more bats were detected at bigger reservoirs. A possible explanation is that bigger reservoirs store more water, can potentially produce more insects and are less likely to fall dry when no water is released from the upstream dam.

I could not find a significant correlation between the flow regulation parameters and the bat activity at the sites. Within the modelling, when the latitudinal effect is accounted for, the amount of zero-flow hours then showed to be a major predictor alongside latitude. My results suggest a negative relationship, meaning higher bat activities at sites with lower counts of zero-flow hours. Since zero-flow hours are a major effect of river regulation, this attests that regulation has a negative effect on bat activity. In this specific case, zero-flow hours mean no water is released from the upstream dam. Depending on how long this lasts, the riparian zone and possibly more of the riverbed might fall dry killing all immobile aquatic flora and fauna that is not adapted to this change. This leads to a loss of biodiversity and ecosystem productivity which then negatively impacts habitat index and thus, bat activity. The amount of zero-flow hours directly reflects how disturbed the river is by regulation, since I assume the unregulated rivers to be perennial. I further found a negative correlation between RBF and zero-flow hours. This means that zero-flow hours might not be the only regulation variable that impacts the riparian habitats. Instead, it likely also represents other changes, e.g. in the discharge fluctuation patterns. However, I propose reducing the amount of annual zero-flow hours at a hydropower plant as an effective measure to support biodiversity in the associated habitats. Renöfält *et al.* (2010) also present the implementation of natural flow patterns to the hydropower operations as a main recommendation to mitigate negative ecological effects. Sites with the most disturbed flow have the highest potential to benefit even from small adjustments. Among my studied region this includes the four northernmost reservoirs at Lule river (20AkUn, 21HsUo, 22PuUo, 23LiUn), 9GjUn at Skellefte river, as well as 15StUo and 16VoUv at Ångerman river (Figure 7). Noticeably, these had also lower bat detection counts compared to other, less severely influenced sites (Figure 17).

In order to evaluate the importance of stream regulation without the overwhelming influence of latitudinal range, however, I advise focusing future research on rivers close to each other (compare Nilsson et al. 1991). With more

detectors along the same stream, a bigger sample size could also increase the resilience of the results. Additionally, the lack of stream flow data represents a major difficulty when analyzing the data. I could only use averages based on an earlier time period (2008-2020). This means I cannot reliably refer the data to the sampling period (2024) to account for special flow events that can vary heavily in timing, duration and frequency (Widén et al. 2021). I invite the companies managing the hydropower plants to share more of their recent flow data in high resolution to enable exact research in the future. This way I could relate the stream behavior to the development stages of the insects as well as the activity of the bats that feed on them.

Besides the aquatic parameters, the characteristics of the riparian zone are detrimental to the associated habitat quality. Horizontal and vertical heterogeneity have been directly linked to biodiversity (Stein et al. 2014; Heidrich et al. 2020). My sites represent a range of within-site variations regarding slope and NDVI. While Stein, Gernster and Kreft (2014) report a positive effect of heterogeneity in microtopography on biodiversity measures, I could not find a connection between slope variability and bat detections. With 1 ha of analyzed area, my studied sites are likely too small to show this effect. Another reason is that forest management operations potentially overthrow such patterns, as they can operate regardless of slope to a large degree. In their large study on 1 ha plots in temperate forest, Heidrich *et al.* (2020) came to similar results as they could not find a correlation between bat diversity or abundance and microscale topography.

In the analysis, only the coefficient of variation for NDVI showed significant negative correlation with bat detections (Figure 19). This suggests that, in contrast to my expectation, sites with a higher diversity in vegetation cover (tree species, ages, shrubs, gaps) had a lower bat activity than those with a uniform plant cover. The current literature, however, points towards a positive influence of plant diversity. In their meta-analysis, Stein *et al.* (2014) found a significantly positive effect of vegetation diversity on species richness in general. Heidrich *et al.* (2020), reported no effect of gap distribution on moth and bat populations. They did, however, find a positive correlation between diversity in bat species and plant diversity. For bats at northern latitudes, Wood *et al.* (2025) also showed an increase in bat activity in more complex forest borders as compared to simple ones. In my data a lack of variation between sites (Figure 8) might be responsible for the different results, giving few sites more power over the correlation (Figure 19). Within the modelling, I found negative as well as positive coefficients for this predictor. This inconsistency requires further research to resolve. Additionally, using NDVI measures as an indicator for plant diversity has limitations (Nagendra 2001; Pettorelli et al. 2005). For example, different species may produce the same NDVI, while patches of the same species and structure can have different values e.g. due to different water availability. This would then also affect the coefficient

of variation in NDVI. The vegetation composition at the sites is a product of the natural site conditions (climate, slope, species communities), forestry (tree species, age, diversity, riparian buffer zones) and river regulation (flood events, discharge fluctuations, channeling, sediment transfer). The variation in NDVI can therefore not fully be explained by the river regulation effort. To increase habitat index, I advise forestry and hydropower activities to focus on increasing the diversity of vegetation within the riparian zones. All regulated sites in my study region would benefit from this since the NDVI CV values are generally low (Figure 8). Sites with the least variation include 2BNU and 4UlU at Ume river and 16VoUv at Ångerman river.

I further analyzed other structures in the riverbanks: the size of the riparian zone, shallow water and the amount of large boulders and deadwood. I found a significant difference, proving that unregulated sites have wider riparian zones and shallower riverbanks than regulated ones (Figure 11). These act as important habitat features for aquatic and terrestrial insects and should therefore influence bat activity. Even though I could not find a strong relationship within my data, increasing these factors has a high potential to increase habitat heterogeneity and thus, biodiversity. Here I want to highlight sites with low values in all of these categories: most sites along Skellefte river (10BtUs, 11GaUn, 12KrUn, 13SeUo), downstream sites at Ume river (1HaU, 2BNU, 3BOU) and 25PiUv at Lule river.

I acknowledge the shortcomings of passive acoustic monitoring. It cannot assess individual bats and therefore fails to provide information about population sizes. Further, species specific information is lost when grouping species in the *Myotis* genus even though they can have different habitat requirements (Wilson & Mittermeier 2019). Combined with the already limited amount of bat species in the studied region, bat diversity approaches are meaningless. Additional mist net explorations could give valuable insight into the exact species composition of the *Myotis* genus in the study region. Another influence is the vicinity of roosting sites, which can increase detections at specific sites (Kotila et al. 2023). Additional searches for roosts can account for this effect but are also connected to immense personnel and time expenditure.

5. Conclusion

In this novel study approach, I tested the influence of hydropower operations on bat activity. I connected flow and habitat parameters of regulated and unregulated streams to the number of bat detections made during the sampling period. I found a strong seasonality in bat activity, peaking in the first half of August. Interestingly, bats of the genus *Myotis* were as abundant as *E. nilssonii* in the whole study region. My data does not show a significant difference in bat activity between regulated and unregulated sites. Instead, it highlights the latitude as the main predictor for bat detections. Through modelling I found a negative impact of heavy river regulation, represented by the amount of zero-flow hours, on bat activity. Habitat heterogeneity seems to be a less important factor. Changes in the flow pattern due to river regulation influence bat presence and should be mitigated.

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Popular science summary

Hydropower plants are an important source for electricity in Sweden. This requires building dams along rivers to hold back water. Many studies show that this river regulation can have negative effects on the river and surrounding ecosystems. The main reason is the change of water flow patterns, to which plants and animals are adapted to. We often use indicator species like bats, which are sensitive to changes in their environment, to understand and monitor human impacts.

In this study I used microphones to detect bats flying along eight rivers in Northern Sweden. I also described the ecological values of each site. I compared unregulated with regulated rivers as well as reservoirs with different levels of regulation. To explain the differences in the amount of bat detections at the sites, I modelled them using variables for the location, flow and habitat.

My results show that bat presence decreases the further north the sites are. This is because the studied region is located at the northern edge of the range in which bats can be found. I also found that bats here are most active in the beginning of August, likely because they avoid the bright nights before that. Besides the effect of the location, reservoirs with the strongest regulation had less bat detections than those with less severe river regulation. This shows that we can trace the negative impact of hydropower plants by monitoring bats. In the future, we can use this to steer and evaluate river restoration efforts.

Appendix I

Table 6. AudioMoth configuration used for all detectors

Setting	Value
Firmware	AudioMoth-Firmware-Basic (1.10.1)
Device time	2024-06-27 08:21:27 (UTC+2)
Sample rate (Hz)	192000
Gain	Medium
Sleep duration (s)	5
Recording duration (s)	25
Active recording periods	2
Recording period 1	02:00 - 04:00 (UTC+2)
Recording period 2	22:00 - 00:00 (UTC+2)
First recording date	2024-07-05 (UTC+2)
Last recording date	----------
Filter	-
Trigger type	Frequency (63.0kHz and window length of 16 samples)
Threshold setting	3%
Minimum trigger duration (s)	2
Enable LED	Yes
Enable low-voltage cut-off	Yes
Enable battery level indication	Yes
Always require acoustic chime	No
Use daily folder for WAV files	Yes
Disable 48Hz DC blocking filter	No
Enable energy saver mode	No
Enable low gain range	No
Enable magnetic switch	No
Enable GPS time setting	No

Appendix II

Table 7. Results of site characteristics

	Location					Flow Parameters				Habitat features							
Site ID	**River catchment**	**Latitude**	**Longitude**	**Elevation**	**Distance to dam (waterline)**	**Mean Annual Flow**	**Reservoir area**	**Zero-flow**	**RBF**	**Slope**		**NDVI**		**Riparian zone area**	**River bed visibility**	**Boulders**	**Dead wood**
	Upstream outlet	WGS 84	WGS84	m asl	m	m^3/s	ha	h per a	d per a	%				ha	ha/ha	per ha	per ha
										Mean		Mean					
										SD	CV	SD	CV				
1HaU	Ume	63,976798	19,623553	91	6200	251	198	1099	218	41,7		0,66		0	0,28	72,3	4,3
	Harrfors									14,3	0,4	0,04	0,06				
2BNU	Ume	64,077814	19,565351	145	3000	246	351	851	244	10,0		0,59		0	0,27	36	0
	Bjurfors nedre									8,7	0,9	0,03	0,05				
3BOU	Ume	64,145295	19,513125	165	1200	246	196	773	230	12,3		0,57		0	0,2	1	0
	Bjurfors övre									12,3	1,0	0,07	0,12				
4UlU	Ume	65,057836	17,105299	319	4000	184	857	1113	148	11,6		0,75		0	0,58	268	30,7
	Umluspen									7,1	0,6	0,03	0,04				
5SsU	Ume	65,035139	17,413403	299,7	8800	196	1458	931	187	19,2		0,57		0	0,4	164	7,2
	Stensele									11,5	0,6	0,03	0,05				
6GuU	Ume	64,946088	17,713525	265,2	6600	198	5264	753	285	10,6		0,74		0,04	0,33	83,5	0,9
	Grundfors									9,3	0,9	0,07	0,09				
7RuU	Ume	64,709099	18,316647	253,3	3000	226	530	1563	180	4,0		0,65		0,29	0,68	81,4	3
	Rusfors									2,8	0,7	0,07	0,11				

8BlU	Ume	64,643373	18,520344	221,9	2000	227	331	1004	208	7,4		0,69		0,09	0,27	259	30,1
	Bålforsen									5,8	0,8	0,06	0,09				
9GjUn	Skellefte	65,086634	19,502978	231	5200	125	733	2720	98	9,0		0,57		0,04	0,53	14,9	0
	Gallejaur									8,7	1,0	0,04	0,07				
10BtUs	Skellefte	64,817621	20,244563	145	2100	162	104	3	198	36,2		0,66		0	0,1	0	1,05
	Båtfors									22,7	0,6	0,06	0,09				
11GaUn	Skellefte	64,776521	20,440563	106	1200	166	122	3	212	38,3		0,83		0	0,08	38,5	6,6
	Granfors									13,5	0,4	0,05	0,06				
12KrUn	Skellefte	64,757877	20,518293	75	1500	166	178	136	215	14,9		0,81		0	0,14	5,3	4,3
	Krångfors									12,2	0,8	0,05	0,06				
13SeUo	Skellefte	64,727127	20,677636	51	2800	166	267	710	217	32,0		0,82		0	0,14	5,3	4,3
	Selfors									19,5	0,6	0,11	0,13				
15StUo	Angerman	64,262066	17,268856	304	3100	148	1027	2881	150	25,2		0,56		0,07	0,27	97,7	50,6
	Stenkulla									13,5	0,5	0,06	0,11				
16VoUv	Angerman	64,488002	16,759785	327	3800	142	3284	2351	119	11,7		0,79		0,1	0,19	15,5	4,2
	Volgsjöfors									6,6	0,6	0,10	0,13				
17LbUv	Angerman	63,61957	16,800924	148	2600	185	269	1674	220	17,2		0,57		0	0,42	255,7	7,6
	Långbjörn									18,1	1,1	0,03	0,05				
18LaUv	Angerman	63,509152	16,814077	94	5400	193	235	971	224	6,5		0,43		0,04	0,11	14,4	0
	Lasele/ Kilforsen									6,2	1,0	0,03	0,07				
19FjUs	Angerman	63,762473	16,443957	200	2800	123	338	1484	194	19,1		0,79		0,06	0,09	0	0
	Fjällsjö									16,5	0,9	0,06	0,08				
20AkUn	Lule	66,600524	19,889409	214	5500	192	1776	2337	142	9,2		0,75		0,03	0,38	19,1	0
	Akkats									9,3	1,0	0,07	0,09				
21HsUo	Lule	66,839630	19,836607	205	5500	279	215	2658	122	6,7		0,52		0	0,54	165,2	1,5
	Harsprånget									5,3	0,8	0,14	0,27				

22PuUo	Lule	66,933993	19,808608	313	3500	273	217	3043	115	24,3	0,64	0	0,6	73,6	18,4
	Porjus									8,3	0,3	0,09	0,14		
23LiUn	Lule	66,784624	19,964304	165	4200	279		2079	223	2,9	0,61	0,46	0,41	81	0
	Ligga						2283			2,1	0,7	0,09	0,15		
24MeUo	Lule	66,622902	20,419503	78	8000	295		478	183	16,9	0,81	0,26	0,61	271,4	12,7
	Messaure						1222			10,8	0,6	0,07	0,09		
25PiUv	Lule	66,404008	20,706825	44	4000	487		56	212	31,8	0,75	0	0,17	7,9	5,6
	Porsi						956			21,7	0,7	0,05	0,07		
26LxUo	Lule	66,191075	20,871348	20	3800	495		13	156	21,1	0,63	0,04	0,46	171	25,8
	Laxede						2544			9,8	0,5	0,08	0,13		
28BsORs	Vindel	65,386442	17,553123	331,5	NA	148		0	0	18,4	0,63	0,34	0,4	133,9	0
	NA (Blattnicksele)						NA			11,5	0,6	0,14	0,22		
29TrORv	Kalix	67,122446	22,60914	159	NA	194		0	0	12,7	0,71	0,2	0,51	85,1	2,7
	NA (Tärendö)						NA			10,3	0,8	0,05	0,07		
30PaORs	Torne	67,239068	23,29982	151	NA	156		0	0	10,4	0,75	0,4	0,44	60,7	1,8
	NA (Pajala)						NA			6,1	0,6	0,13	0,17		
42KkORv	Torne	65,919074	24,113061	4,1	NA	448		0	0	7,5	0,86	0,33	0,67	192,5	10,4
	NA (Kukkola-forsen)						NA			6,3	0,8	0,04	0,05		
43KfORv	Kalix	66,145896	22,784211	28,3	NA	308		0	0	9,4	0,73	0,3	0,57	171,4	1,4
	NA (Kälvfors)						NA			8,6	0,9	0,05	0,07		
44AlORv	Pite	65,585820	21,121279	27,8	NA	168		0	0	22,2	0,57	0,27	0,73	32,9	12,3
	NA (Älvsbyn)						NA			15,6	0,6	0,03	0,05		

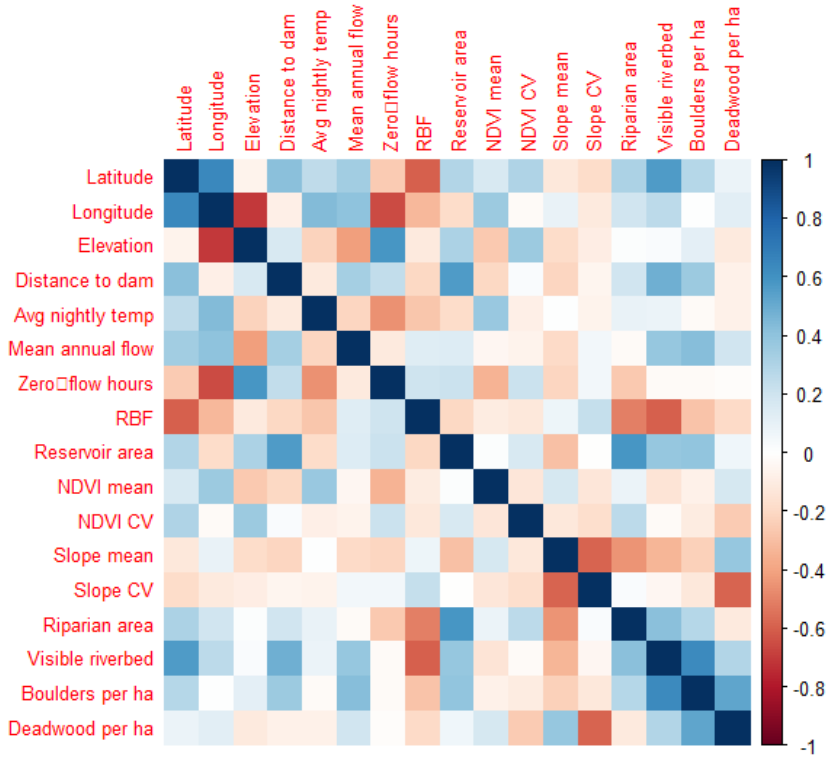


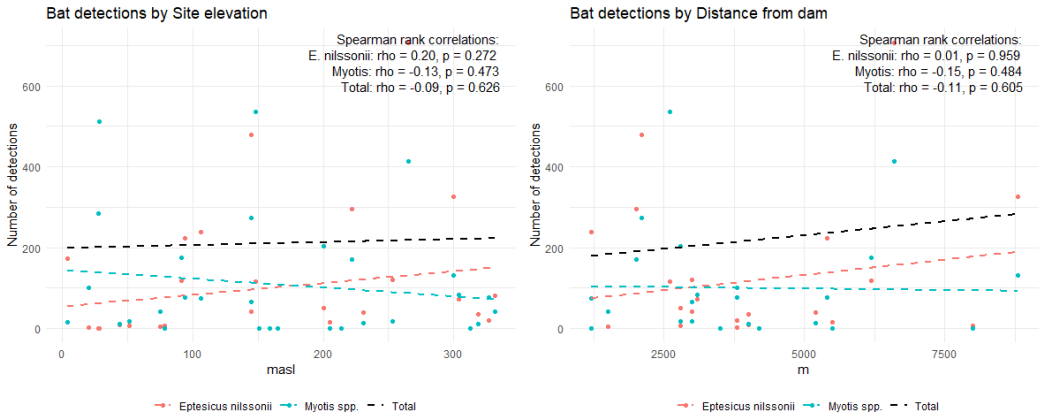
Figure 20. Predictor correlation matrix based on Spearman rank correlations. Colours represent strength and direction of correlation, regardless of statistical significance.

Appendix III

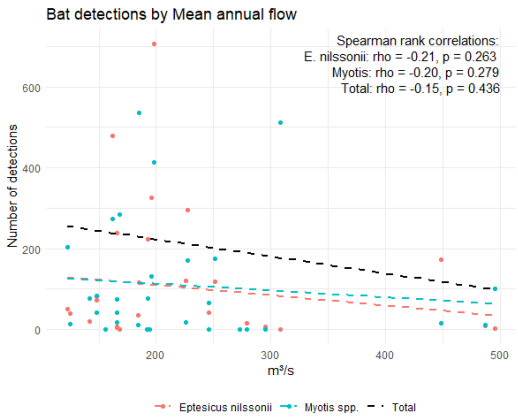
Table 8. Audio detector results

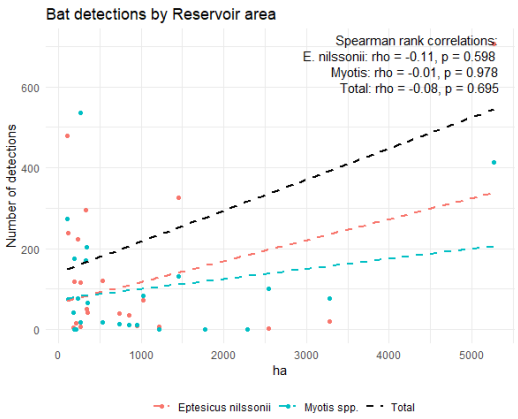
Site	Catchment	Upstream outlet	Latitude	Longitude	Night of first call	Total detections	Enil detections	Myotis detections	Total feeding buzzes	Enil feeding buzzes	Myotis feeding buzzes
1HaU	Ume	Harrfors	64,817621	20,244563	2024-07-10	295	119	176	41	17	24
2BNU		Bjurfors nedre	64,776521	20,440563	2024-07-10	107	41	66	22	7	15
3BOU		Bjurfors övre	64,757877	20,518293	-	0	0	0	0	0	0
4UlU		Umluspen	64,727127	20,677636	2024-07-22	47	35	12	4	4	0
5SsU		Stensele	64,262066	17,268856	2024-07-27	457	325	132	156	122	34
6GuU		Grundfors	64,488002	16,759785	2024-07-16	1120	707	413	272	160	112
7RuU		Rusfors	63,61957	16,800924	2024-08-02	139	120	19	29	26	3
8BlU		Bålforsen	63,509152	16,814077	2024-07-24	467	296	171	111	89	22
9GjUn	Skellefte	Gallejaur	63,762473	16,443957	2024-07-25	53	39	14	7	5	2
10BtUs		Båtfors	63,976798	19,623553	2024-07-23	751	478	273	178	135	43
11GaUn		Granfors	66,600524	19,889409	2024-07-28	313	238	75	38	30	8
12KrUn		Krångfors	66,83963	19,836607	2024-07-14	45	4	41	5	0	5
13SeUo		Selfors	66,933993	19,808608	2024-08-03	25	8	17	1	1	0
15StUo	Ångerman	Stenkulla	66,784624	19,964304	2024-07-28	155	72	83	42	30	12
16VoUv		Volgsjöfors	66,622902	20,419503	2024-07-14	99	21	78	19	2	17
17LbUv		Långbjörn	66,404008	20,706825	2024-07-10	652	116	536	113	15	98
18LaUv		Lasele/Kilforsen	66,191075	20,871348	2024-07-10	302	224	78	39	27	12
19FjUs		Fjällsjö	65,386442	17,553123	2024-07-04	254	51	203	65	10	55
20AkUn	Lule	Akkats	67,122446	22,60914	2024-08-10	2	1	1	0	0	0
21HsUo		Harsprånget	64,077814	19,565351	2024-07-31	16	16	0	3	3	0
22PuUo		Porjus	67,239068	23,29982	-	0	0	0	0	0	0
23LiUn		Ligga	64,145295	19,513125	-	0	0	0	0	0	0

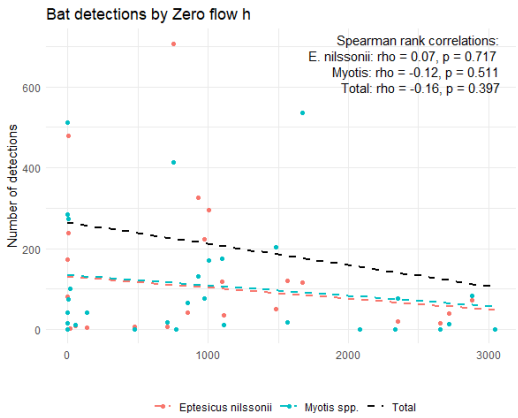
24MeUo		Messaure	65,919074	24,113061	2024-07-26	7	7	0	1	1	0
25PiUv		Porsi	66,145896	22,784211	2024-07-31	22	10	12	2	0	2
26LxUo		Laxede	65,58582	21,121279	2024-07-24	102	2	100	15	0	15
28BsORs	Vindel	NA (Blattnicksele)	65,057836	17,105299	2024-07-28	124	81	43	12	10	2
29TrORv	Kalix	NA (Tärendö)	65,035139	17,413403	-	0	0	0	0	0	0
30PaORs	Torne	NA (Pajala)	64,946088	17,713525	2024-08-11	1	1	0	0	0	0
42KkORv	Torne	NA (Kukkolaforsen)	64,709099	18,316647	2024-07-29	189	173	16	42	41	1
43KfORv	Kalix	NA (Kälvfors)	64,643373	18,520344	2024-07-19	511	0	511	48	0	48
44AlORv	Pite	NA (Älvsbyn)	65,086634	19,502978	2024-07-18	285	0	285	57	0	57

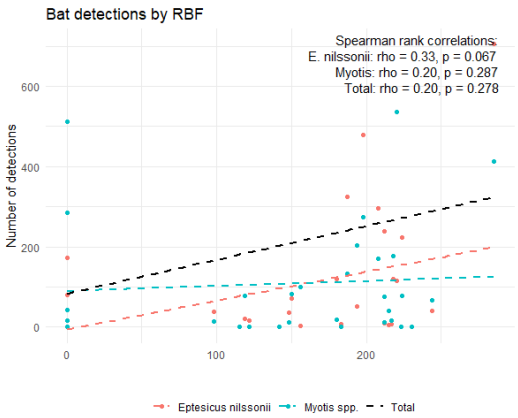

Bat detections by Site elevation
Spearman rank correlations:
E. nilssonii: rho = 0.20, p = 0.272
Myotis: rho = -0.13, p = 0.473
Total: rho = -0.09, p = 0.626
Number of detections
masl
Eptesicus nilssonii
Myotis spp.
Total

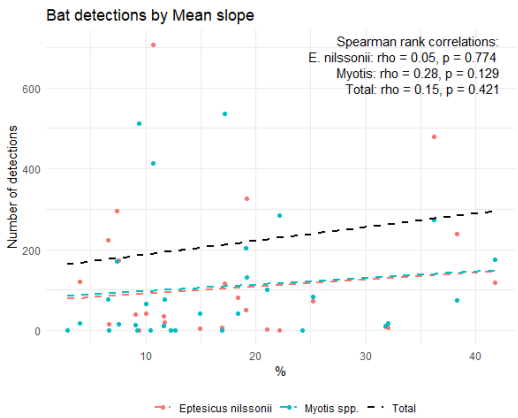
Bat detections by Distance from dam
Spearman rank correlations:
E. nilssonii: rho = 0.01, p = 0.959
Myotis: rho = -0.15, p = 0.484
Total: rho = -0.11, p = 0.605
Number of detections
m
Eptesicus nilssonii
Myotis spp.
Total

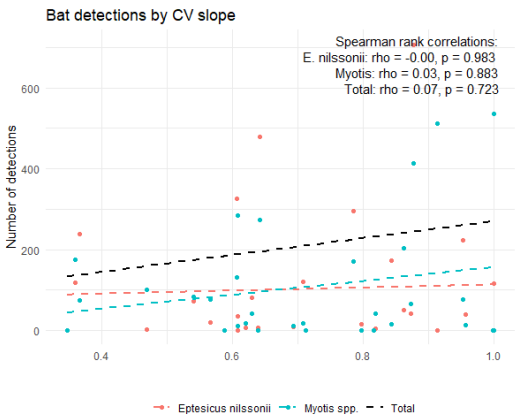

Bat detections by Mean annual flow
Spearman rank correlations:
E. nilssonii: rho = -0.21, p = 0.263
Myotis: rho = -0.20, p = 0.279
Total: rho = -0.15, p = 0.436
Number of detections
m³/s
Eptesicus nilssonii
Myotis spp.
Total


Bat detections by Reservoir area
Spearman rank correlations:
E. nilssonii: rho = -0.11, p = 0.598
Myotis: rho = -0.01, p = 0.978
Total: rho = -0.08, p = 0.695
Number of detections
ha
Eptesicus nilssonii
Myotis spp.
Total


Bat detections by Zero flow h
Spearman rank correlations:
E. nilssonii: rho = 0.07, p = 0.717
Myotis: rho = -0.12, p = 0.511
Total: rho = -0.16, p = 0.397
Number of detections
Eptesicus nilssonii
Myotis spp.
Total


Bat detections by RBF
Spearman rank correlations:
E. nilssonii: rho = 0.33, p = 0.067
Myotis: rho = 0.20, p = 0.287
Total: rho = 0.20, p = 0.278
Number of detections
Eptesicus nilssonii
Myotis spp.
Total


Bat detections by Mean slope
Spearman rank correlations:
E. nilssonii: rho = 0.05, p = 0.774
Myotis: rho = 0.28, p = 0.129
Total: rho = 0.15, p = 0.421
Number of detections
%
Eptesicus nilssonii
Myotis spp.
Total


Bat detections by CV slope
Spearman rank correlations:
E. nilssonii: rho = -0.00, p = 0.983
Myotis: rho = 0.03, p = 0.883
Total: rho = 0.07, p = 0.723
Number of detections
Eptesicus nilssonii
Myotis spp.
Total

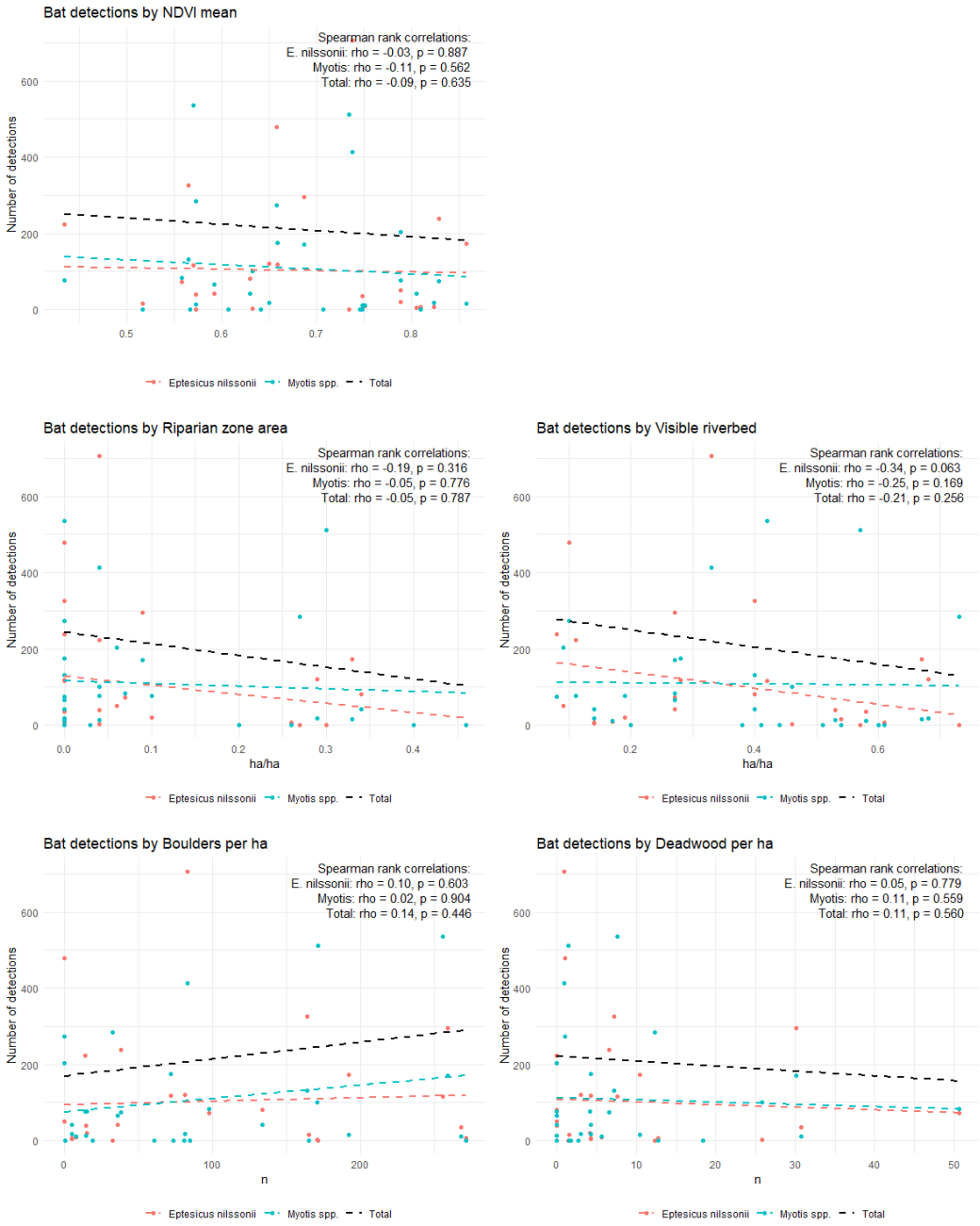


Figure 21. Relationships between bat detections and the predictor variables based on a linear regression (dashed lines). Red markers represent Northern bats, blue - Myotis and black - the total amount of bat detections. Correlations were tested using Spearman rank correlations and are not significant.

Table 9. Spearman rank correlation table

Response	Predictor	rho	p-value	Significance
Total detections	N_WGS84	-0,54	0,002	**
	E_WGS84	-0,29	0,115	ns
	Temp_min_avg	0	0,987	ns
	MAS	-0,09	0,626	ns
	Distance	-0,11	0,605	ns
	MQ	-0,15	0,436	ns
	Res_Area_ha	-0,08	0,695	ns
	Zero_flow_h	-0,16	0,397	ns
	RBF_y	0,2	0,278	ns
	Slope_mean	0,15	0,421	ns
	Slope_cv	0,07	0,723	ns
	NDVI	-0,09	0,635	ns
	NDVI_cv	-0,43	0,015	*
	Rip_zone_area	-0,05	0,787	ns
	Visible_riverbed_percent	-0,21	0,256	ns
	Boulders_per_ha	0,14	0,446	ns
	Deadwood_per_ha	0,11	0,56	ns
Enil detections	N_WGS84	-0,54	0,002	**
	E_WGS84	-0,48	0,007	**
	Temp_min_avg	-0,19	0,295	ns
	MAS	0,2	0,272	ns
	Distance	0,01	0,959	ns
	MQ	-0,21	0,263	ns
	Res_Area_ha	-0,11	0,598	ns
	Zero_flow_h	0,07	0,717	ns
	RBF_y	0,33	0,067	.
	Slope_mean	0,05	0,774	ns
	Slope_cv	0	0,983	ns
	NDVI	-0,03	0,887	ns
	NDVI_cv	-0,27	0,147	ns
	Rip_zone_area	-0,19	0,316	ns
	Visible_riverbed_percent	-0,34	0,063	.
	Boulders_per_ha	0,1	0,603	ns
	Deadwood_per_ha	0,05	0,779	ns
Myotis detections	N_WGS84	-0,57	0,001	***
	E_WGS84	-0,29	0,118	ns
	Temp_min_avg	0,01	0,971	ns
	MAS	-0,13	0,473	ns
	Distance	-0,15	0,484	ns
	MQ	-0,2	0,279	ns
	Res_Area_ha	-0,01	0,978	ns
	Zero_flow_h	-0,12	0,511	ns
	RBF_y	0,2	0,287	ns
	Slope_mean	0,28	0,129	ns
	Slope_cv	0,03	0,883	ns
	NDVI	-0,11	0,562	ns
	NDVI_cv	-0,37	0,04	*
	Rip_zone_area	-0,05	0,776	ns
	Visible_riverbed_percent	-0,25	0,169	ns
	Boulders_per_ha	0,02	0,904	ns
	Deadwood_per_ha	0,11	0,559	ns

Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (.) $p < 0.1$, ns = not significant.

Table 10. Model evaluation results

Data subset	Response variable	Model Nr	AICc	Predictors	Estimate coefficient	p-value	Significance
full	Enil	1	310,56	N_WGS84	-1,54	0,0000	***
		2	311,01	N_WGS84	-1,43	0,0000	***
				Zero_flow_h	-0,49	0,0900	.
		3	311,51	N_WGS84	-1,79	0,0000	***
				Boulders_per_ha	0,47	0,1200	
	Myotis	1	317,03	N_WGS84	-1,92	0,0000	***
				Zero_flow_h	-1,02	0,0020	**
				Regulation (Unr)	1,39	0,0900	.
		2	317,44	N_WGS84	-1,66	0,0000	***
				Zero_flow_h	-1,26	0,0000	***
		3	318,04	N_WGS84	-2,44	0,0000	***
				MQ	0,54	0,0770	.
				Zero_flow_h	-0,75	0,0324	*
				Regulation (Unr)	1,93	0,0260	*
	Total	1	367,77	N_WGS84	-1,51	0,0000	***
				Zero_flow_h	-0,81	0,0007	***
				Boulders_per_ha	0,52	0,0270	*
		2	368,02	N_WGS84	-1,33	0,0000	***
				Zero_flow_h	-0,82	0,0008	***
		3	369,66	N_WGS84	-1,38	0,0000	***
				Zero_flow_h	-0,83	0,0007	***
				Slope_cv	0,29	0,2320	
north	Enil	1	123,09	N_WGS84	-1,69	0,0002	***
		2	124,16	N_WGS84	-1,57	0,0002	***
				Boulders_per_ha	0,78	0,0589	.
		3	124,55	N_WGS84	-1,78	0,0001	***
				MQ	0,67	0,1180	
	Myotis	1	126,65	N_WGS84	-2,97	0,0000	***
				MAS	-1,63	0,0002	***
				Zero_flow_h	-1,25	0,0270	*
		2	128,86	N_WGS84	-3,70	0,0000	***
				MAS	-2,45	0,0000	***
				NDVI_cv	0,51	0,3560	
		3	128,86	N_WGS84	-3,44	0,0000	***
				MAS	-1,98	0,0000	***
				Temp_min_avg	0,35	0,3400	
	Total	1	156,43	N_WGS84	-3,12	0,0000	***
				MAS	-1,79	0,0000	***
				NDVI_cv	0,92	0,0084	**
		2	158,73	N_WGS84	-2,19	0,0000	***
				MAS	-1,10	0,0004	***
		3	159,39	N_WGS84	-2,33	0,0000	***
				MAS	-1,36	0,0000	***
				Boulders_per_ha	0,89	0,0014	**
				Deadwood_per_ha	-0,78	0,0104	*
south	Enil	1	186,56	Zero_flow_h	-0,50	0,1410	
		2	186,91	N_WGS84	0,35	0,3060	
		3	187,87	MAS	0,29	0,4070	
	Myotis	1	185,02	Boulders_per_ha	0,44	0,1140	
		2	185,28	NDVI_cv	-0,57	0,0429	*
		3	185,57	MAS	0,58	0,0408	*
				NDVI_cv	-0,87	0,0023	**
	Total	1	208,57	Boulders_per_ha	0,35	0,2410	
		2	208,83	NDVI_cv	-0,46	0,1290	
		3	209,43	Zero_flow_h	-0,24	0,4380	
regulated	Enil	1	264,44	N_WGS84	-1,01	0,0001	***
				MAS	1,05	0,0021	**
				Zero_flow_h	-1,00	0,0043	**
		2	265,73	N_WGS84	-1,38	0,0000	***
				MAS	1,08	0,0014	**
				Zero_flow_h	-1,22	0,0012	**

			NDVI_cv	0,43	0,1855	
	3	266,79	N_WGS84	-0,99	0,0003	***
			MAS	1,10	0,0011	**
			Zero_flow_h	-1,01	0,0036	**
			Rip_zone_area	-0,34	0,2397	
Myotis	1	248,63	N_WGS84	-2,01	0,0000	***
			Zero_flow_h	-0,88	0,0006	***
			Res_Area_ha	0,69	0,0041	**
	2	248,8	N_WGS84	-2,04	0,0000	***
			Temp_min_avg	-0,46	0,0318	*
			Zero_flow_h	-0,98	0,0001	***
			Res_Area_ha	0,67	0,0029	**
	3	249,37	N_WGS84	-2,02	0,0000	***
			Zero_flow_h	-0,94	0,0002	***
			Res_Area_ha	0,65	0,0048	**
			Deadwood_per_ha	0,35	0,1094	
Total	1	298,73	N_WGS84	-1,17	0,0000	***
			MAS	0,66	0,0361	*
			Zero_flow_h	-0,99	0,0021	**
	2	299,64	N_WGS84	-1,35	0,0000	***
			Zero_flow_h	-0,58	0,0170	*
			Res_Area_ha	0,36	0,1350	
	3	300,1	N_WGS84	-1,54	0,0000	***
			MAS	0,69	0,0257	*
			Zero_flow_h	-1,19	0,0006	***
			NDVI_cv	0,42	0,1500	

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