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Non- Invasive Monitoring of Insectivorous Bats and Insects in Boreal Forest Habitats

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Abstract

1. All the Norwegian bat species depend on forest habitats in some parts of their annual cycle. Despite many of the Norwegian bat species being categorised as threatened on the Norwegian Red List and playing key roles as controllers of insect populations, lack of knowledge about their ecological role in forests leads to them often being overlooked in management decisions. Bats can be grouped into foraging guilds depending on their foraging behaviors and call structure. This study focuses on short- range echolocating (SRE) bat species foraging on insects in open forest habitats.

2. The overall aim of the study is to gain more knowledge about the relationships between SRE bat activity and insect abundance within boreal forests of varying tree density. More specifically this study investigates (1) if and how the activity of SRE bats is influenced by forest density (canopy openness) and environmental variables (temperature, moisture), and if these relationships differs between feeding and commuting behaviours, (2) if and how the abundance of insects is influenced by canopy openness and environmental variables, and (3) whether there is a stronger positive correlation between bat feeding activity and insect abundance than between bat commuting activity and insect abundance.

3. Data was retrieved from sampling plots located in forest gaps in eleven mixed boreal forest sites in south-eastern Norway between May and September 2022. Bat activity and insect abundance were monitored with non- invasive methods, using bat acoustic detectors and insect camera traps. Site- specific soil moisture and temperature data were sampled using data loggers deployed into the soil. Hemisphere photos were taken at each site to calculate canopy openness as a proxy for forest density.

4. Results from this study show that forest density and environmental variables influenced bat feeding- and commuting activity differently. Bat feeding activity increased with higher canopy openness and decreased with higher temperatures. Bat commuting activity decreased with increasing soil moisture and temperatures. Insect abundance was positively influenced by moisture and had a negative relationship with temperature. The relationship between bat activity and insect abundance was positively influenced by low canopy openness but disappeared at higher openness. For commuting behaviour there was no clear relationship between bats and insects. Results from this study show that there are relationships between insect abundance and bat activity in forests that can be quantified with non- invasive monitoring. However, to fully understand this relationship, one must account for the influence of biotic and abiotic environmental variables.

Key words: Insectivorous bats, flying insects, short- range echolocators, passive acoustic monitoring, insect camera traps, non- invasive, canopy openness, boreal forests

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1 Introduction

Forest ecosystems constitute important habitats for many bat species, offering key resources of both roosting and foraging grounds (Dietz & Kiefer, 2016). All Norwegian bat species are insectivores and exploit forest habitats in some parts of the year. During the summer, bats in temperate regions rely on stable abundances of insects to accumulate the fat reservoirs required to survive the long winters (Vesterinen et al., 2016). Norway's eleven bat species are all nocturnal and use echolocation in navigation and to catch their prey (Perks & Goodenough, 2020). Species in this study (*Myotis* spp. and *Plecotus auritus*) are short- range echolocation (SRE) species that typically catch their prey by aerial hawking or gleaning (Ancillotto & Russo, 2020; Perks & Goodenough, 2020).

In recent years there has been an increasing concern for trends of decline in global insect populations (e.g., Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021). Main causes of insect declines includes habitat loss, degradation, climate change and agriculture (Wagner et al., 2021). Lower abundances of insects also affect insectivorous species that rely on access to insect prey. For example migratory insectivorous birds have experienced significant declines in North America (Spiller & Dettmers, 2019). A study, from Denmark, found flying insect declines to be strongly correlated with the decline of the insectivorous barn swallows (*Hirundo rustica*) (Møller, 2019). However, insectivore declines are not only caused by a decrease in abundance of insects. Many insectivorous species are also declining as they are forced to shift their diet to less preferable prey of lower caloric value (Pomfret et al., 2014; Twining et al., 2016). To date, several studies have investigated relationships between insect abundance and bat activity (e.g., Bolliger et al., 2020; Fukui et al., 2006; Kolkert et al., 2020; Müller et al., 2012; Verboom & Spoelstra, 1999; Wolbert et al., 2014). However, there are few studies on bat- insect relationships that are carried out in boreal forests and higher latitudes (but see Vesterinen et al., 2018; Vesterinen et al., 2016). It is therefore a need for more research in these ranges, as they represent living areas with unique environmental constraints for many bat species.

Research on factors influencing bat activity show that the distribution and activity of bats are more determined by forest structural features than insect abundance (Brigham et al., 1997; Cox et al., 2016; Müller et al., 2012). Studies have also shown that different forest structures can be used as proxies for bat activity (e.g., Carr et al., 2023). Many forest dwelling bats have a preference for open habitats, with increasing vegetation density negatively affecting bat foraging activity (Brigham et al., 1997). Open forest habitats, with higher canopy openness,

allow for better manoeuvrability of bats and easier detection by ultrasonic bat recorders. Erasmý et al. (2021) found that natural canopy gaps increased forest bat diversity in coniferous forests, although this also depended on the bat guild. A limiting factor of bat forest activity is the number of potential roosting places (i.e., dead wood, hollow trees, crevices) (Crampton & Barclay, 1998; Ruczyński & Bogdanowicz, 2005). Trees with suitable microhabitats for bat roost sites are typically associated with older, natural forests (Basile et al., 2020; Mölder et al., 2020; Vuidot et al., 2011) and bats within the boreal zone have indicated a preference for mature forests (Vasko et al., 2020). However, there is a growing recognition that production forests might be more suitable for bats than previously thought (Kirkpatrick et al., 2018; Rachwald et al., 2021). Forests managed for timber production are typically denser and thus potentially constitute a less manoeuvrable foraging habitat compared to forests with a more natural forest dynamic. It is therefore especially important to understand if- and- how forest density influences bat activity in these habitats. Reconsidering and understanding the importance of these forest habitats will thus be vital in future management.

Bat activity and insect abundance are also affected by abiotic factors, such as moisture and temperature. Soil moisture can be used as a proxy for precipitation (P. Froidevaux et al., 2014). Insectivorous bats have shown to be negatively correlated with precipitation (Erickson & West, 2002; Voigt et al., 2011), both because it causes physical constraints in bats flying abilities and suppresses insect abundance (Snively et al., 2021). On the contrary, insect abundance is generally positively correlated with increasing moisture. For example, many Dipteran species (i.e., mosquitos) rely on access to water in their larval stage (Oldroyd, 1999). Temperature tends to be positively correlated with bat activity (Erickson & West, 2002; Snively et al., 2021), especially in northern latitudes (Perks & Goodenough, 2020; Wolbert et al., 2014) where temperatures are generally lower compared to lower latitudes. Higher ambient temperatures also promotes insect activity in northern latitudes (Burles et al., 2009). In this study, soil moisture and temperature are included to control for the effect of environmental variables on the relationship between bat activity and insect abundance.

With the development of new wildlife monitoring technology and a stronger focus on animal welfare, non- invasive methods have become increasingly popular. A commonly used method in bat monitoring is the use of passive acoustic recording detectors (hereafter referred to as “detectors”), where acoustic detectors are programmed to collect recordings of sound produced by bats (ultrasonic activity as well as sound within the human auditory range). In addition to being non- invasive, advantages with this technique are that it is cost-effective and allows for

collection of large datasets (J. S. P. Froidevaux et al., 2014; Kotila et al., 2023). The method has certain advantages over other methods, such as live capturing, as it can also be used in more cluttered habitats and detects significantly more species per sampling night (MacSwiney G. et al., 2008). Within insect monitoring, recent studies have shown the potential of cameras monitoring nocturnal insect abundance with insect camera traps (Ruczyński et al., 2020). This technique can be used to collect data with high spatial and temporal resolution that displays dynamic changes in insect abundances (Ruczyński et al., 2020). Since the cameras register data on time- and- date, the method also allows for investigating relationships with data collected with other high- resolution monitoring techniques (i.e., bat activity), where recordings can be compared at time scales of within a few minutes.

There is a lack of studies that investigate relationships between bats and insects in boreal habitats. Based on current knowledge, no previous published study has been carried out to understand the potential modifying effects of forest density, temperature, and moisture on the relationship between bats and insects in boreal forests. This study focuses on the typically forest- dwelling species, *P. auritus* and *Myotis* spp. and how their activity patterns relate to insect abundance throughout the boreal summer. Secondly the study focuses to gain a better understanding of how forest density (canopy openness) influence SRE bat activity and insect abundance, while accounting for environmental factors: temperature, and moisture. More specifically, three research questions have been outlined for this study:

- 1) *How is the activity of SRE bats influenced by canopy openness and the environmental factors (soil moisture and temperature), and does this relationship differ between feeding and commuting behaviours?*
- 2) *How is the abundance of insects influenced by canopy openness and environmental factors?*
- 3) *Is there a stronger positive correlation between bat feeding activity and insect abundance than between bat commuting activity and insect abundance?*

Related to each of these research questions, I have the following hypotheses:

- I. An increase in canopy openness and temperature will promote bat activity, but moisture will have a negative effect on bat activity.
- II. Moisture and temperature will have a positive effect on insect abundance and increasing canopy openness will have a negative effect on insect abundance.
- III. There will be a higher positive correlation between bat feeding activity and insect abundance than between bat commuting activity and insect abundance.

2 Materials and methods

2.1 Study area and site selection

The study area (**Figure 1**) stretches through Nordre Follo, Ås, Vestby and Frogn municipalities in the south-eastern part of Norway in Viken county. The eleven sites researched in this study are production forests that include mixed boreal forests (i.e., a mix of coniferous and deciduous trees) of similar age, productivity, and height. Main land cover is categorised as boreal forests dominated by Norway Spruce (*Picea abies*), Scots pine (*Pinus Sylvestris*) and a mix of deciduous trees (NIBIO, 2023). The area is located within the hemiboreal zone with relatively mild climate. Daylength in the northern hemisphere varies through the summer, peaking in mid-June with daylength at approximately 18 hours and 45 minutes in Ås (Timeanddate.no, 2023).

Given the information available on abundance of bat populations in Norway (Artsdatabanken, 2023) as well as suitable climatic conditions in the region, the study area has the potential to include all bat species currently known to occur in Norway. The sites were also selected because they are near the Norwegian University of Life and Sciences (NMBU) which eased the access to the sites. Additionally, the sites were representative for the mixed production forests in the region.

To extract information about the forests in the study area, SR16 and SR16beta Norwegian forest maps (Astrup et al., 2019) and national resource maps of Norway AR5 maps (Ahlstrøm et al., 2019) were processed in the mapping software QGIS (QGIS Development Team, 2021). Sites were then selected on a forest density gradient calculated from basal area and crown cover, based on Eid (2001). They were all located within an area of 40km², at least 50 metres from the coastline or water bodies, and 50 metres from the forest edge to control for edge effects. Each site was located between 1 and 17 km apart from each other.

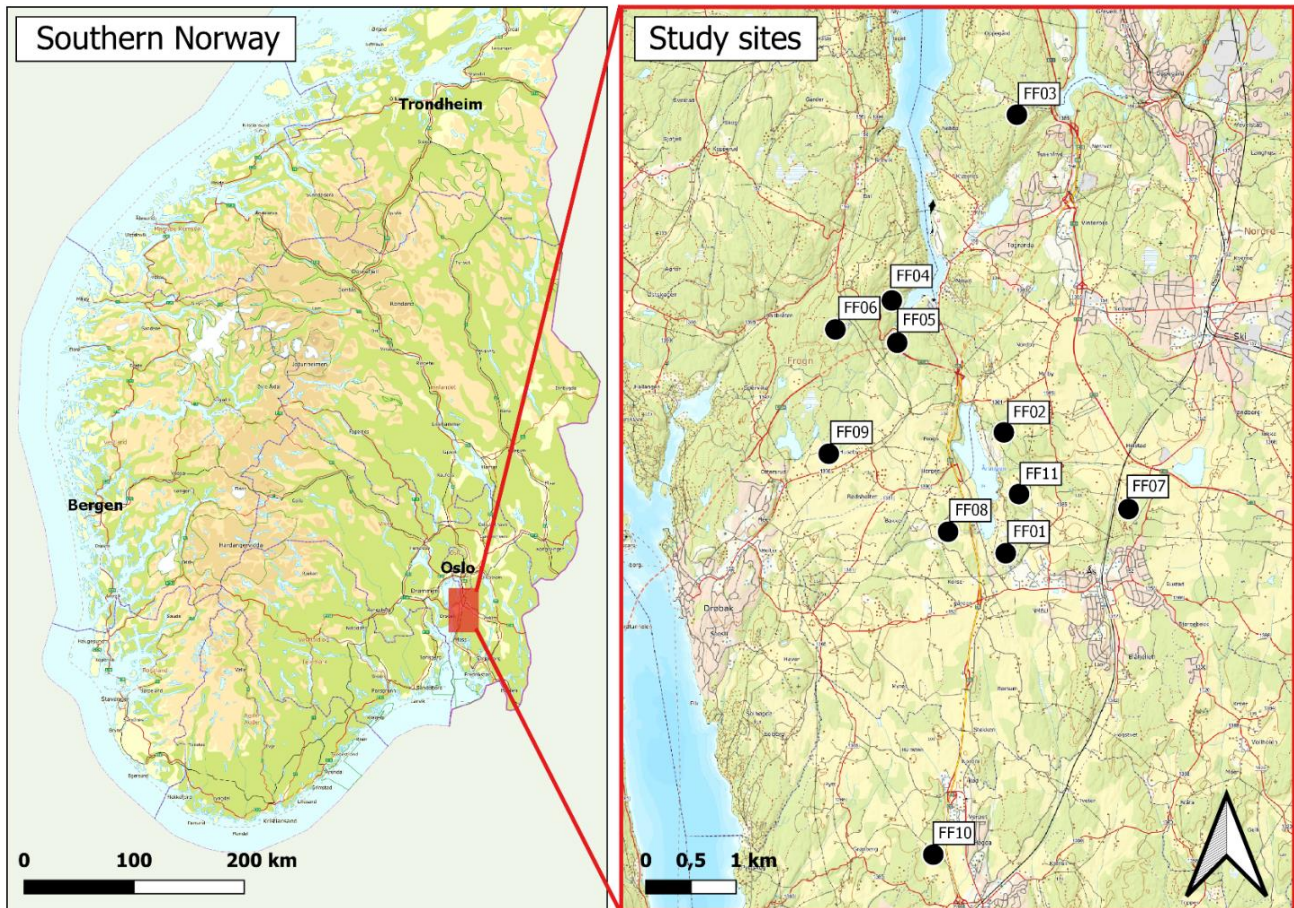


Figure 1: Study area map. Map to the left is showing Southern Norway with study area outlined in the red box. Map to the right is showing the study area with site locations (FF01-FF11). Coordinates for each site can be found in **Appendix 1, Table A1**. Maps are generated in QGIS with WMTS background map from Norgeskart (Norgeskart Bakgrunn).

2.2 Study species

2.2.1 Bats

Only five of the eleven bat species found in Norway (**Table 1**) are considered least concerned (LC) on the Norwegian National Red List (Artsdatabanken, 2021). However, within the European distribution area of these species, all except the *Barbastella barbastellus* (Near Threatened) are considered LC throughout their range (IUCN, 2023). Bats can be observed all over Norway; however, they are more abundant in the southern parts of the country.

Table 1: Overview of bat species found in Norway. Their common names are given in Norwegian. Foraging guilds are divided into three categories: **SRE**= Short- range echolocators, **MRE**= medium- range echolocators and **LRE**= long- range echolocators. The foraging guild monitored in this study (=SRE) is outlined in bold. Red list status is based on the Norwegian Red list (Artsdatabanken, 2021) and are here represented by five categories: **CR**=critically endangered, **EN**= endangered, **VU**= vulnerable, **NT**= Near threatened, **LC**= least concern. The presence- column indicates the likelihood of the bat species appearing within our study area based on current knowledge about abundance of the species.

<i>Scientific name</i>	<i>Common name</i>	<i>Foraging guild</i>	<i>Red list status</i>	<i>Presence</i>
<i>Barbastella barbastellus</i>	Bredøre	SRE	CR	Unlikely
<i>Eptesicus nilsonii</i>	Nordflaggermus	LRE	VU	Common
<i>Myotis brandtii</i>	Skogflaggermus	SRE	LC	Common
<i>Myotis daubentonii</i>	Vannflaggermus	SRE	LC	Common
<i>Myotis mystacinus</i>	Skjeggflaggermus	SRE	LC	Common
<i>Myotis natterii</i>	Børsteflaggermus	SRE	CR	Unlikely
<i>Nyctalus noctula</i>	Storflaggermus	LRE	EN	Common
<i>Pipistrellus nathusii</i>	Trollflaggermus	MRE	NT	Potential
<i>Pipistrellus pygmaeus</i>	Dvergflaggermus	MRE	LC	Common
<i>Plecotus auritus</i>	Brunlangøre	SRE	LC	Common
<i>Vespertilio murinus</i>	Skimmelflaggermus	LRE	NT	Potential

Within research, bat species with similar physiological and behavioural adaptations are often assigned to different guilds or functional groups, independent of their phylogeny (Denzinger & Schnitzler, 2013). In this study, bat passes were grouped into three foraging guilds (short-, medium-, and long- range echolocators) originally defined by Frey-Ehrenbold et al. (2013). Parameters for separating between these guilds were adapted based on the bat community in our study area, using (Russ, 2021) as a reference for species specific acoustic metrics. Long-range echolocator (LRE) bat calls primarily consist of frequency modulated quasi constant frequency (FM-QCF) calls with peak frequencies below 32 kHz. Species belonging to this guild are typically well adapted to flying in open space environments. Medium- range echolocator (MRE) bats rely on FM-QCF calls with peak frequency above 34 kHz and are well adapted to flying in edge space environments. Short- range echolocator (SRE) species relies mostly on low intensity, high interpulse interval, frequency modulated (FM) call types. SRE bats are often well adapted to forage in the interior forest, having short and rounded wings that improve

manoeuvrability in more cluttered environments (Marinello & Bernard, 2014; Norberg et al., 1987).

Of the six SRE species in **Table 1**, individuals of *M. brandtii*, *M. daubentonii*, *M. mystacinus*, *P. auritus* and *B. barbastellus* were all expected to occur within the study area. *M. natterii* was not expected due to uncertain distribution of the species in Norway (Eldegard et al., 2021) (**Table 1**). FM calls produced by SRE bats can be identified in spectrograms of the recorded call (see **Figure 5**). In this study *Myotis* spp. were categorised to genus rather than species level due to overlapping call structures between the species. *Myotis* spp., in contrast to *P. auritus* and *B. barbastellus*, produce distinctive feeding buzzes that can be used to identify feeding behaviour. Because of this, the recorded feeding activity in this study only reflects behaviour of *Myotis* spp. The SRE species *B. barbastellus* separate from the other SRE species by having a more varied call structure, with a stronger quasi constant frequency (QFC)- component in their calls in addition to the FM call. They produce a very low intensity call type, which is quiet and of short range. However, *B. barbastellus* was not recorded in this study.

SRE bats are chosen as study guild for this study by practical reasons. Since their peak frequency is lower than the other bat guilds (i.e., LRE, MRE), there is also a higher chance that the bat calls from SRE bats are produced by individuals operating close to the detector. This enable comparisons between bat activity, insect abundance and environmental variables that is monitored close to the bat detector.

2.2.2 Insects

The insects of interest in this study are flying, nocturnal insects such as *Lepidoptera* (butterflies) and *Diptera* (true flies), that could be recorded by the insect camera traps. A previous study conducted in south-western Finland, near the same latitude as our study area, found that the insect orders butterflies and true flies also composed the main diet for SRE bat species (Vesterinen et al., 2018). Other potential prey includes insects from the orders *Coleoptera*, *Ephemeroptera*, *Hemiptera*, *Orthoptera* and *Trichoptera*, all of which are present within our study area. Even though this study does not aim to identify the insect taxa recorded, one would expect to find a similar taxonomic composition of insects within our study area.

Since the camera lens on the insect camera traps faced the sky, the measures of insects in this study are limited to flying insects. Accordingly, certain insect taxa will not occur in the images,

even though they still might be important prey for the bats. Due to low resolution of camera trap images, there is a high chance of taxonomic identification bias. Thus, the insects were only detected by presence in each image and overall abundance of flying insects were calculated.

2.3 Data collection

At each site a bat acoustic detector, an insect camera trap and a soil sensor were deployed. The bat acoustic detector was deployed at plots in the forest with canopy gaps and exposed sky. To measure the influence of temperature and moisture on bat activity and insect abundance, a soil sensor was deployed within 10 metres of the detector and insect camera trap. In **Figure 2** you see an overview of the equipment setup. To measure the influence of canopy coverage on bat activity and insect abundance, a hemisphere image was taken at each site at the end of the season.

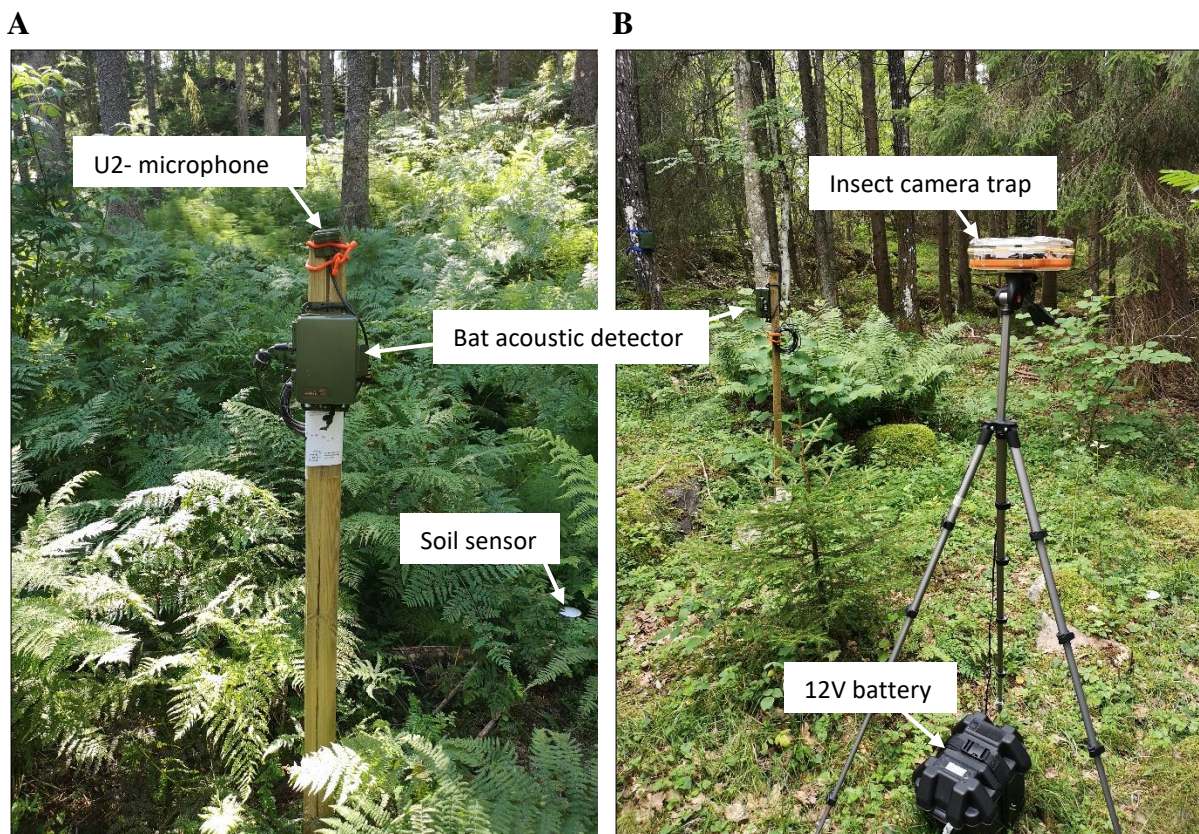


Figure 2: Overview of equipment set-up in the field. A U2-microphone was attached to an acoustic bat detector on top of a wooden pole (A). Soil sensors were deployed into the soil close to the detector. An insect camera trap was installed on top of a tripod (B) and a 12V gel battery, protected by a black box, was used as power source. In B one sees an example of how detectors and camera traps were deployed only a few metres apart. Photos are from site FF04 (A) and site FF01 (B). Photos by Mathilde Klokkeveen Thomle

2.3.1 Acoustic monitoring

Bat activity was monitored at each site using SM4BAT- FS bioacoustics recorders (hereafter referred to as detectors) from Wildlife Acoustics Inc. All detectors were deployed with omnidirectional SMM-U2 (U2) microphones except when U2 microphones failed and needed to be replaced with unidirectional SMM-U1 (U1) microphones (FF09 and FF10). U2-microphones were oriented towards the sky, while U1- microphones pointed towards the most open habitat oriented approximately 45 degrees upwards from the pole.

Detectors were deployed in the first week of May 2022 and retrieved at the end of September 2022. Added together, the detectors were active for 141 days. Acoustic detector maintenance was carried out every 2-3 weeks to monitor for technical issues and to collect data. The standard maintenance procedure included checking the detectors date and time settings, register the detectors power status (battery voltage), check and/or retrieve memory cards, calibrating microphones and making sure that all the gear was in place. Batteries and memory cards were changed frequently throughout the field season.

The detectors were placed on top of a wooden pole approximately 1,5 m tall and 5 metres away from surrounding vegetation. Detectors were scheduled to monitor between one hour before sunset and one hour after sunrise, making triggered recordings (minimum frequency: 12 kHz) of ultrasonic sound. The GPS location of the detector adjusted the monitoring schedule accordingly in relation to changing sunset and sunrise time throughout the season. To secure the detectors from environmental conditions and unauthorized personnel a 3- digit code lock was attached to the cover of the detector. A full overview of the detector settings can be found in **Appendix 2, Table A2**.

2.3.2 Insect camera trap monitoring

Insect camera traps were deployed in early June and retrieved in the end of July, with a total monitoring period of approximately seven weeks. Regular maintenance was carried out once a week except for two weeks in the end of June, where we had no recordings. Images from the insect camera traps were used to calculate the abundance of flying insects.

Insect monitoring in this study was similar to what is described in Ruczyński et al. (2020). The cameras (Ricoh WG-6 (Digital) Waterproof 20m/65.6ft; Model R02050 2019) were installed as close as possible to the bat acoustic detector, facing towards the sky, on top of a tripod, about 80 cm from ground level. Cameras were connected to an external battery (Biltema motorcycle

gel battery, 12V, 15Ah-21Ah) power source. The cameras were programmed to take pictures with flash on every 10 minutes, 24 hours a day. Additional camera settings can be found in **Appendix 3, Table A3**.

The weekly maintenance included checking batteries, camera settings, cleaning the camera lens and- lid, retrieving memory cards, and making sure that the equipment was properly secured. The batteries were placed in black plastic boxes to protect them from weather and reduce the risk of wildfire (**Figure 2**).

2.3.3 Sampling of environmental and canopy data

One TMS-4 TOMST datalogger (Wild et al., 2019) (**Figure 3**) was deployed at each site. The dataloggers (hereafter referred to as soil sensors) were deployed within 2-5 metres from the bat detector. Soil sensors were programmed to collect data every 10 minutes on temperature and moisture. The sensor measured temperatures at three levels of depth: -6, +2 and +15 cm, relative to the soil surface. Moisture was measured right under the surface. To shovel the sensor into the soil, we first made a hole using a metal stick with the same size as the soil sensor. The soil sensors were retrieved from field at the same time as the bat detectors.

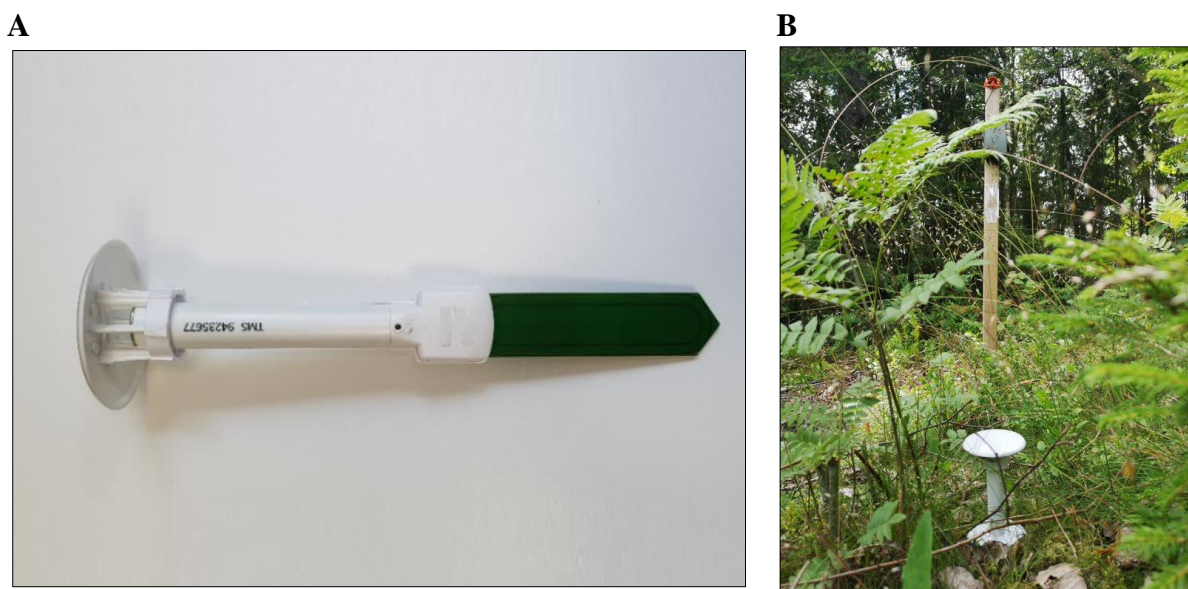


Figure 3: A. TMS-4 TOMST soil sensor. Photo by: TOMST® B. Soil sensor in relative position to the acoustic bat detector. Photo by: Mathilde Klokkersveen Thomle

Hemisphere photos (**Figure 4**) were taken in the beginning of September using a PENTAX K-5II DSLR camera with a 4.5 mm f/2.8 EX DC HSM circular fisheye camera lens. The camera was attached on top of a 130 cm high tripod with the lens orientated at the sky. The photos were taken at open canopy gaps, as close to the bat acoustic detectors and insect camera traps as possible to allow for data comparisons. The photos were taken at each site within the same week and in days with similar weather conditions. Cloudy weather without too much sunlight was considered the optimal conditions for photos. Photos were used to measure canopy openness as a metric for forest density.

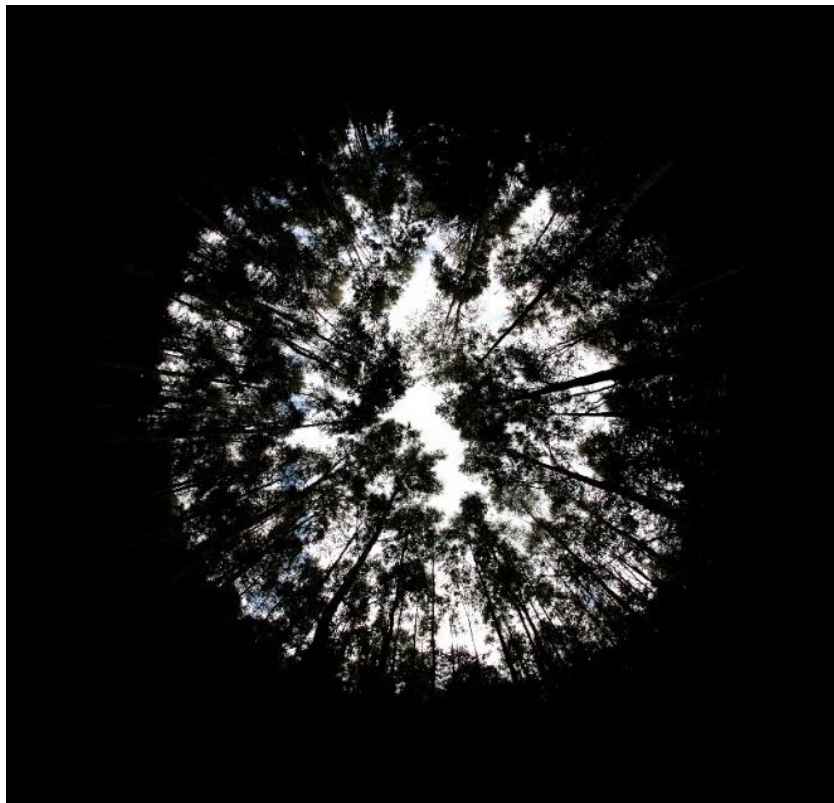


Figure 4: Photo of forest canopy at site FF07. Photo is taken with a fisheye camera attached to a tripod. Photo by Reed April Mckay.

2.4 Data management and preparation

All the raw data collected was backed up on a NMBU large file with at least one accessible backup in OneDrive. Data maintenance and management checks were regularly carried out during the field work period. This included reviewing the data, backing up and storing data properly and identifying any missing data.

2.4.1 Bat acoustic data

A “bat pass” is defined as a sequence of bat calls/pulses emitted by a bat as it flies by the detector (Wildlife Acoustics, 2023a). In this study one bat pass included any recording that had at least two consecutive pulses and lasted for minimum 2 seconds. Recordings were then trimmed to 5 second passes. **Figure 5** gives an example of multiple bat calls (or pulses) that together constitute one bat pass. Insectivorous bats tend to use echolocation consistent enough across different environments and even within species such that it can be possible to identify characteristics, such as behaviour (commuting/ feeding) and its guild, genus and/or species of the bat that produced the call. These characteristics can be identified by automatic classifiers (auto identification) using machine learning or by trained analysts which use a range of tools including spectrograms (**Figure 5**) of the recorded bat passes to interpret the information about bat activity from recordings (manual identification).

Since this study investigates relationships between bat feeding activity and insect abundance, the feeding behaviour was of special interest. Feeding behaviour was identified by manually looking for “feeding buzzes” in the spectrogram of the recorded bat pass. In order to be categorized as a feeding buzz, it needed to be preceded by an “approach”, where the time between each bat call is getting shorter. Other behaviours that can be displayed in a spectrogram can be “commuting” or “social calls”. Only *Myotis* spp. are included in our sample of feeding activity because *P. auritus* and *B. barbastellus* do not exhibit the classical feeding buzzes.

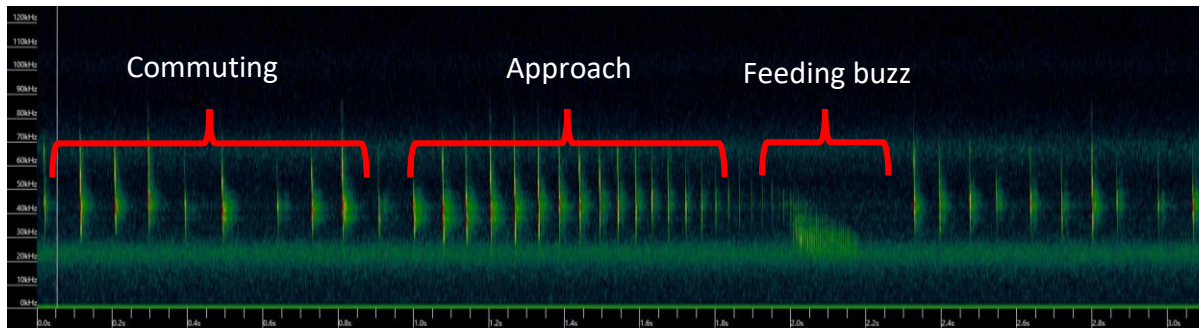


Figure 5: Spectrogram of a 5-second-long bat pass produced by an individual of a *Myotis* spp. recorded within the study area. Different behaviours (commuting, approach and feeding) of the individual are indicated with the red curly brackets.

The bat acoustic data was processed in Kaleidoscope Pro Analysis Software (Wildlife Acoustics, 2023b). Each 5 seconds long bat pass were automatically classified to estimate the bat species of each AutoID using the “AutoID for bats feature” with classifier Bats of Europe 5.2.1. AutoID’s were then grouped by species or genus into guilds. A list of the bat species included in the classifier and how they were grouped into guilds (LRE, MRE, SRE) is listed in **Appendix 4, Table A4**.

After the AutoID, a total of 19 811 bat passes (.wav files) were manually identified (ManualID) by species and behaviour by one analyst (Reed April McKay). The manual analysis were analysed following the instructions in Amichai (2022). Passes of *Myotis* spp. were classified to genus rather than species level due to overlapping call structures of species within the study area.

A dataset with all recordings, including bat passes, noise files, insect recordings and unidentified noise were plotted against date and site to see when each detector was actively recording. The dates with no recordings (zeros) were checked to see whether they were caused by “false zeros” or “true zeros”. False zeros (i.e., missing data) were identified by looking at the field log, and was generally caused by dead batteries, microphone failures or full SD-cards. True zeros were categorised as nights when the detectors were active and working but did not collect any bat passes. The dates with true zeros were inserted in the full SRE bat dataset to be included in further analyses.

2.4.2 Insect camera trap data

Raw images from insect camera traps (N=15 680) were sorted into separate folders for each site. Image files were then given a unique name-ID, and sorted by date, time and location in RStudio (RStudio Team, 2023). Before further processing the images were placed into separate folders containing only nocturnal images. Two sites (FF09 and FF05) had incorrect date and time stamps due to incorrect camera settings. The date and time for these two sites were adjusted using the Python programme Spyder (Raybaut, 2009) before processed in RStudio in the same way mentioned above.

All nocturnal (n= 4 785) images were manually annotated by one analyst (Mathilde Klokkersveen Thomle) using VGG Image Annotator (Dutta & Zisserman, 2019), to identify the number of insects in each image. Any potential insects were circled (**Figure 6**) and grouped based on the certainty of the object being an insect. Detections with 40-60% certainty were labelled “No” and detections with >60% certainty were labelled “Yes”. Detected objects <40% certainties were ignored. Image quality was also categorized as either “Good”, “Poor” or “Bad”, using reference images. “Bad” and “Poor” images often had water droplets, glare or other debris covering the lens view. Only images labelled with “Yes” and with “Good” or “Poor” image quality were included in further analysis. After annotation, a csv. file with annotation results for each site was produced. These files were combined, using RStudio, into one large dataset containing annotation results from all eleven sites. Based on the full dataset, insect abundance was aggregated to number of insects per date for each site to allow for analyses of relationships with bat and environmental data. After being combined, two sites (FF06 and FF09) had incorrect date and time stamps. Due to limited time available to fix the bug, these sites were excluded from further analysis comparing date and time.



Figure 6: Flying nocturnal insect (circled in red) captured in images at FF09 (upper photo), and FF10 (lower photo). Photos are taken with flash. Note the difference in detectability of insects in front of clear sky (upper photo) compared to vegetation (lower photo).

2.4.3 Environmental data and hemisphere images

Soil moisture and temperature data were obtained from soil sensors at each site. The data was combined into one file including temperature and moisture data from all eleven sites. A subset of the soil sensor data was then made to include only measures from between 18:00 in the night and 6:00 in the morning. This was done to better match the monitored hours of bats activity and insect abundance in this study. Temperature in degrees Celsius ($^{\circ}\text{C}$) 15 cm above ground was used to calculate average temperature at each site, for each night. Volumetric soil moisture was measured with the time- domain transmission (TDT) method (Wild et al., 2019). Both moisture

and temperature data were aggregated to average moisture and temperature per site for each night.

Hemisphere images were prepared for analysis by one analyst (Jenna Fairchild) by removing disturbing elements and darken light surfaces and areas that could give the impression of being open sky. The images were thereafter analysed in RStudio using the R package “Hemiphot” (Ter Steege, 2018). After the analysis a csv. file with calculated canopy openness and Leaf Area Index (LAI) for each site was retrieved. LAI was excluded from further analysis due to missing values in the data. Canopy openness is therefore the only variable used for canopy coverage in this study.

2.5 Statistical modelling

All statistical modelling was carried out in the programme R (RStudio Team, 2023). Generalized linear mixed models (GLMMs) were used to model the relationships between i) bat activity and explanatory variables (canopy openness, temperature, and soil moisture), ii) insect abundance and explanatory variables, and iii) bat activity and insect abundance. If explanatory analyses (scatterplots) indicated non- linear relationships between the response variable and the candidate explanatory variables, these were dealt with by including the explanatory variable as a quadratic term in the full models. The R-package DHARMA (Hartig, 2022) was used for model validation, to investigate residuals and check for overdispersion. When overdispersion was detected in Poisson models, GLMMs were fitted with a negative binomial distribution using the R package glmmTMB (Brooks et al., 2017). Zero- inflated negative binomial models were fitted if a standard negative binomial model did not provide a good fit to the data.

Before fitting the full (most complex) models, candidate explanatory variables were modelled against the response variable in single variable models to test the effect of each candidate variable. To reduce the risk of leaving out important explanatory variables from the models, the significance level was set to $\alpha=0.1$ instead of the more commonly used $\alpha=0.05$. Only candidate variables having a significant effect on the response were included in the full model. Site was included as random effect in all models to account for among-sites variation. To account for different numerical scales among the environmental variables, each variable was standardised before inclusion in the models.

2.5.1 Relationship between bat activity and explanatory variables

Bat feeding activity was modelled with canopy openness and temperature as explanatory variables. The candidate variable soil moisture (hereafter: “moisture”) was excluded from the full model as it did not show any significant effect ($p= 0.376$) on bat feeding activity when testing in a single- variable model.

The following R code was used to assess the influence of canopy openness and temperature on bat feeding activity:

```
n.bat.passes ~ CanOpen.std + mean_temp.std + (1 | Site)
```

Bat commuting activity was modelled as a function of the explanatory variables, moisture and temperature. The candidate variable canopy openness was excluded from the full model as it did not have a significant effect ($p=0.121$) on bat commuting activity when testing in a single-variable model.

The following R code was used to assess the influence of environmental variables on bat commuting activity:

```
n.bat.passes ~ mean_moist.std + mean_temp.std + (1 | Site)
```

2.5.2 Relationship between insect abundance and explanatory variables

Insect abundance was modelled as a function of moisture and temperature to estimate the effect of environmental variables on insect abundance. Canopy openness was excluded from the full model as it had no significant effect ($p= 0.133$) on insect abundance when testing in a single-variable model. Temperature was included in the model as both a linear and a quadratic term to account for a non- linear relationship between insect abundance and temperature detected in the explanatory analyses.

The following R code was used to assess the effect of environmental variables on insect abundance:

```
nCertain ~ mean_moist.std + mean_temp.std + I(mean_temp.std^2) + (1 | Site)
```

2.5.3 Relationship between bat activity and insect abundance

To model the relationship between bat activity and insect abundance, and to assess whether the strength and direction of this relationship depended on bat behaviour, a zero-inflated negative binomial model was fitted with bat behaviour, insect abundance, and the behaviour \times insect abundance interaction was included as fixed explanatory terms, using the R package glmmTMB (Brooks et al., 2017). SiteID and Date (i.e., observation night) nested in SiteID were included as random intercepts to account for among-sites and among-date variation. Due to many zero values and a skewed distribution of the insect abundance variable (i.e., number of insects counted on photos), the insect abundance variable was $\log_{10}+1$ transformed before fitting the model. Secondly, a more complex zero-inflated negative binomial model was fitted to account for any modifying influence of canopy openness; with bat behaviour, insect abundance, canopy openness, and all possible interaction terms as fixed effects.

3 Results

3.1 Overview of results

A total of 222 535 recordings were collected by acoustic detectors at in forest gaps. This included recordings from bats, insects, and unidentified noise. A full overview of the number of recordings per detector is available in **Appendix 5, Table A5**. A subset of 17 640 bat passes includes only the bat passes of SRE bat species (*Myotis* spp. and *P. auritus*) (**Table 2**).

Table 2: Overview of sampling results from each study site. *N bat passes*= total number of (5 sec) bat passes by short-range echolocating (SRE) bats. *N insects*= total number of certain observations of insects identified in insect camera trap images. *Mean moisture*= volumetric soil moisture measured with the time- domain transmission (TDT) method, the higher mean moisture value, the higher the soil moisture content is. *Mean T(°C)* = mean temperature (T) in degrees Celsius measured by soil sensors 15 cm above the ground. *Canopy Openness*= calculated canopy coverage based on hemisphere images. Values range from 0.17 to 0.53 from lowest to highest degree of openness. Scatterplots and Spearman correlation coefficients between all pairs of variables in this table are included in **Appendix 6, Figure A1**.

<i>Site</i>	<i>N bat passes</i>	<i>N insects</i>	<i>Mean moisture (TDT)</i>	<i>Mean T (°C)</i>	<i>Canopy Openness</i>
FF01	1275	144	2598.08	12.24	0.27
FF02	1290	109	2024.80	11.35	0.36
FF03	451	7	1801.92	11.44	0.40
FF04	4668	174	2462.43	11.15	0.43
FF05	818	104	2118.27	12.18	0.30
FF06	603	83	2005.33	11.44	0.51
FF07	896	51	1772.61	12.43	0.26
FF08	3353	32	2111.28	11.09	0.53
FF09	2520	170	1862.27	12.07	0.39
FF10	483	245	2509.00	12.17	0.17
FF11	1283	133	1931.74	12.24	0.31
Sum/Average	17640	1252	2108.88	11.80	0.36

Activity of short-range echolocating bats (i.e., SRE bat activity) (**Figure 7**) varied substantially between the sites throughout the summer season. Sites FF04, FF08 and FF09 stand out as sites with generally high activity level, while site FF03 and FF10 have relatively few recordings and little variation throughout the season, compared with the other sites. Site FF06 had zero recordings before mid-June, due to equipment failure.

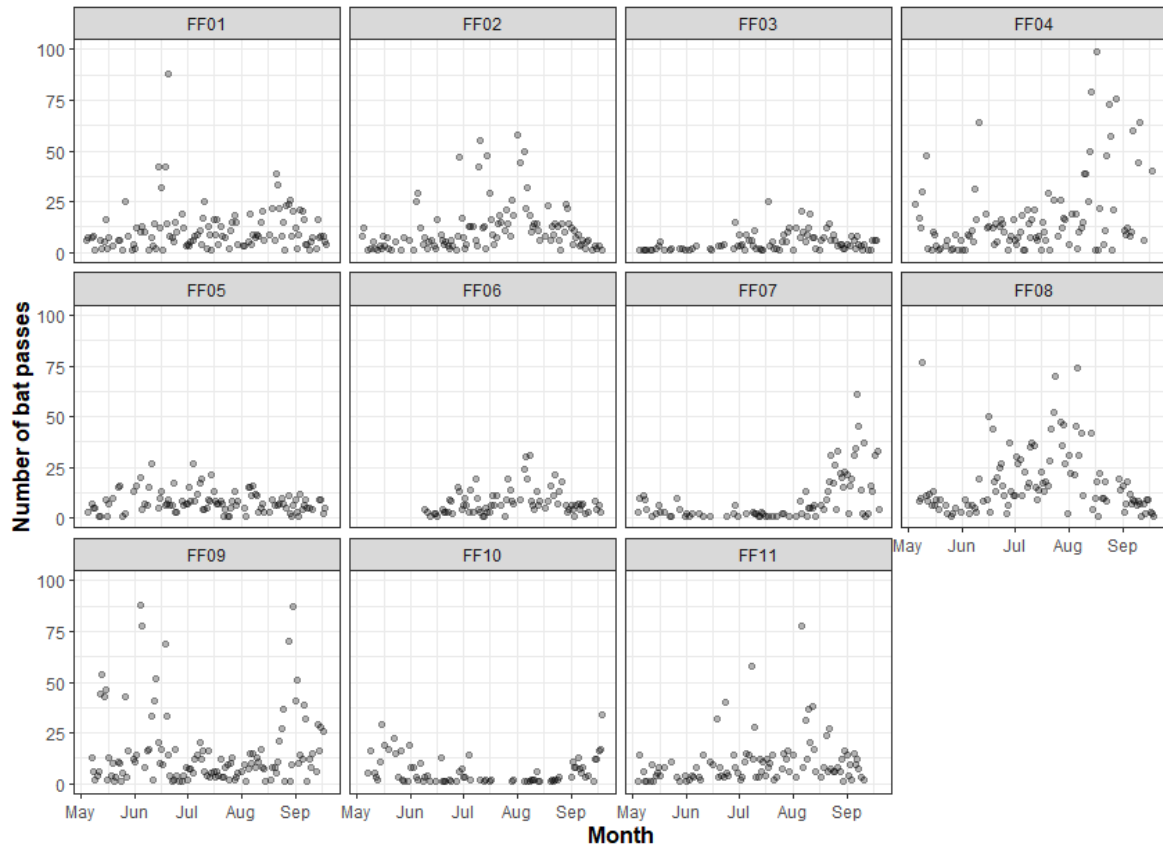


Figure 7: Activity patterns of SRE bats at each site. Each point represents the number of bat passes recorded that date. One bat pass= one 5 secs recording of a bat. NB: 24 observations with number of bat passes >100 was omitted to better visualise the variation among the sites.

Of the SRE bat passes, 16 947 were produced by *Myotis* spp. and 693 by *P. auritus*. 14 295 bat passes represented commuting behaviour, 3131 was feeding behaviour (**Figure 8**), 199 were social behaviour and 15 were both feeding and social together. The behaviour category “Both” includes both social and feeding behaviour, thus this was only recorded among *Myotis* spp. There were no recordings of the SRE bat species *B. barbastellus*.

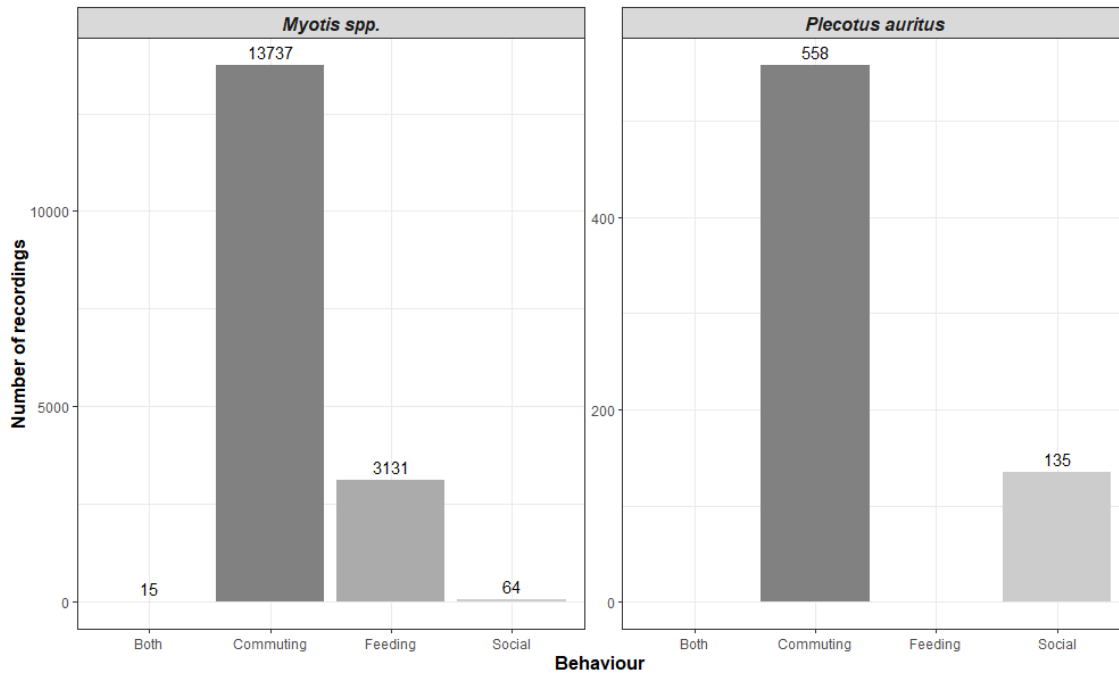


Figure 8: Overview of recorded behaviour among SRE bat; *Myotis spp.* (left) and *Plecotus auritus* (right). Behaviour “Both” means that commuting and feeding behaviour was displayed in the same recording. Feeding buzzes are only produced by *Myotis spp.*, consequently there are no recordings of “Both” and “Feeding” for *P. auritus*. Note that the range of values along the y-axis differ for *Myotis spp.* and *P. auritus*.

Insect abundance varied among the sites (**Table 2, Figure 9 and 10**) throughout the sampling period. The first insects were recorded on June 7th and the last observations were recorded on July 21st. Due to two weeks of inactive cameras, there were no recorded observations of insects between June 17th and July 4th. The overall insect abundance ranged from 0 to 60 observed insects per sampling night. However, only sites FF01 and FF02 had sampling nights with >30 observed insects. Site FF03, FF07 and FF08 had the lowest number of recorded insects; 10 or fewer insects observed at any sampling night.

Batteries were replaced once a week and lasted on average 2 days (between 0-6 days) before they needed to be replaced with fresh batteries. This affected the continuity of the recordings. Thus, there are no complete weeks with recorded insect observations every night for any site.

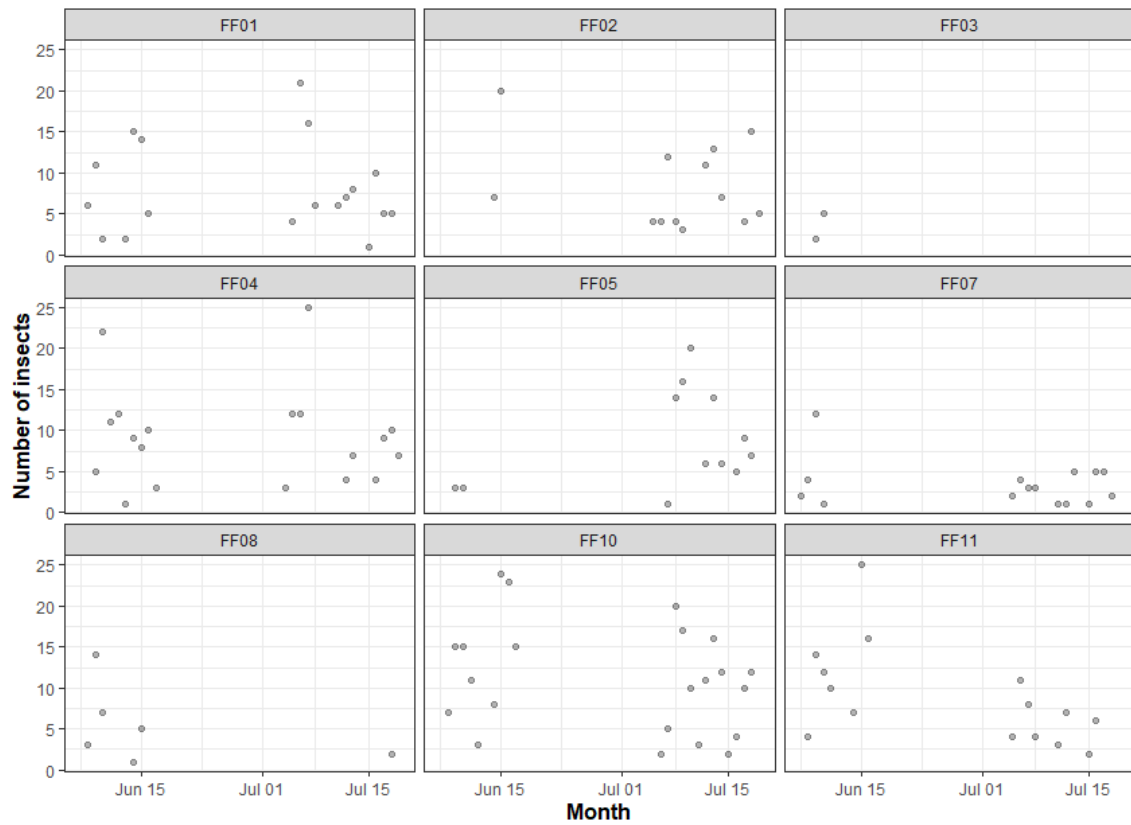


Figure 9: Distribution of sampling nights throughout the sampling period and number of insects observed on images per site (FF01-FF11). Number of insects observed include both certain (>60% certainty) and uncertain (40-60% certainty) observations. Note that sites FF06 and FF09 were excluded from the plot due to errors in the date and time stamps in the recordings.

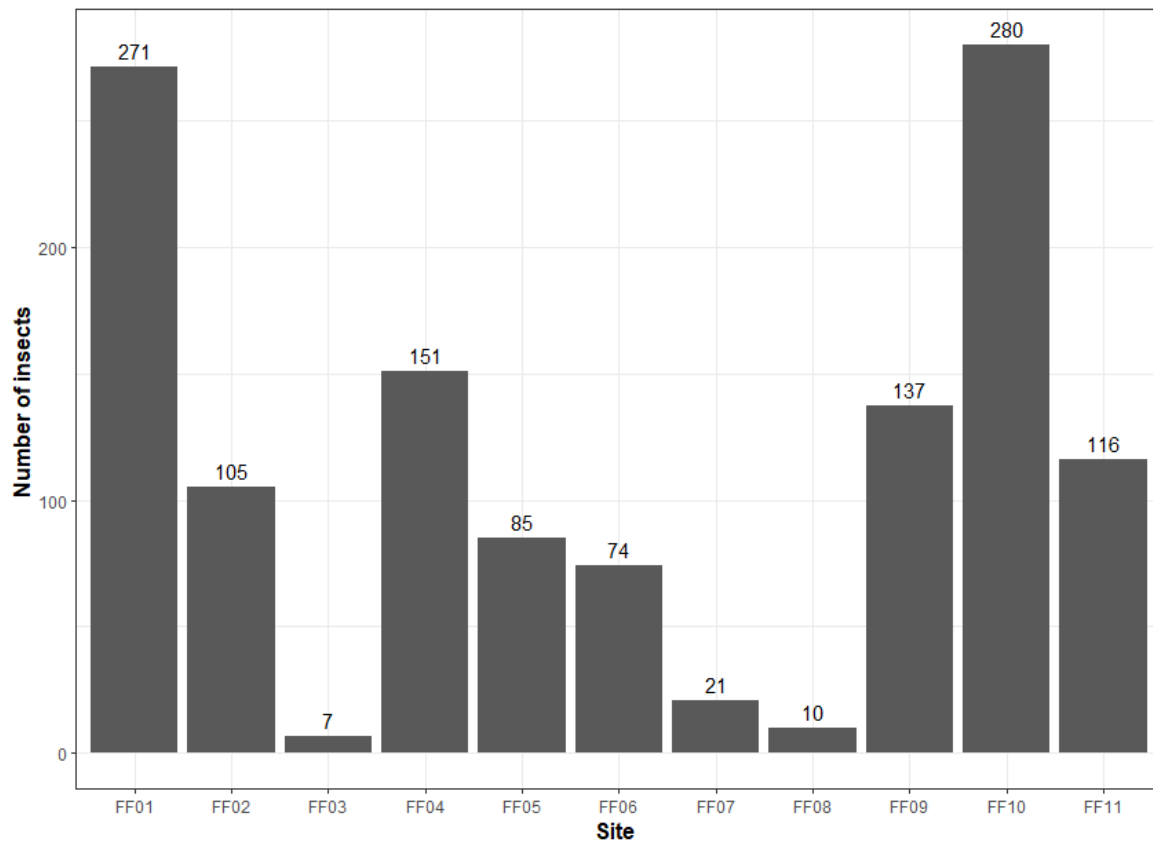


Figure 10: Total number of certain (>60% certainty) observations of insect on each site. Note that Sites FF06 and FF09 were not included in the statistical models due to errors in the date and time stamps in recordings.

3.2 Relationship between bat activity and explanatory variables

3.2.1 Bat feeding activity

Analysis results gave evidence for an increase in bat feeding activity with increasing canopy openness; feeding activity was higher in sites with more open canopy cover (**Table 3, Figure 11**). Additionally, there was also evidence of a negative influence of temperature on bat feeding activity (**Table 3, Figure 11**).

Table 3: Analysis of factors influencing feeding activity of short-range echolocating (SRE) bats. Output from negative binomial model (GLMM) with log link function. Continuous explanatory variables were standardized before analysis. SiteID was included as random intercept to account for among-site variation. Analysis of 628 observations from 11 sites. Marginal $R^2 = 0.111$ / Conditional $R^2 = 0.346$. The candidate explanatory variable “soil moisture” was excluded in the full model because it had no significant effect ($p = 0.38$) on bat feeding activity when included in a single-variable model.

Variable	Estimate	Std. Error	z	p
Fixed effects				
Intercept	1.19	0.17	6.95	<0.0001
Canopy openness	0.33	0.16	2.1	0.039852
Temperature	-0.16	0.048	-3.33	0.000881
Random effect				
SiteID	Variance	St.Dev		
	0.29	0.54		

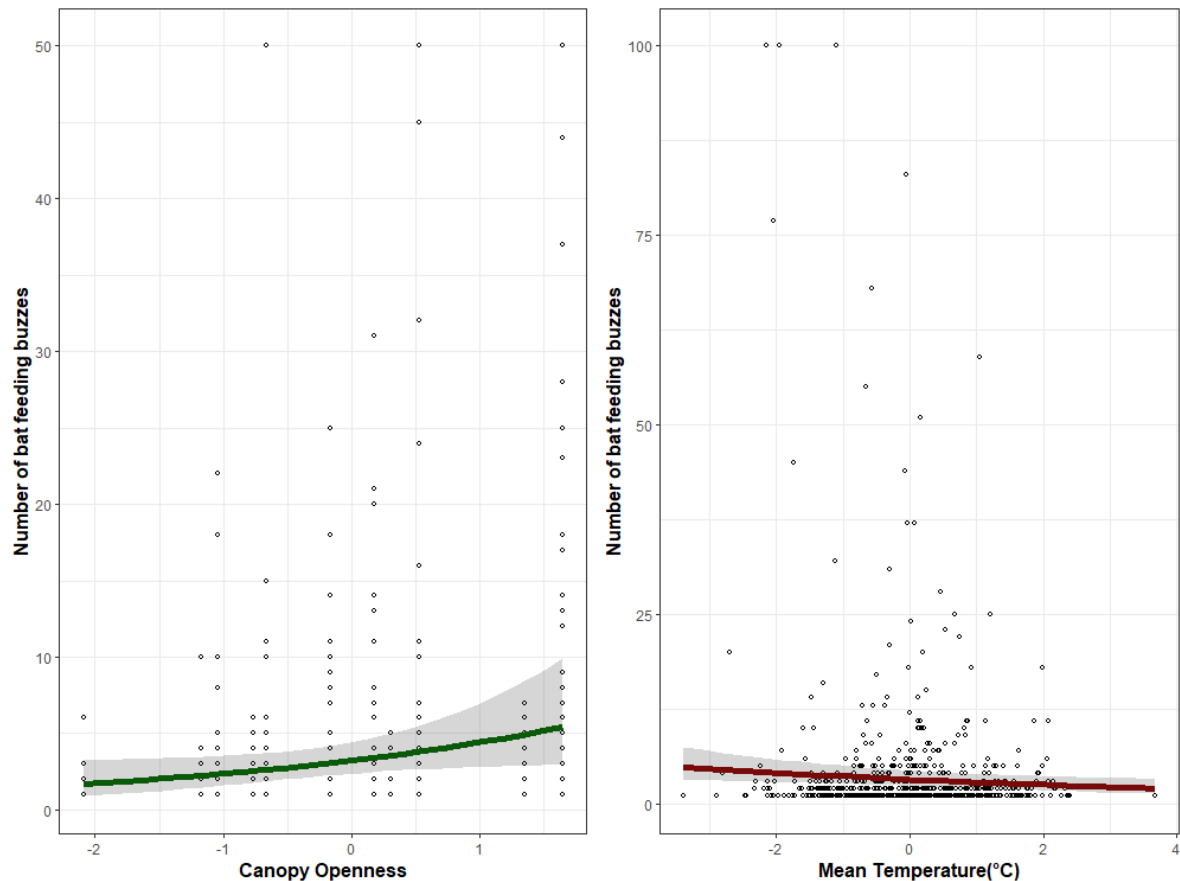


Figure 11: Predicted relationships (solid lines) between bat feeding activity and canopy openness (left), and mean temperature during the observation night (right). Predicted relationship between bat feeding activity and canopy openness is for average temperature and predicted relationship between bat feeding activity and temperature is for average canopy openness. Grey polygons show 95% confidence limits. Points are observed values. Note that observations > 50 bat passes were assigned the value 50 to improve data visualisation. Explanatory variables were standardised to allow for comparison of influence of variables of different numerical scales.

3.2.2 Bat commuting activity

Results from analysis display a negative relationship between bat commuting activity and moisture; decrease in bat commuting activity with increasing levels of moisture (**Table 4, Figure 12**). There was also evidence of a negative influence of temperature on bat commuting activity, with lower bat activity with higher temperatures (**Table 4, Figure 12**).

***Table 4:** Analysis of factors influencing commuting activity of short-range echolocating (SRE) bats. Output from negative binomial model (GLMM) with log link function. Continuous explanatory variables were standardized before analysis. SiteID was included as random intercept to account for among-site variation. Analysis of 1086 observations from 11 sites. Marginal $R^2 = 0.045$ / Conditional $R^2 = 0.382$. The candidate explanatory variable “canopy openness” was excluded from the full model because it had no significant effect ($p = 0.12$) on bat commuting activity when included in a single-variable model.*

Variable	Estimate	Std. Error	z	p
Fixed effects				
Intercept	2.245	0.19	11.99	<0.0001
Moisture	-0.203	0.04	-4.87	<0.0001
Temperature	-0.092	0.03	-2.74	0.00614
Random effect				
SiteID	Variance	St.Dev		
	0.37	0.61		

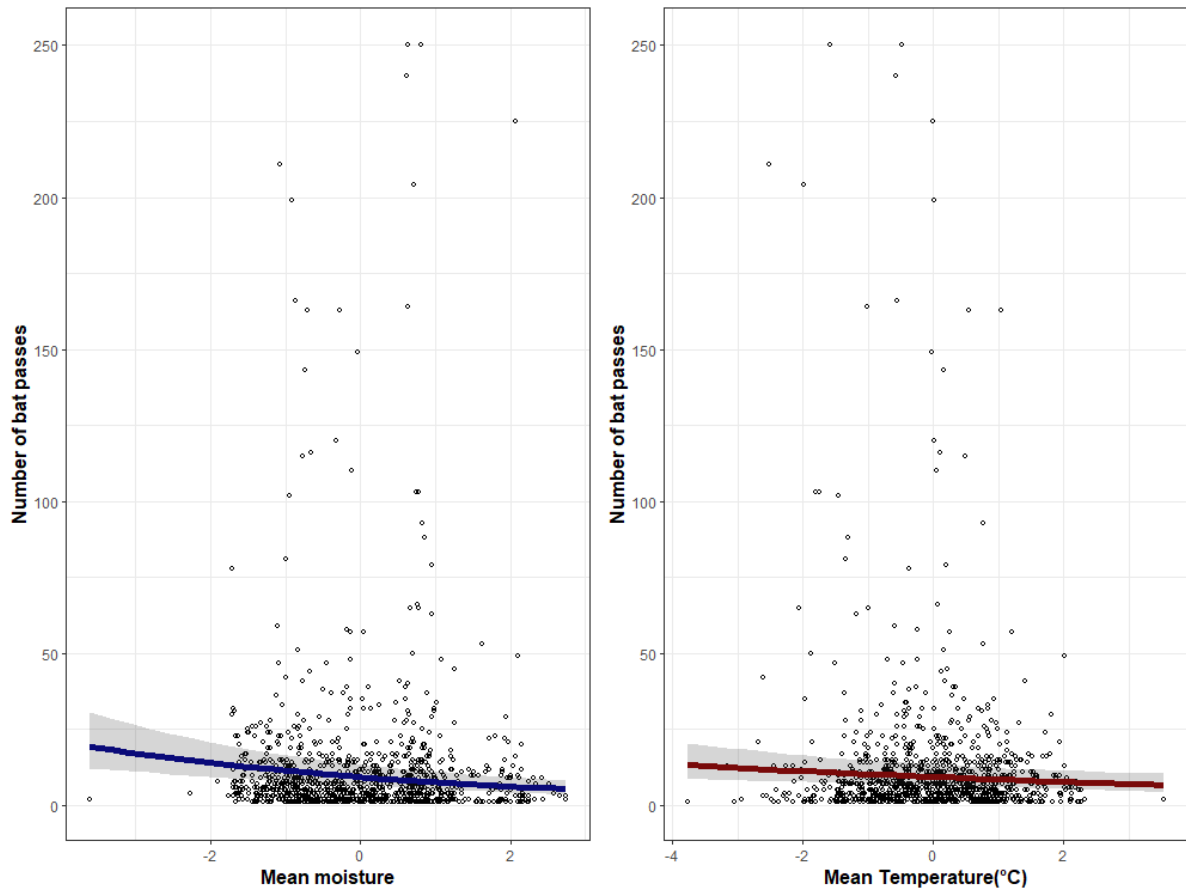


Figure 12: Predicted relationships (solid lines) between bat commuting activity and mean moisture (left), and mean temperature (right) during the observation night. Predicted relationship between bat commuting activity and moisture is for average temperature and predicted relationship between bat commuting activity and temperature is for average moisture. Grey polygons show 95% confidence limits. Points are observed values. Note that observations > 250 bat passes were assigned the value 250 to improve data visualisation. Explanatory variables were standardised to allow for comparison of influence of variables with different numerical scales.

3.3 Relationship between insect abundance and explanatory variables

Moisture had a significant positive influence on insect abundance, with higher insect abundance with increasing levels of moisture (Table 5, Figure 13). Temperature had no significant influence on insect abundance (Table 5), but the insect abundance was highest around intermediate temperatures Figure 13.

Table 5: Analysis of variables influencing abundance of insects. Output from negative binomial GLMM with log link function. Continuous explanatory variables were standardised before analysis. The explanatory variable “Temperature” was included as both a quadratic and linear term because of non-linear relationship between temperature and insect abundance. SiteID was included as random intercept. Marginal $R^2 = 0.201$ / Conditional $R^2 = 0.470$. Candidate explanatory variable “canopy openness” was excluded from the full model as it had no significant effect on insect abundance when included in a single-variable model ($p=0.133$). 125 observations, 9 Sites.

Variable	Estimate	Std. Error	z	p
Fixed effects				
Intercept	1.902	0.21	9.02	<0.0001
Moisture	0.428	0.15	2.87	0.00412
Temperature	0.064	0.09	0.69	0.48845
Temperature^2	-0.087	0.06	-1.41	0.15920
Random effect				
SiteID	Variance	St.Dev		
	0.283	0.532		

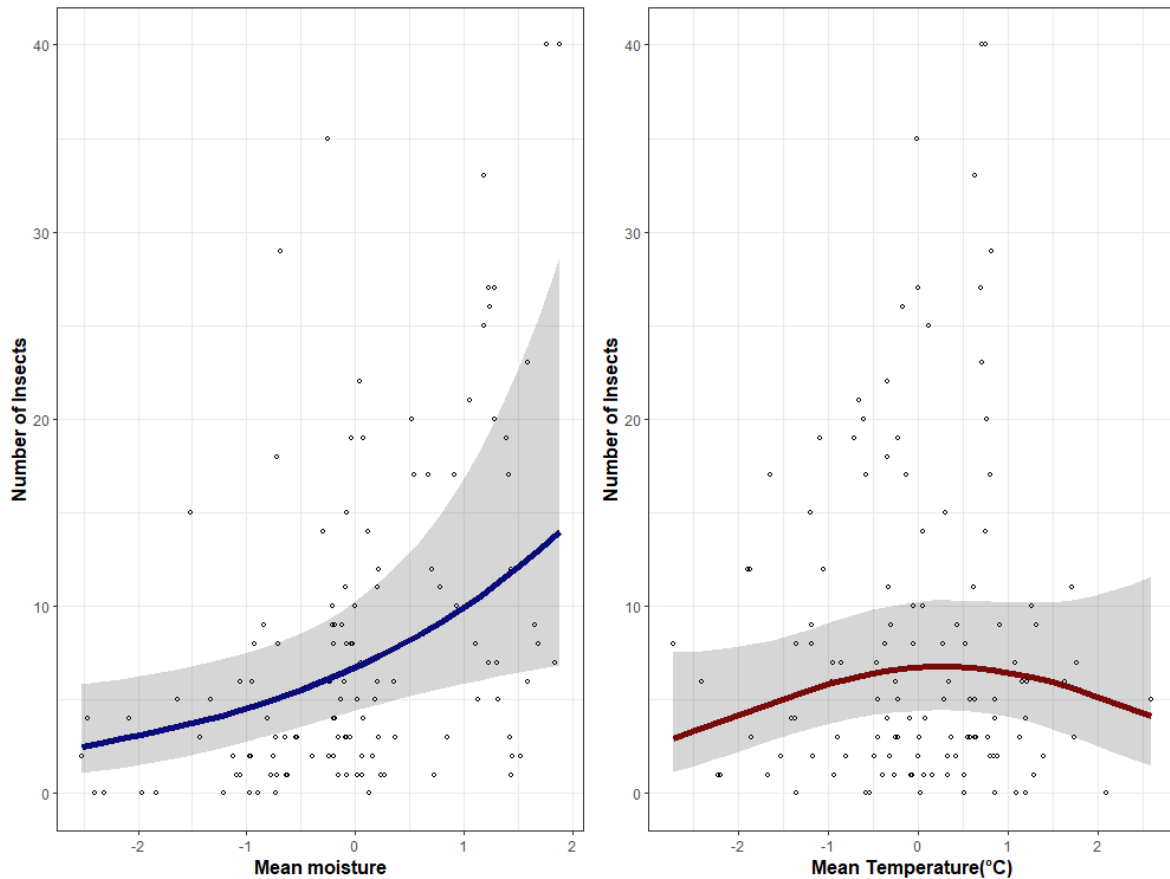


Figure 13: Predicted relationships (solid lines) between insect abundance and mean moisture (left), and mean temperature (right) during the observation night. Predicted relationship between insect abundance and moisture is for average temperature and predicted relationship between insect abundance and average temperature is for moisture. Grey polygons show 95% confidence limits. Points are observed values. Note that observations > 40 insects were assigned the value 40 to improve data visualisation. Explanatory variables were standardised to allow for comparison of influence of variables of different numerical scales.

3.4 Relationship between bat activity and insect abundance

Insect abundance influenced commuting and feeding behaviours differently (Table 6 and 7, Figure 14). Generally, there was a stronger influence of insect abundance on bat feeding activity than on commuting (Table 5, Figure 14), but the direction and strength of the insect-bat relationship depended on the degree of canopy openness (Table 7, Figure 14). At low canopy openness there was marked positive relationship between insect abundance and bat feeding activity, whereas the relationship disappeared at intermediate canopy openness, and was negative at high canopy openness (Figure 14). Candidate explanatory variables temperature and moisture was not included in this model, as they had no significant influence on insect abundance when tested in single- variable models.

Table 6: Analysis of influence of insect abundance on number of bat passes (commuting and feeding activity). Output from zero-inflated negative binomial model with log link function. SiteID and DateID nested in Site ID were included as random intercepts in the model to account for among-site and among-date variation. Analysis of 244 observations from 9 sites.

Variables	Estimate	Std. Error	z	p
Fixed effects				
Intercept (Behaviour Commuting)	1.0667	0.4718	2.261	0.023759
Insect abundance	0.0300	0.1381	0.217	0.828017
Behaviour Feeding	-0.9338	0.2540	-3.677	0.000236
Insect abundance × Behaviour Feeding	-0.2789	0.1326	-2.104	0.035388
Random effects				
	Variance	St.Dev		
DateID nested in SiteID	0.7487	0.8653		
SiteID	1.2540	1.1198		

Table 7: Analysis of influence of insect abundance and canopy openness on number of bat passes (commuting and feeding activity). Output from zero-inflated negative binomial model with log link function. SiteID and DateID nested in Site ID were included as random intercepts in the model to account for among-site and among-date variation. Analysis of 244 observations from 9 sites.

Variables	Estimate	Std. Error	z	p
Fixed effects				
Intercept (Behaviour Commuting)	-0.1931	1.3831	-0.140	0.88897
Insect abundance	-0.3695	0.5537	-0.667	0.50452
Behaviour Feeding	-3.6096	0.8938	-4.039	<0.001
Canopy openness	3.9305	3.9652	0.991	0.32156
Insect abundance × Behaviour Feeding	1.0582	0.4549	2.326	0.02000
Insect abundance × Canopy openness	1.2641	1.7156	0.737	0.46125
Behaviour Feeding × Canopy openness	6.7149	2.0651	3.252	0.00115
Insect abundance × Behaviour Feeding × Canopy openness	-3.5257	1.2228	-2.883	0.00394
Random effects				
	Variance	St.Dev		
DateID nested in SiteID	0.7929	0.8904		
SiteID	0.6546	0.8090		

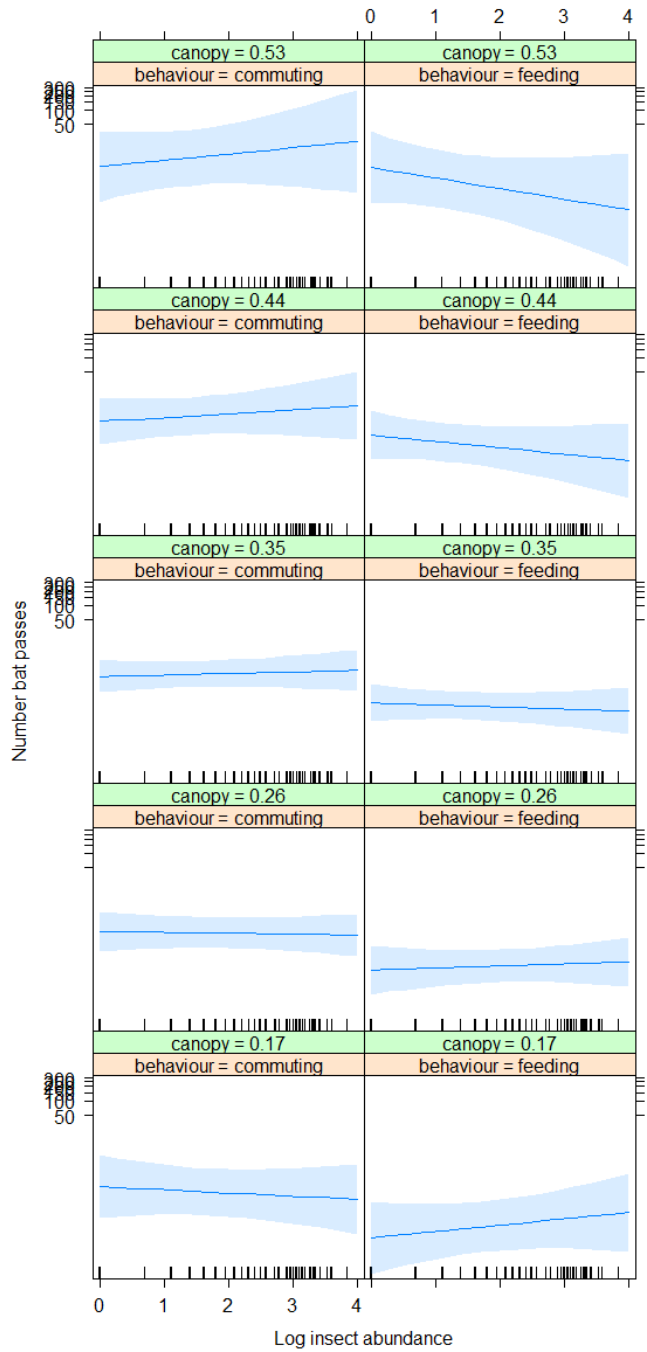
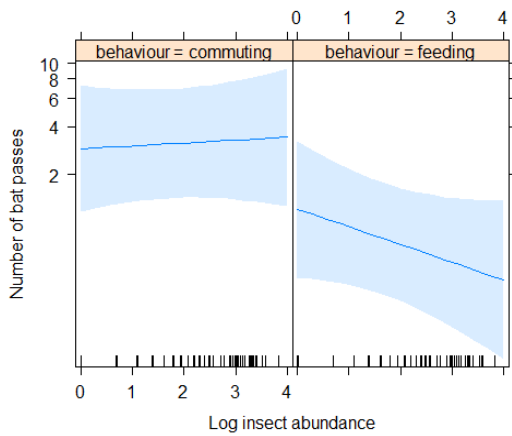


Figure 14: *Upper left.* Predicted relationship between number of bat passes (commuting and feeding buzzes) and insect abundance, when canopy cover was not included as explanatory variable in the model. Predicted relationship (solid blue lines) and 95% confidence interval (light blue polygons) are based on the zero-inflated negative binomial model in **Table 6**. *Right.* Predicted relationship between number of bat passes (commuting and feeding buzzes) and insect abundance, at various levels of canopy openness. Predictions are based on the zero-inflated negative binomial model in **Table 7**.

4 Discussion

4.1 Key findings

SRE bat feeding- and commuting behaviours were influenced by environmental factors and canopy openness in different ways. Canopy openness had a positive effect on bat feeding activity but did not significantly influence commuting activity. Moisture had a negative influence on bat commuting activity but did not significantly influence feeding activity. Unexpectedly, both bat behaviours displayed a negative relationship with temperature. Insect abundance was positively correlated with moisture, but neither temperature nor canopy openness had any significant effect on insect abundance in the most complex models. The relationship between bat activity and insect abundance depended on the bat behaviour. Insect abundance generally had a stronger influence on bat feeding activity than on commuting, but the strength and direction of the relationship depended on the degree of canopy openness. The relationship between bat feeding activity and insect abundance was more strongly influenced by the degree of canopy openness than bat commuting activity.

4.2 Relationship between bat activity and explanatory variables

Canopy openness had a positive effect on bat feeding activity but had no significant effect on bat commuting activity. For bat feeding activity, this is in line with the hypothesis that an increase in canopy openness would promote bat activity. Canopy openness was excluded from the full model with commuting activity as it had a p- value of 0.121 when tested in a single-variable model. However, the estimate was still positive, indicating that canopy openness also had a weak positive effect on bat commuting activity. Higher bat activity with increasing canopy openness (decreasing forest density) can be supported by both methodological and ecological explanations. Detectors will record poorer quality bat passes in cluttered environments because the echoes of the bat calls themselves will also be recorded, resulting in a noisier recording. In addition, bats have better possibilities of manoeuvring in more open habitats. A similar master's study to the present study, investigated bat- insect relationship at the same sites in 2021 displayed the same trend; more bat activity in plots with higher canopy openness (Sætre, 2022). Other studies have similar results, e.g., Erasmy et al. (2021) found that small-scale natural canopy gaps increased forest bat diversity, which emphasise the importance of preserving natural broadleaved forests for temperate bat communities. Consequently, harvested forests are often looked at as poor habitats for many bat species, even though they

provide important habitats for many bat species in temperate regions (Kirkpatrick et al., 2018). As suggested by (Russo et al., 2010), reconsidering the importance of managed forests is therefore important to preserve forests dwelling bat species.

Moisture had no significant effect on bat feeding activity but had a negative influence on bat commuting activity. For bat commuting activity, this is in line with the hypothesis that moisture would negatively affect bat activity. The negative relationship between bat commuting activity and moisture might be explained by soil moisture being a proxy for precipitation. Bat activity are known to decrease with precipitation (e.g., Burles et al., 2009; Voigt et al., 2011). In example, Rostovskaya et al. (2000) found that the number of bat calls produced by *P. auritus* decreased considerably during heavy rain. As bats orientation in the forest is highly dependent on sound, high levels of noise are also known to decrease bat echolocation activity (Bunkley et al., 2015) making it harder to capture insects. Precipitation leads to physical constraints for bats, as their fur and wings get wet (Voigt et al., 2011) and flight becomes more physically demanding. It is therefore not unlikely that, at least nights with heavy (noisy) rainfall might be a contributing factor to the negative relationship.

Temperature had a significantly negative effect on both bat behaviours. This contradicts the hypothesis that temperature would have a positive effect on bat activity. Previous studies have shown temperature to be positively associated with bat activity in northern latitudes (Perks & Goodenough, 2020; Wolbert et al., 2014). A previous master's study associated with the same study group as the present study also found temperature to have a positive influence on bat activity (Johns, 2021). A possible explanation to the negative relationship in this study is that the more open sites, which also had the highest activity levels, had higher heat radiation to the atmosphere during the night compared to plots with more dense canopy coverage. Another potential explanation is that the difference between the lowest and highest temperatures among the sites is very small, with measured average temperatures between 11.1°C and 12.4°C. As it is highly unusual for bat activity to decrease with increasing temperatures in the latitudes where this study was carried out, it can also be that the dataset of simply lacked enough data to see the true trend in the relationship.

4.3 Relationship between insect abundance and explanatory variables

Moisture had a significantly positive effect on insect abundance. This is in accordance with the hypothesis that there would be an increase in insect abundance with higher moisture levels. In addition, as soil moisture is closely related to precipitation (P. Froidevaux et al., 2014), results from the current study might indicate that certain insect species are more active under- or shortly after rainfall events (when soil moisture levels are higher). Insects can also be difficult to distinguish from other objects in insect camera trap images, especially water droplets that reflects the flash from the camera in similar ways as flying insects. A possible, methodological explanation for the positive relationship might therefore be that some raindrops was mistaken for insects in images, leading to an impression that the insect activity was higher than it actually was. Few other studies have used this methodology for quantifying abundance of flying insects, however Ruczyński et al. (2020) also found that water droplets could be hard to distinguish from insects. More testing of insect camera traps in different weather conditions would be needed to better evaluate the risk of this type of misidentification.

Canopy openness and temperature did not significantly influence insect abundance in this study. Although canopy openness was excluded from the full model ($p= 0.133$), the estimate from the single- variable model was negative, indicating that canopy openness had a weak negative influence on insect abundance. This is in line with the hypothesis that an increase in canopy openness would have a negative influence on insect abundance. This is expected based on the knowledge that higher structural complexity and heterogeneity of the canopy tend to increase insect activity in forest habitats (Haddad et al., 2009; Müller et al., 2012; Ober & Hayes, 2008). Another, methodological explanation for the weak negative trend could be that more insects were detected in front of the vegetation and that images with increasing openness had fewer insects. Combining the insect camera traps with other insect monitoring techniques (e.g., malaise traps, window traps or light traps) could have provided additional information about insect species composition and insect biomass, which could have strengthened the robustness of the results.

Temperature had no significant effect on insect activity in the full, most complex model. Contrary to the hypothesis that higher temperatures would increase insect abundance, the quadratic effect of temperature in the model showed a weak negative estimate, and the peak insect activity seemed to be highest at intermediate temperatures. In temperate regions one would generally expect insect activity to increase with higher temperatures (Wilson & Maclean, 2011). Ruczyński et al. (2020) also found insect activity in insect camera traps to increase with

increasing ambient temperatures in forest habitats in north-eastern Poland. However, a higher activity around intermediate temperatures in this study might indicate that insects are most active around a certain optimal thermal range, and that insects are less active at particularly low or high temperatures. Studies from Jones et al. (1995) and Taylor (1963) have shown that temperature threshold for many insect species lay around 6-10°C. The non-linear relationship between insect abundance and temperature might thus be explained by insects preferring intermediate temperatures.

4.4 Relationship between bat activity and insect abundance

The relationship between bat activity and insect abundance differed between commuting and feeding behaviours and depended on the degree of canopy openness. Generally, there was a stronger influence of insect abundance on bat feeding activity than on commuting. Insect abundance had a weak positive influence on bat commuting activity, although the relationship was not significant. On feeding activity, the influence of insect abundance was significantly negative when not accounting for canopy openness. These findings are not in line with the hypothesis that there would be a stronger positive relationship between insect abundance and feeding activity than with commuting. A reason for this could be that there were relatively few nights with recorded insect abundance compared to nights with recorded bat activity. There were also more nights with recordings of commuting behaviour than feeding. A larger sample size of insects and more recordings of feeding behaviour could possibly have displayed another relationship. Few studies have accounted for differences in bat behaviours when looking at relationships between bat activity and insect abundance. However, several studies (e.g., Brigham et al., 1997; Carr et al., 2020; Jung et al., 2012) have shown that the relationship between overall bat activity and insect abundance is also influenced by habitat factors, which is why the relationship was modelled with the effect of canopy openness.

At low canopy openness, the relationship between insect abundance and bat feeding activity was positive, but at high openness it displayed a negative trend. For commuting activity, the relationship was positive at high openness, but disappeared at other levels of openness. Based on these results one can address the following question: is the influence canopy openness a real effect, or is it caused by insects having different detectability with different levels of canopy openness? If it is caused by detectability the results might imply that there are more insects at sites with low canopy openness (high canopy density). More insects with low openness could

be supported by abundance of insect generally being higher with increasing vegetation density (Müller et al., 2012). It can also be that some flying insect taxa flies higher in more open habitats, which can be too high for the cameras to detect. However, several studies have found forest structure to have a larger influence on bat activity than insect abundance (Bender et al., 2021; Carr et al., 2020; Cox et al., 2016). Cluttered habitats, with high vegetation density, promote insect abundance but reduce bat access to prey (Rainho et al., 2010) as it becomes more difficult for bats to manoeuvre and echolocate. The influence of habitat clutter on manoeuvrability depends on the species and guild. Bats recorded in this study are all SRE species known to forage in the interior forest, meaning that they have specialized morphology and foraging techniques to forage in more dense vegetation. Both *P. auritus* and *Myotis* spp. are shown to be positively related to higher tree densities (Fuentes-Montemayor et al., 2013). Bat species from guilds adapted to forage in more open habitats (i.e., LRE, MRE), would likely be more negatively affected by lower canopy openness. To better understand how the relationship between bats and insects is affected by forest density further studies should include more explanatory variables on forest. For example, Carr et al. (2023) found that understory vegetation and number of stems per plot were the most important woodland characteristics to explain variations in bat species richness. However, it seems that a combination of canopy openness and insect abundance together can work as a good proxy for bat feeding activity. This also matches with findings in Bender et al. (2021) who found that vegetation characteristics and insect abundance together best explained the occupancy of bats in managed pine forests.

Although forests features are important explanatory factors for bat activity, there is still a need for more research on the relationship between bat activity and insect abundance in forest habitats. Multiple studies are indicating worrying declines in global insect populations, especially among flying insects in the northern hemisphere (Eggleton, 2020). As flying insects constitute key prey resources for insectivorous bat species it is important to gain a better understanding of the relationships between insectivorous bats and insects. Bats are also in decline and understudied. Over a third of bat species assessed by the International Conservation of Nature (IUCN) are considered threatened or data deficient (IUCN, 2023). Frick et al. (2020) identified logging and harvesting of plants, agriculture, hunting and collecting animals, human intrusion and disturbance, and urban development as the most important threats for bats today.

Based on current knowledge, there are few studies that have proven declines in insects and insectivorous bats to be connected (but see Vesterinen et al., 2020). However, studies on insectivorous birds are displaying negative trends. For example, a study by Pomfret et al. (2014)

on population declines in the insectivorous bird Vaux's Swifts suggested that a reduction in diet quality caused by insect declines could be the reason for the decline for this bird species. They further suggested that their findings could be an explanation for declines in other aerial insectivore species (Pomfret et al., 2014), such as bats. Another study by Tallamy and Shriver (2021) showed that for terrestrial birds of which insects are an essential food source, the population had experience massive declines over the past 50 years. With clear declining trends in insectivore birds associated with insect declines, it is reasonable to believe that also insectivorous bats will be negatively affected by insect declines. Although this was used in the context of acoustic monitoring Russo et al. (2018) stated that "bats are still not birds". It is therefore an acute need for more specific research on insectivorous bats and their relationship with insect declines. Bats are critically understudied relative to birds and other mammal groups (Frick et al., 2020) . More region-specific knowledge about insectivorous bats, and their relationships with insects in forest ecosystems is needed.

5 Conclusion

Results from this study highlight the importance of accounting for the modifying influence of biotic and abiotic environmental variables to understand relationships between response and explanatory variables in ecosystem research. It is also one of the first studies that is using only non-invasive techniques to investigate the relationship between bat activity and insect abundance, while accounting for forest density and environmental conditions. The findings in this study are in line with what previous research have found; that forest structure is an important explaining factor for bat activity. The study also provides new insight, showing that forest density (canopy openness) influences the relationship between bat activity and insect abundance in boreal forests, and that this relationship also depend on bat behaviour. Based on results from this study it is suggested that further research take both forest density and bat behavioural differences into account when assessing relationships between bat activity and insect abundance.

6 Appendix

Appendix 1: Site coordinates

Table A1: Overview of site location with Lat (latitudinal) and Long (longitudinal) coordinates for each site.

Site	Lat	Long
FF01	59.67191	10.75547
FF02	59.69584	10.75482
FF03	59.75864	10.75996
FF04	59.72194	10.71087
FF05	59.71358	10.71299
FF06	59.71621	10.68844
FF07	59.71621	10.68844
FF08	59.67617	10.73294
FF09	59.6916	10.68612
FF10	59.61217	10.72714
FF11	59.68363	10.76077

Appendix 2: Bat detector settings

Table A2: Settings of Wildlife Acoustics Song Meter SM4BAT FS Bioacoustics Recorder

Firmware	2.3.1
Time zone	UTC +2
Schedule	1 hour before sunset – 1 hour after sunrise
Gain	12 dB
16k high filter	off
Sample rate	256 kHz
Min duration	1.5 ms
Max duration	none
Min trig frequency	12 kHz
Trigger level	12 dB
Trigger window	3 s
Max length	15 s
Compression	none

Appendix 3: Insect camera trap settings

Table A3: Insect camera settings. Camera model: Ricoh WG-6 (Digital) Waterproof 20m/65.6ft; Model R02050 2019

Program settings	
Scenery Interval Shooting (SCN). Every 10 min. 1000 shots	
Shooting settings	
Focus	Infinity
AF	Multi
Focus assist	Off
Flash mode	Flash on
Face detection	Off
Blink detection	Off
Digital zoom	Off
Quality level	*** (tree stars)
Image Tone	“Natural”
Custom settings	
CALS Pixels	L
CALS Quality	*** (tree stars)
Setup settings	
Embed Info	On
Power saving	5 sec
Operation Volume	Off
Playback Volume	Off
Sounds	Off
Auto Power Off	Off

Appendix 4: Overview of bat species included in classifier

Table A4: List of bat species included in the classifier of bat species and how they are grouped into guilds. Bat species found in Sweden were included in the automatic classification process but only bat species found in Norway were found in the manual acoustic analysis.

Species	Guild
<i>Barbastella barbastellus</i>	SRE
<i>Eptesicus nilssonii</i>	LRE
<i>Eptesicus serotinus</i>	LRE
<i>Myotis alcathoe</i>	SRE
<i>Myotis bechsteinii</i>	SRE
<i>Myotis brandtii</i>	SRE
<i>Myotis dasycneme</i>	SRE
<i>Myotis daubentonii</i>	SRE
<i>Myotis myotis</i>	SRE
<i>Myotis nattereri</i>	SRE
<i>Nyctalus leisleri</i>	LRE
<i>Nyctalus noctula</i>	LRE
<i>Pipistrellus nathusii</i>	MRE
<i>Pipistrellus pipistrellus</i>	MRE
<i>Pipistrellus pygmaeus</i>	MRE
<i>Plecotus austriacus</i>	SRE
<i>Plecotus auritus</i>	SRE
<i>Vespertilio murinus</i>	LRE

Appendix 5: Acoustic detector recordings

Table A5: Total number of recordings by bat acoustic detectors at in forest gaps for each site. N recordings include total number of automatically classified recordings including recordings of all bats, insects, noise, and no identity recordings.

Site	N recordings
FF01	8850
FF02	13320
FF03	4642
FF04	28372
FF05	8012
FF06	4233
FF07	8371
FF08	107291
FF09	14466
FF10	8033
FF11	16945
Sum	222535

Appendix 6: Supplementary figures

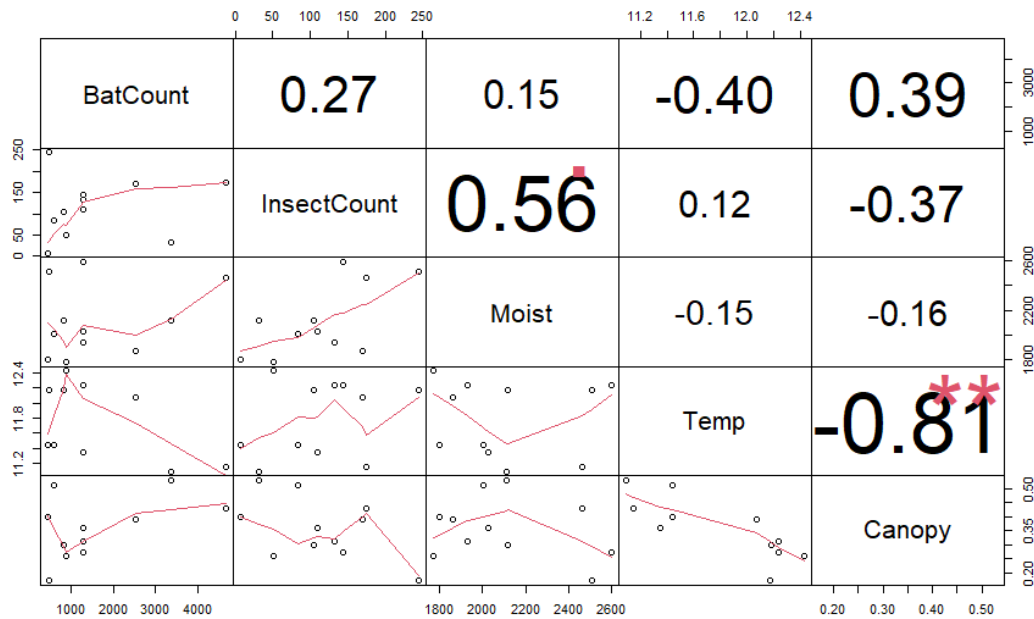


Figure A1. Scatterplots and Spearman correlation coefficients between pairs of variables aggregated per site for the whole sampling period in 2022. BatCount= total number of (5 sec) bat passes by short-range echolocating (SRE) bats. InsectCount = total number of certain observations of insects identified in Insect camera trap images. Moist = Volumetric soil moisture measured with the time-domain transmission (TDT) method, the higher mean moisture value, the higher the soil moisture content is. Temp = mean temperature (T) in degrees Celsius measured by soil sensors 15 cm above the ground. Canopy = calculated canopy coverage based on hemisphere images. InsectCount versus Moist: $r_s = 0.56$, $p = 0.076$; Temp versus Canopy: $r_s = -0.81$, $p = 0.0024$. On a site level, there was moderate evidence for a positive relationship between soil moisture and insect abundance; and strong evidence for a negative relationship between canopy openness and temperature. For the other variables, relationships were not statistically significant on a site level.

7 Reference list

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