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Monitoring Bat-Insect Relationships in Boreal Forest Habitats

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Abstract

Insect populations have over the last decades experienced global declines caused by anthropogenic disturbances, e.g., land-use changes, habitat loss, deforestation, and agricultural intensification. Consequently, insectivore populations are vulnerable because of reduced prey populations. Bats living at northern latitudes are especially vulnerable to changes in their food resources, as they experience shorter nights in the summer months compared to conspecifics living at lower latitudes. Additionally, bats living at northern latitudes are often constrained by less preferable weather conditions under the same high energy demands as those conspecifics. Evidence-based conservation of insectivorous bats requires knowledge about changes in both bat and insect abundance. There is a strong need for efficient methods for monitoring insect-insectivore relationships at different spatial and temporal scales. Non-invasive techniques have with time become a more accessible and affordable tool providing knowledge about wildlife populations with minimal degree of disturbance. Here I have investigated the ability of insect camera traps and ultrasonic acoustic recorders to capture these insect-insectivore relationships at 12 sites of boreal mixed forest habitats in Norway. In addition, I have looked at how bat activity and insect abundance are affected by environmental context, i.e., forest density (leaf area index), day length, temperature, soil moisture and ground cover. I also studied whether the relationships between insect abundance and bat activity differs among bat foraging guilds, i.e., short range echolocators (SRE), medium range echolocators (MRE) and long range echolocators (LRE). I conducted sweep net sampling of insects to compare the effectiveness of the non-invasive camera traps with a more conventional insect sampling method. I found an overall positive relationship between insect abundance and bat activity, but the relationship depended on leaf area index. There was a clear positive relationship between insect abundance and bat activity when leaf area index was low, but not at high leaf area index values. There was a clear negative relationship between leaf area index and bat activity for all guilds, but the decline was steeper for the MRE guild. Day length and soil moisture were negatively related to bat activity. Sites with a tall vegetation ground cover had higher insect abundance and bat activity than sites with low vegetation ground cover. In conclusion, I found that using automatic camera traps can be a useful method for quantifying food abundance for insectivorous forest-dwelling bats, but for the method to work, the camera must be deployed in open areas (gaps) in the forest.

Key words: Insects, Bats, Non-Invasive Techniques, Boreal Forest Habitats, Norway

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Table of contents

1. Introduction

Insect taxa have in more recent times been experiencing major declines in regard to both abundance (population size) and species richness (Benton et al., 2002; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019). These declines include both specialist and generalist species groups (Sánchez-Bayo & Wyckhuys, 2019). Considered to be among the main drivers of species declines are habitat loss and land-use changes (Sánchez-Bayo & Wyckhuys, 2019). As the world's largest group of animals, insects provide many important ecosystem services, e.g., pollination, natural pest control, decomposition, and nutrient cycling. Insects also play an important role in ecosystems as food for insectivores (Jones et al., 2009; Sánchez-Bayo & Wyckhuys, 2019). As insects play an important role in a variety of ecosystem functions and food webs, and are widely geographically distributed, they are often considered to be a good indicator taxa for assessing ecosystem health (Jones et al., 2009; McGeoch, 2007; Moreno et al., 2007).

Bats are the world's second largest order of mammals, with more than 1400 different species (Hutson & Mickleburgh, 2001; Trust, 2022). They are widely geographically distributed, have a rich diversity in diet and are the only mammal capable of active flight (Dietz & Kiefer, 2016). Their use of ultrasonic echolocation as means of orientation is also unique among terrestrial animals (Dietz & Kiefer, 2016), and enables them to navigate and locate prey in the dark (Law et al., 2016). In Norway we have 13 species of bats which all feed on insects (Miljødirektoratet, 2021). Activity and diversity of insectivorous bats are strongly correlated to the abundance of their insect prey (Kunz et al., 2011; Wickramasinghe et al., 2003). The amount of insects they consume also varies between bat species, depending on the season and the reproductive cycle (Kunz et al., 2011). Insectivorous bats that predate exclusively on insects and arachnids can provide an indication of ecosystem changes (Jones et al., 2009), and their potential as bioindicators should be further explored.

Much of the terrestrial biodiversity are found in forests (Duraiappah et al., 2005; Kortmann et al., 2018). Forests are important habitat for insectivorous bats, providing foraging opportunities, roost sites and protection from predators (Dietz & Kiefer, 2016; Kirkpatrick et al., 2018; Law et al., 2016). The boreal forest ecosystem in Fennoscandia is home to a variety of species, including bats and insects (Rouvinen & Kouki, 2008). Bats are an important part of the forest ecosystem and can provide top-down control of herbivorous insects when foraging (Jung et al., 2012). Forest bats, like forest birds, typically need a large three-dimensional space to meet their life requisites (Law et al., 2016). When insectivorous bats are foraging, they use vocalizations to navigate through this habitat and locate prey (Guo et al., 2021), and patches of forest landscape with diverse habitat composition is preferred by insectivorous bats when foraging (Charbonnier et al., 2016). Bats can be divided into guilds based on how they utilize the foraging space, depending on prey preferences, echolocation and wing morphology (Aldridge & Rautenbach, 1987; Dietz & Kiefer, 2016). Some bat species prefer open spaces, some tend to utilize edge-spaces and others are adapted to cluttered spaces.

The overall declines in insect biomass, and the fact that both specialist and generalist species groups are declining, is as cause of concern (Sánchez-Bayo & Wyckhuys, 2019). Declines in bats populations have also been reported as a response to human induced environmental stressors (Jones et al., 2009). As bats are sensitive to a range of environmental stressors and are affected by decline of their insect prey, they can be important environmental indicators (Jones et al., 2009). More studies on bat and insect populations can help understand the complex bat-insect relationships.

Ecological research has in recent time increased the use of passive acoustic monitoring (PAM) and camera traps, as the acoustic sensors have become more accessible (Gibb et al., 2019). Some of the strongest benefits of using PAM techniques to study wildlife's reactions to environmental changes, are that they are non-invasive, cost-effective and allows collection of large datasets (Froidevaux et al., 2014; Parsons & Szewczak, 2009). The accuracy of results from passive acoustic methods and camera traps will among other things depend on the study species activity patterns and habitat utilization (Froidevaux et al., 2014; Ruczyński et al., 2020). Most techniques for monitoring flying nocturnal insects have restrictions to how well they capture overall insect abundance and changes in abundance, in addition to affecting insect distribution (Ruczyński et al., 2020). To quantify the abundance of nocturnal flying insects, non-invasive camera traps can therefore be a useful alternative method (Ruczyński et al., 2020).

The aim of the study was to use non-invasive methodology to increase our knowledge of bat-insect relationships in forest habitats in Norway. I wanted to see if the use of insect camera traps and ultrasonic acoustic bat recorders could tell us anything about these relationships in a range of forest densities. I also wanted to see how bat-insect relationships were affected by other environmental factors including day length, temperature, soil moisture, canopy openness, leaf area index (LAI) and ground cover. To gain more knowledge about the insect community at the study sites and to compare a non-invasive approach to a more traditional approach I also sampled insects using sweep nets. Similar studies have been conducted by (Ruczyński et al., 2020), who used camera transects to monitor flying nocturnal insects, and (Johns, 2021) who used camera traps and acoustic detectors to monitor bats and insects at a Norwegian wind facility. This method has however, to my knowledge, not been tested in a Norwegian forest habitat.

The overall aim for this thesis was to find out if camera traps can be used to quantify food resources for insectivorous bats in forest habitats. Specifically, I asked the following research questions:

1. Is bat activity influenced by insect abundance measured with camera traps, and is the influence of insect abundance affected by the amount of canopy coverage?
2. Does bat activity vary among foraging guilds and are the foraging guilds similarly affected by the amount of canopy coverage?
3. How is bat activity influenced by other biotic (amount of ground cover) and abiotic environmental variables (temperature, soil moisture, day length)?
4. How do different measures of insect abundance (sweep net data or camera trap data) relate to bat activity?

2. Materials and methods

2.1. Study area

The study was conducted in the Follo region of eastern Norway from May 14th to September 14th of 2021. The study area included 12 sites of mixed boreal forests of similar height and productivity. The sites were approximately 1 km apart from each other and with similar distance to water bodies and the coastline of the inner Oslo Fjord (Figure 1).

At each of the 12 forest sites, bats and birds were monitored using stationary acoustic recording units, Wildlife Acoustic Inc Song Meters; including one bird detector (SM4) and three bat acoustic detectors (SM4-BATFS) sampling different forest structure, i.e., forest gap, forest interior and forest canopy. The sites also had an arthropod camera trap, an arthropod trapping transect and a data logger. A detailed example of a site layout is shown in Figure 2. All 12 sites were monitored by three nights of mist net surveys to capture bats throughout the summer. I will focus on the 12 'open' forest sites, which includes one bat detector, one arthropod camera trap, a data logger and a 20 m long arthropod trapping transect, placed within a forest gap with exposed sky. The size of the gap varied between sites, depending on the density of the forest.

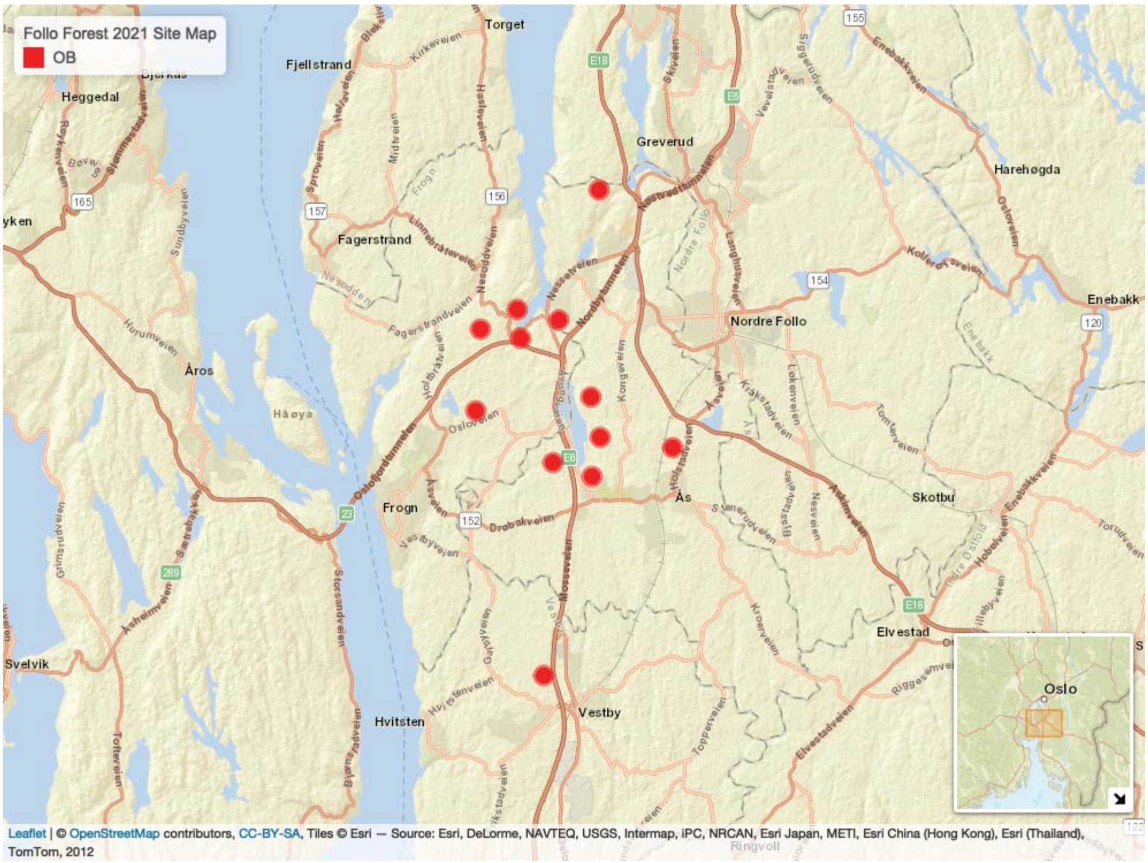

Figure 1. Map of the study area including GPS points from the open bat detectors for each of the 12 mixed boreal forest sites within the Follo region in Norway. Map was created using the Leaflet package in R Studio (RStudio, 2020).

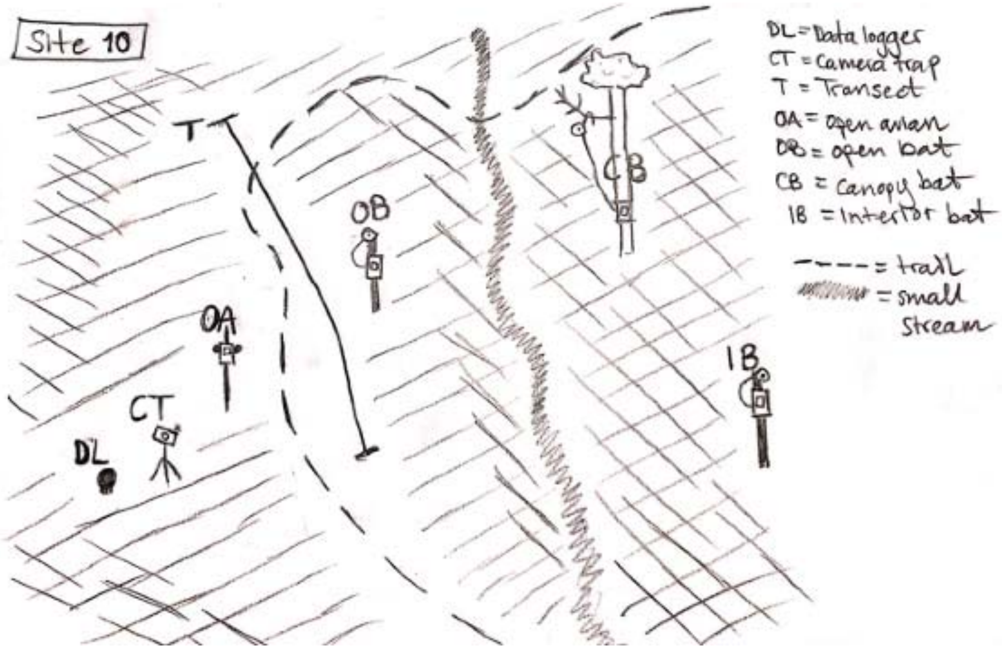

Figure 2. Layout of a forest site, with site FF10 as an example, including placement of all detectors, the data logger, the camera trap and the arthropod trapping transect.

2.2. Study species

2.2.1.Bats

In Norway there are 13 documented bat species, all belonging to the family *Vespertillionidae* and all are insectivorous (Artsdatabanken, 2021). 11 of these bats have documented reproducing populations, while two, *Eptesicus serotinus* and *Pipistrellus pipistrellus,* are known only to occur irregularly in the country (Eldegard K, 24.11.2021). As shown in Table 1, four of the bats are considered vunerable, endangered or critically endangered in Norway. In the rest of Europe, most of these species are considered to be of least concern (IUCN, 2021).

Table 1. Bat species found in Norway, their status on the Norwegian red list of species from 2021 (Artsdatabanken, 2021) and their assignment into foraging guilds (Froidevaux et al. 2014). The abbreviations on the red list: CR = Critically Endangered, VU = Vulnerable, NA = Not Applicable, LC = Least Concern, EN = Endangered, NT = Near Threatened (NT^{o} = Downgraded)(IUCN, 2021). Assignment into guilds and guild abbreviations: SRE = Short range echolocators, MRE = Medium range echolocators and LRE = Long range echolocators.

Scientific name	**English common name**	**Norwegian common name**	**Cathegory on the Norwegian red list 2021**	**Guild**
Barbastella barbastellus	Western Barbastelle	Bredøre	CR	SRE
Eptesicus nilssonii	Northern Bat	Nordflaggermus	VU	LRE
Eptesicus serotinus	Serotine Bat	Sørflaggermus	NA	LRE
Myotis brandtii	Brandt's Bat	Skogflaggermus	LC	SRE
Myotis daubentonii	Daubenton's Bat	Vannflaggermus	LC	SRE
Myotis mystacinus	Whiskered Bat	Skjeggflaggermus	LC	SRE
Myotis nattereri	Natterer's Bat	Børsteflaggermus	CR	SRE
Nyctalus noctule	Noctule Bat	Storflaggermus	EN	LRE
Pipistrellus nathusii	Nathusius's Pipistrelle	Trollflaggermus	NT^{o}	MRE
Pipistrellus pipistrellus	Common Pipistrelle Bat	Tusseflaggermus	NA	MRE
Pipistrellus pygmaeus	Soprano Pipistrelle Bat	Dvergflaggermus	LC	MRE
Plecotus auratus	Brown Long-eared Bat	Brunlangøre	LC	SRE
Vespertilio murinus	Parti-Coloured Bat	Skimmelflaggermus	NT	LRE

2.2.2.Arthropods

Common orders of insects eaten by bats are beetles (Coleoptera), flies (Diptera), mayflies (Ephermeroptera), true bugs (Hemiptera), butterflies and moths (Lepidoptera), grasshoppers, crickets and locusts (Orthoptera), and caddisflies (Trichoptera). Bats can also eat spiders (Araneae) and harvestmen (Opiliones). A study by Rydell (1992) investigating the diet of the parti-coloured bat in southern Sweeden using fecal samples, found small dipterans to dominate, but also found the diet to include moths, caddis-flies and dung beetles. Using continent-wide DNA metabarcoding of fecal samples, Alberdi et al. (2020) found the diet of European bats were dominated by Lepidoptera and Diptera. Lee and McCracken (2005) found the diet of Brazilian free-tailed bats to be dominated by moths, beetles and true bugs.

2.3. Field data collection

2.3.1. Acoustic bat monitoring

One acoustic bat detector was placed at ground level, approximately 2 m above ground, at every site and a minimum of 1 m away from vegetation clutter (Figure 3). It was deployed on a wooden pole with an external SMM-U2 or an SMM-U1 ultrasonic microphone from Wildlife Acoustic Inc attached at the top of the pole. We mainly used U2 microphones that were pointing straight upwards, but a few U1 microphones pointing 45 degrees upwards from the top of the pole and away from clutter were also used. The detectors started recording if they were triggered by bat activity during the time frame of one hour before sunset to one hour after sunset. They were deployed in May and were left out continuously during the summer until retrieval in September. Routine maintenance checks on detectors occurred on a biweekly basis to check for loss in microphone sensitivity, check for functional errors and collect data. A microphone calibration test was conducted twice throughout the study period.

Figure 3. Setup of SM4-BATFS acoustic bat detector deployed with a U2 microphone at an open forest site.

2.3.2. Arthropod camera trap monitoring

The arthropod camera traps were deployed between June 23rd and June 25th and retrieved on average 40 days later between August 30th and September 7th. The study design is inspired by (Ruczyński et al., 2020), who did a similar study across different habitat types. The camera traps were placed in a forest gap with exposed sky in the background, 3-15 m away from the 'open' bat detectors. The setup consisted of a tripod secured to the ground by tent poles with a waterproof camera box attached on top, approximately 2 m above ground when fully extended (Figure 4) The camera box was facing north and tilted slightly downwards to let raindrops run off. The camera was taking one photo every 10 minutes with a flash during a 24-hour cycle for as long as the battery lasted, on average three days. The power converter was placed inside the camera box together with a silica pad to absorb condensation. A waterproof battery box with a 12V 19- or 21-Ah motorcycle gel battery was placed between the tripod legs. Equipment was marked with placards informing the public that it was part of a research project related to the Norwegian University of Life Sciences. There was a tiny hole on the side of the front of the camera box, where the power cord went out and down into the ventilation holes under the lid of the battery box. The power cord was attached to the motorcycle battery using a screwdriver. GPS points were collected for all the camera trap locations. Maintenance checks of the camera traps were conducted once a week, which included changing the battery and collecting data.

Figure 4. Arthropod camera trap setup. Study design inspired by (Ruczyński et al., 2020).

Figure 5. Arthropod camera trap example photo of flying nocturnal insects.

2.3.3. Arthropod sampling

Physical arthropod trapping was conducted using a sweep net and a butterfly net (Figure 6). Sampling was done once at each site during the day in both July and August, and once during the night at all sites. Each site had a 20 m transect approximately 0.5-8 m away from the arthropod camera traps, with a semi-homogenous vegetation cover. The vegetation cover varied between sites. All the open plots had full (100%) ground cover vegetation, but the pots were either characterized as having low vegetation (bilberry/small ferns/forbs) or tall (tall ferns and forbs). Transect GPS points were collected, with at least three points per transect. Daytime sampling was conducted by myself and nighttime sampling was conducted by Rebekka Bedringås, April McKay and myself during mist net surveys over the course of the summer. One sweep was done per step, where two steps accounted for approximately one meter combined. Sweep- and butterfly net samples were emptied into resealable plastic bags with cotton pads soaked in nail polish remover containing acetone inside to kill the arthropods. The bags were marked with site name, date, time and crew member and were then stored in a freezer at –20 degrees Celsius.

Figure 6. Arthropod trapping equipment and an example photo of a transect from site 3.

2.3.4. Environmental variables

Each site had a TMS-4 TOMST® datalogger (Wild J. et al., 2019) that was deployed at the same date as the camera trap and was left out until the acoustic detectors were retrieved (Figure 7). It was inserted into the soil approximately 1-10 m from the arthropod camera trap and collected data continuously. The datalogger registered soil moisture in addition to temperature both in and above ground. Date and time of deployment and retrieval, in addition to the serial number of the data logger was noted. The temperature registered highest above ground will be used in analysis (T3).

Figure 7. TOMST TSM4 soil moisture and temperature data logger before (left) and after (right) deployment with the specific serial number.

To document canopy cover (leaf area index) and canopy openness at the 12 forest sites, hemisphere images were collected using a fish-eye lens camera for each site (Figure 8). Day length data were obtained from SeNorge, corresponding it to dates of the study and GPS location of the study area. Ground cover vegetation was documented for all sites with common plant species groups and then assigned a rank score.

Figure 8. Hemisphere photos from fish-eye lens camera documenting tree crown cover at the forest sites.

2.4. Laboratory work

All arthropod samples from the sweep netting were sorted by myself in the NMBU entomology lab from August to December of 2021. I started by separating arthropods from vegetation, where the vegetation was thrown away after. Sweep- and butterfly net samples from one transect survey were pooled together and put into a glass tube with 80% ethanol. The tubes were marked with date and time, site name and collector ID, both on the tubes and on a paper note inside the tube. Samples were then stored at room temperature (22 degrees Celsius) until further handling. I classified arthropods into orders, following taxonomic keys in Sømme (2015). All the contents inside the glass tube were emptied out into a petri dish. I used a tweezer, needle, pipette, paper towel and a Leica MS5 stereo microscope with 4X magnification placed in front of a suction for ventilation. Arthropods in one sample were classified and then put into glass tubes or SafeSeal Micro Tubes with 80% ethanol according to order, or into the categories ‘uncertain’ or ‘smaller than 2 mm’. The arthropods that were in the < 2mm category were counted without being sorted into orders. External verification from expert colleagues was used to classify the uncertain category specimens which I was unable to classify confidently. The total number of arthropods in a sample were noted.

2.5. Data management

2.5.1. Acoustic data

The bat detectors recorded data between one hour before sunset to one hour after sunset, if they were triggered by bat activity. This results in bat data being sampled across two dates, which we accounted for by adding a new date column where the day (or night) started and ended at noon. A bat pass can include a series of bat calls. We used a 5 second cut off, because this makes bat passes more comparable between each other and is well suited to quantifying bat activity in more cluttered environment. Acoustic bat data (.wav files) were processed with the Auto ID function in Kaleidoscope Pro Analysis Software from Wildlife Acoustic, Inc. Signal parameters were used to distinguish between bat calls and noise files, which includes everything that is not a bat call. We used the following signal parameters: 8-120 (kHz) as minimum and maximum frequency range, 2-500 (ms) as minimum and maximum length of detected pulses, 500 (ms) as maximum inter-syllable gap and 2 as minimum number of pulses. Noise files were removed in R Studio. The auto IDs were then clustered into bat guilds (SRE, MRE and LRE).

2.5.2. Arthropod camera trap data

Raw images from all camera traps were sorted by site, date and time. Images that were shot from one hour before sunset to one hour after sunset were selected for further data management. To get a count of insects, these images were manually annotated in VGG Image Annotator (Dutta & Zisserman, 2019). Insects in images were annotated with circles, and they were categorized as being certain, 'Yes' or 'No'. 'Yes' meant that you were more than 60% sure that the object was an insect, and 'No' meant that you were between 40-60% certain that it was an insect. No objects were circles if you were less than 40% sure it was an insect. Image quality was also selected for each image, where the categories were 'Good', 'Poor' or 'Bad'. 'Good' had little to no, 'Poor' images had 10-30% , and 'Bad' images had more than 30% of the frame altered by a glare or water droplets. Reference images were used as a guide. Only images annotated as 'Good' were used in analysis.

2.5.3.Environmental variables

Soil moisture and the above ground temperature (T3) data from the TMS-4 TOMST® dataloggers was collected continuously while the insect camera traps were out in the field, so there were no gaps in the data. At a later point these data were aggregated by hour in R Studio, to coincide with dates with insect camera trap images, which were used in analysis. Hemisphere photos were taken once for each site and used for obtaining leaf area index values and assessing canopy openness to be used in analysis.

2.6. Statistical analysis

Statistical analyses were carried out in R Studio version 1.4.1717 © 2009-2021 RStudio, PBC. Bat activity was measured as number of bat passes per night, where a bat pass can be multiple bat calls within a five second bat pass recording. Bat acoustic data were aggregated to number of bat passes per night (Figure A1). Two sites (FF03 and FF11) were excluded from the statistical analyses, because they had only 4 and 5 nights of data recorded, respectively). In addition, 9 outliers, i.e., observations with >300 bat passes per night, were excluded from the statistical analyses. The distribution of insect counts was heavily skewed with many zero and low values. To avoid statistical problems, insect abundance was log +1 transformed before statistical analysis. Exploratory analyses also revealed that leaf area index and canopy openness were highly correlated ($r>0.7$), and therefore only leaf area index was included in the statistical analysis.

For the statistical analysis, a Negative Binomial Generalized Linear Mixed Model (NB) GLMM model was used because overdispersion was detected when fitting a Poisson model. The NB GLMM cannot be overdispersed, as it has an extra parameter theta. The full (most complex model) included fixed effect terms insect abundance, guild (SRE, MRE, LRE), leaf area index, soil moisture, daylength, ground cover (tall vegetation, low vegetation), and the interaction terms guild × leaf area index, and insect abundance × leaf area index. SiteID was included as random intercept to account for among-site variation.

To check if the model fitted the data, a model validation for the NB GLMM was carried out, plotting plotted residuals versus fitted values and residuals versus each covariate in the model. This graphical model validation did not reveal any serious violations of model assumptions.

3. Results

From the 12 'open' bat recorders that were left out during the four-month study period from May 14th to September 14th, there were a total of 209652 bat passes after filtering out incomplete nights and noise using Auto ID in the Kaleidoscope Pro Software from Wildlife Acustics, Inc. A bat pass is here referred to as a sound file with a five second cut off, which can include a series of bat calls. There were 85147 LRE, 40961 MRE, 33115 SRE and 50429 No ID bat passes. 'No ID' bat passes refer to files that did not receive an auto ID which are not noise files. The average nightly bat pass at the OB detector sites was 1000. Activity varied among the 12 study sites, with site FF08 being the most active and FF11 the least active site. Sites with tall ground cover vegetation showed significantly more bat activity overall than sites with low ground cover vegetation. The two study sites FF03 and FF11 were excluded from analysis as they had much lower bat activity and insect abundance compared to the other sites and would have given an unbalanced study design.

When the acoustic bat data were prepared for analysis, only bat pass data from nights with corresponding insect camera trap data were used. After doing this, there was a minimum of 975 and a maximum of 41973 total bat passes at site FF11 and site FF08 respectively, where FF11 had the least nights of recordings with 64 and FF08 had the most nights of recordings with 114. The average nightly bat pass ranged from a minimum of 15 (rounded up from 14.7) at FF07 to a maximum of 368 bat passes per night at site FF08. The total number of insects and arachnids combined were the highest at site 973 at site FF09 and lowest at site FF08 with 115. The Diptera count was at a minimum of 42 at site FF08 and maximum of 467 at site FF09. The number of unique taxa ranged from a minimum of 11 at FF03 to a maximum of 18 at FF10.

The full (most complex) model

BatPassN ~ s.logSumIns + Guild + s.LAI + Guild * s.LAI + s.logSumIns * s.LAI + s.SoilMoisture + s.day_length + GroundCover + (1 | SiteID),

included the explanatory variables insect abundance, guild (SRE, MRE, LRE), leaf area index, soil moisture, daylength, ground cover (tall vegetation, low vegetation), and the interaction terms guild × leaf area index, and insect abundance × leaf area index.

I found that on average per site, bat activity differed amongst bat guilds (LRE>SRE>MRE). This was measured as number of bat passes per night. Sites with a tall ground cover vegetation had higher bat activity than sites with low ground cover vegetation (Table 2, Figure 9). Bat activity decreased with daylength (Figure 10, Table 2) and soil moisture (Table 2). The relationship between bat activity and insect abundance depended on leaf area index, where there was a clear positive relationship between insect abundance and bat activity when leaf area index was low, whereas the relationship disappeared at high leaf area index values (Table 2, Figure 11). There was a clear negative relationship between leaf area index and bat activity for all the guilds, but the decline in bat activity with increasing leaf area index was steeper for the MRE guild (Table 2, Figure 12).

Table 2. Analysis of factors influencing number of bat passes. Bat guilds LRE, MRE and SRE are long, medium and short-range echolocators. Continuous variables were scaled before analysis. Analysis of 753 observations from 10 sites. Two sites (site FF03 and FF11) were excluded from analysis due to data deficiency compared to the other 10 sites. Conditional $R^2 = 0.77$, Marginal $R^2 = 0.71$. Candidate explanatory term Temperature was dropped during model selection with backward elimination using AIC. Output from negative binomial model with log link function, dispersion parameter $\theta = 0.747$. SiteID was included as random intercept to account for among-site variation.

Fixed effects	**Estimate**	**Std. Error**	**z**	**p**
Intercept	2.48	0.19	13.23	<0.0001
Insect abundance	0.14	0.07	2.04	0.042
Guild MRE (*versus* LRE)	-1.19	0.12	-9.76	<0.0001
Guild SRE (*versus* LRE)	-0.46	0.11	-4.01	<0.0001
Leaf area index	-1.05	0.16	-6.41	<0.0001
Soil moisture	-0.34	0.12	-2.91	0.0037
Daylength	-0.22	0.06	-3.52	<0.0001
Ground cover Tall vegetation (*versus* Low vegetation)	1.02	0.32	3.17	0.0015
Guild MRE (*versus* LRE) × Leaf area index	-1.04	0.13	-7.70	<0.0001
Guild SRE (*versus* LRE) × Leaf area index	-0.08	0.11	-0.73	0.464
Insect abundance × Leaf area index	-0.21	0.07	-2.92	0.0035
Random effect	**Variance**	**St.Dev**		
SiteID	0.19	0.44		

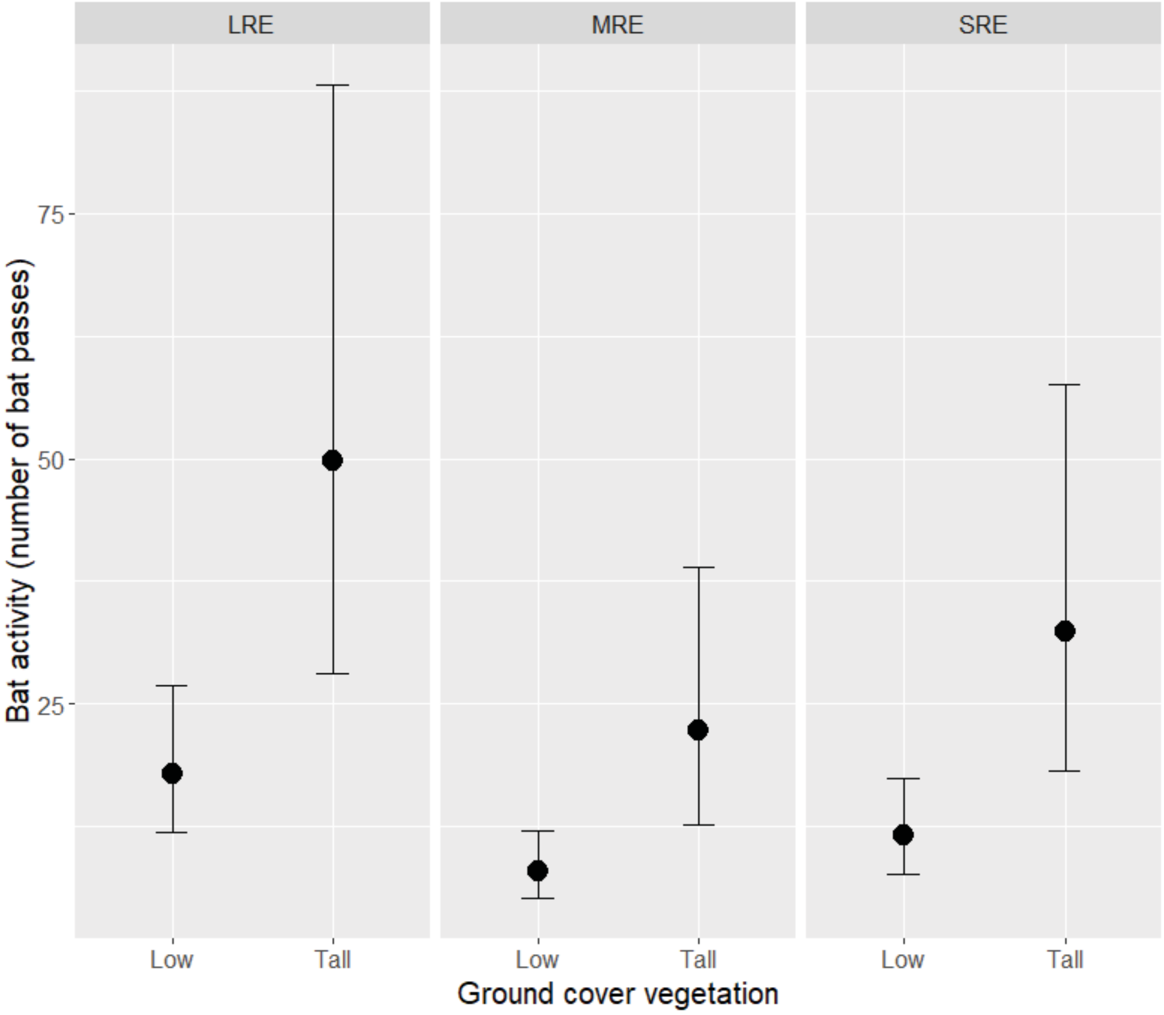

Figure 9. Predicted effects of guild and ground cover on bat activity at median values of the other variables. Points are estimated means, error bars show 95% confidence intervals. Based on the statistical model in Table 2.

Figure 9 displays bat activity in relation to ground cover vegetation, being either low or tall, between the three guilds. Ground cover vegetation was classified as tall or low depending on the rank score from the vegetation analysis. Tall got the score 5 and low had the score 4. Both were fully vegetated but with some differences in plant community composition. MRE and SRE bats show similar trends, while LRE bats had a bit higher activity, in particular for the tall ground cover vegetation.

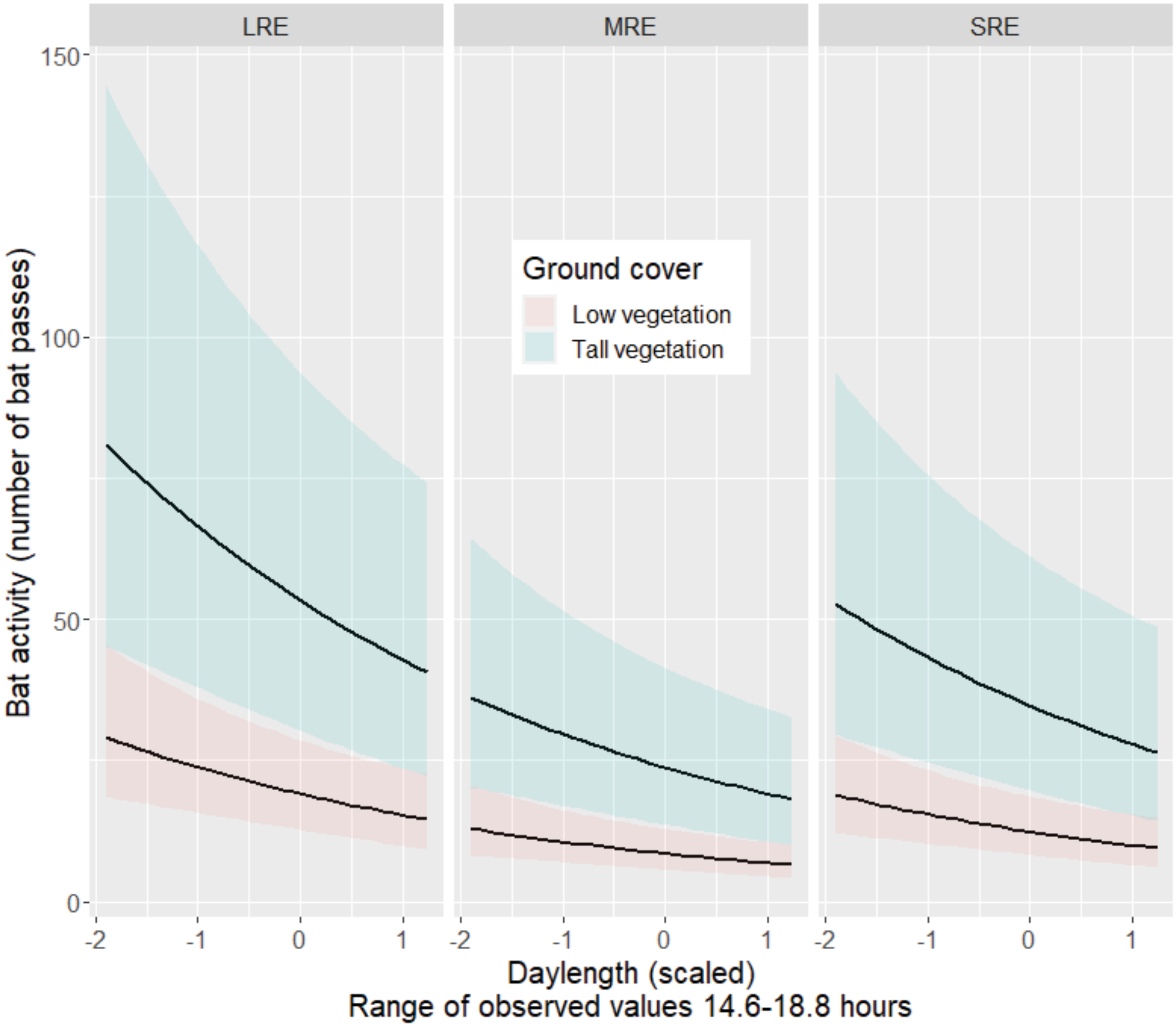

Figure 10. Predicted effects of daylength on bat activity for all levels of guild and ground cover, at median values of the other variables. Black lines are estimated relationships, shaded polygons show 95% confidence intervals. Based on the statistical model shown in Table 2.

Figure 10 displays bat activity in relation to daylength between 14.6 to 18.8 hours for both tall and low ground cover vegetation for all three bat guilds. There is a clear negative relationship for all guilds, whereas the nights get shorter the total bat activity per night decreases.

To measure insect abundance, the 12 camera traps took a total of 17046 total unique images throughout the study period from June 23rd to September 7th. These photos were classified into having good, poor or bad image quality, where only the good ones were used in analysis. The number of insects found in photos varied from a minimum of 0 to a maximum of 213. Insect abundance and bat activity were statistically correlated. They were also both related to the abiotic environmental factors, temperature and soil moisture, and the biotic factors, leaf area index and ground cover vegetation in a similar manner.

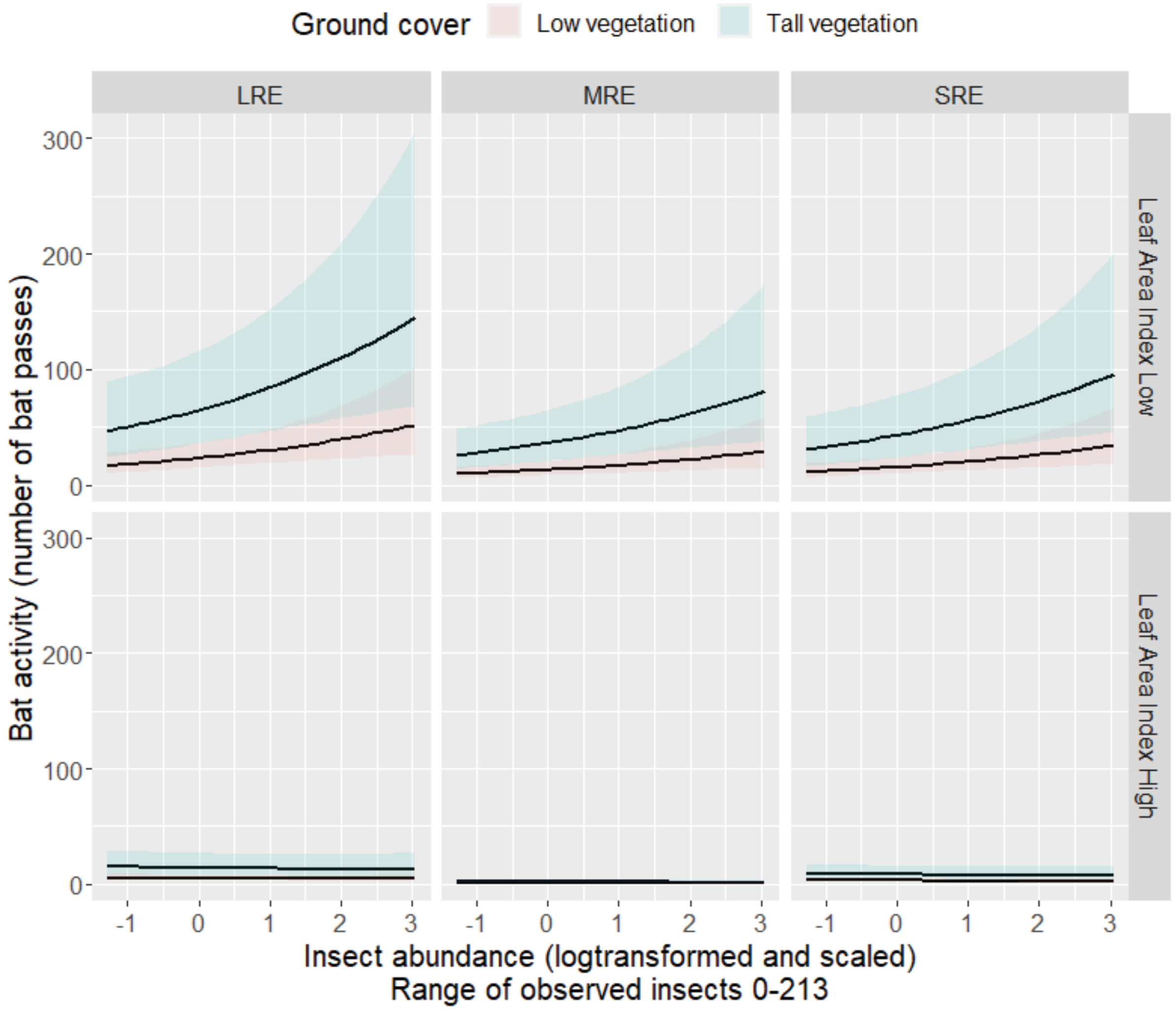

Figure 11. Predicted effects of insect abundance on bat activity at high (4th quantile) and low (2nd quantile) leaf area index, for each of the three guilds and for median values of the continuous variables. Based on the statistical model shown in Table 2.

In figure 11 we can see bat activity compared to insect abundance within the range of 0-213 individuals for the three bat guilds and for either low or high leaf area index. There is a positive trend in bat activity for all guilds and insect abundance with low leaf area index and no clear relationship at high leaf area index.

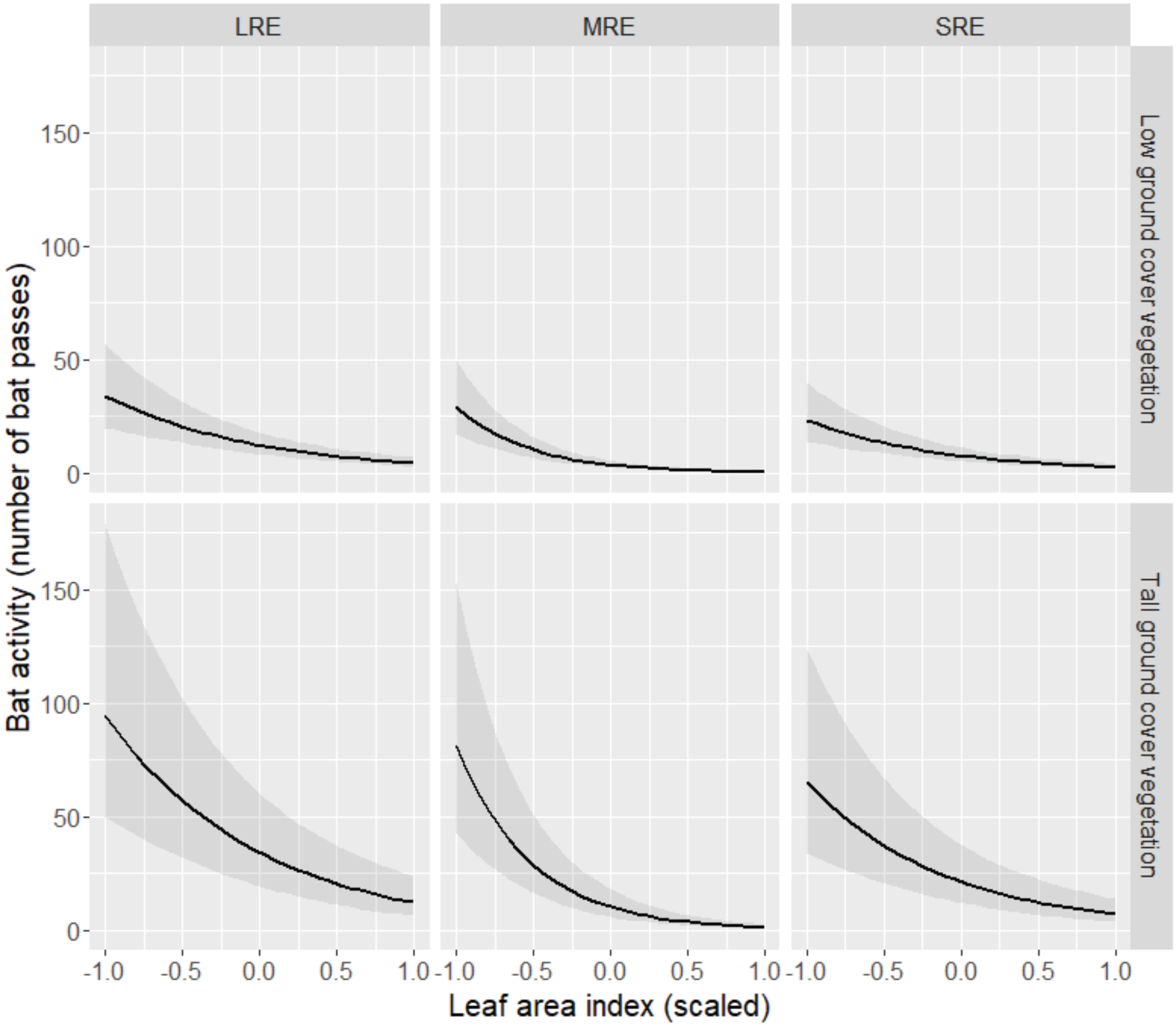

Figure 12. Predicted effects of leaf area index (predicted for interval -1 to 1) on bat activity, for each of the three guilds and for median soil moisture and daylength. Based on the statistical model shown in Table 2.

Bat activity in relation to leaf area index at low or high ground cover vegetation is displayed in figure 12. There is a clear negative relationship in all instances and for all guilds, however it is strongest for the tall ground cover vegetation.

There was a total of 6749 arthropods from the sweep net samples of all 12 sites. Of these, 639 belonged to class arachnids and 4824 to class insects. There were 5463 insects and arachnids. There was a lot of variation in abundance (number of specimens) among sites, but not much variation in taxon richness. I did not find a very obvious relationships between the sweepnet data and the bat data.

4. Discussion

4.1.Main findings

I found that bat activity was affected by insect abundance and abiotic environmental variables such as temperature, day length and soil moisture. The degree to which bat activity was affected by insect abundance depended on the amount of canopy cover (leaf area index). At low leaf area index values, there was a clear positive relationship between bat activity and insect abundance, whereas this relationship disappeared at high values. On average per site, bat activity differed among the three bat guilds. All guilds were negatively affected by higher amount of canopy cover; however, the effect was strongest for MRE bats. Sites with tall ground cover vegetation had overall higher bat activity than at sites with low ground cover vegetation. Activity was a bit higher for LRE bats, particularly for sites with tall ground cover vegetation, whereas SRE and MRE bats showed similar trends. Bat activity was negatively affected by daylength and soil moisture.

4.2.Bat and insect relationships

Boreal forests in Scandinavia are spruce and pine dominated (Law et al., 2016). European commercial plantations are generally considered to be poor habitats for bats (Kirkpatrick et al., 2018; Russo et al., 2010). As the trees usually are densely planted, a bats access to insect prey is limited (Jung et al., 2012; Kirkpatrick et al., 2017; Kirkpatrick et al., 2018). Therefore, bats tend to be less associated with closed canopy conifer stands (Kirkpatrick et al., 2018). I found that insect abundance measured with camera traps had an influence on bat activity in mixed-boreal forest, but the influence of insect abundance was affected by the amount of canopy coverage. The relationship between bat activity and insect abundance depended on leaf area index, where it was clearly positive at low leaf area index values but disappeared at high leaf area index values. This means that as the number of insects at a site increased, bat activity also increased when the canopy cover was low. With a high amount of canopy coverage, I did not find the same trend.

The accessibility of food resources by insectivorous bats are affected by plant density, canopy cover and temperature (Rojo Cruz et al., 2019). Rojo Cruz et al. (2019) found that forests with high canopy cover or high plant density tended to increase more in activity. Brigham et al. (1997) found that small bats were negatively affected by increased clutter when foraging. High amount of vegetation clutter can mask the echoes returning from insect prey, decreasing the foraging efficiency for bats (Law et al., 2016; Schnitzler et al., 2003). Increased canopy cover in the background of images also makes it more difficult to detect insects.

I found that on average per site, bat activity differed among foraging guilds, where LRE bats had the highest amount of activity. MRE bats in my study had the second highest total number of bat passes followed by SRE bats. Patriquin and Barclay (2003) found that the bat species in their study utilized the harvested forest habitat differently. Vasko et al. (2020) suggested that all bat species in their study foraged in forest gaps, but also utilized the space differently. Smaller, more maneuverable species were less influenced by clutter than the larger, less maneuverable bat species which preferred more open habitat with less clutter (Patriquin & Barclay 2003). All guilds in my study were negatively affected by higher amount of canopy coverage; however, the effect was strongest for MRE bats. LRE bats showed the greatest increase in bat activity in relation to insect abundance at low leaf area index values, while SRE and MRE bats showed very similar responses. Kortmann et al. (2018) and Jung et al. (2012) found foraging activity for *Barbastella barbastellus*, a *SRE bats*, to increase with increased canopy opening. This was more likely a result of increased accessibility of the prey and not higher prey abundance.

It is important to consider some expected biases that comes with using passive acoustic bat detectors. Bats belonging to different foraging guilds vary in the way they echolocate; i.e., long or short call duration, high or low frequency and large or small bandwidth (Dietz & Kiefer, 2016). These echolocation traits have correlations with wing morphology, where more maneuverable bats tend to be small with large wing area while fast flying bats are larger with small wing area (Arita & Fenton, 1997; Dietz & Kiefer, 2016). Maneuverable species are adapted to flying in cluttered spaces at lower speeds, and fast flying species to open spaces with less clutter (Dietz & Kiefer, 2016). Larger insectivorous bats often also eat larger prey than smaller bats, detected using low frequency calls in more open habitats (Aldridge & Rautenbach, 1987; Arita & Fenton, 1997). Detectability of bat calls by ultrasonic acoustic bat recorders vary between bat species and habitat, where it is higher in open areas and LRE bats are more easily detected from longer distance than SRE and MRE bats (Aldridge & Rautenbach, 1987; Dietz & Kiefer, 2016). Acoustic bat data collection will be affected by the detector placement and presence of linear features that may have higher levels of insect activity (Perks & Goodenough, 2020). It is also expected of activity studies to have some pseudoreplication, as one can’t differentiate between individual recorded bats during a night (Hope & Jones, 2013).

Conducting acoustic surveys in the summer, when nights are at their shortest at northern latitudes, may be advantageous as activity tend to be higher and more concentrated (Perks & Goodenough, 2020). Scandinavian summer nights are short, with the darkest time being around midnight bats often forage at the lowest light level rather than at peak insect activity (Rydell et al., 1996). (Rydell et al., 1996) found that moths had highest activity around midnight while other flying nocturnal insects peaked in activity closer to dusk. Bats tend to emerge at lower light levels rather than earlier in the evening if they are not in need of crepuscular insect prey (Jones & Rydell, 1994; Vasko et al., 2020). The study of (Rydell et al., 1996) found areal-hawking bats to begin foraging short after sunset, when small dipterans are active. The foliage gleaning bat in the study however, emerged later when moth activity was higher. Light levels are likely to effect emergence time of insectivorous bats, as bats will be more visible for predators earlier in the night (Rydell et al., 1996). I found that daylength was negatively correlated to bat activity, where shorter nights had a negative effect on bats.

The composition of understory vegetation in a forest habitat affects the availability of insect prey and a bats ability to access the forest interior (Law et al., 2016). How bats use a forest also depend on their foraging behavior and wing morphology, where some prefer open spaces with little cover and others rely on dense ground cover vegetation (Law et al., 2016; Müller et al., 2012). I found that sites with a tall ground cover vegetation had higher bat activity than sites with low ground cover vegetation. MRE and SRE bats show similar trends, while LRE bats had a bit higher activity, in particular for the tall ground cover vegetation. Bat activity in relation to leaf area index at low or high ground cover vegetation had a clear negative relationship in all instances and for all guilds, however it was strongest for the tall ground cover vegetation. Edge-space and gleaning species have been shown to prefer a well-developed understory cover, while open space foragers prefer more open parts of the forest (Jung et al. 2012)(Fuentes-Montemayor et al., 2013).

Müller et al. (2012) found insect abundance to be higher in dense vegetation (Froidevaux et al., 2016). Forest gaps with less crown cover and better light conditions allows for more rapid vegetation succession (Froidevaux et al., 2016), which may result in more heterogenous ground cover vegetation (Bouget & Duelli, 2004). As many insects thrive in habitats with herbaceous plants (Kortmann et al., 2018; Vaughan, 1997), these gaps may attract bats that prefer foraging in forest openings (Froidevaux et al., 2016). (Kirkpatrick et al., 2018) mentions the importance of investigating fine scale variations in microhabitats in managed forest stands (Arrizabalaga-

Escudero et al., 2014), as they will vary in abundance and accessibility of bat prey species. Great emergence of insects in boreal forest habitats during the summer may cause prey abundance to generally be high, making the difference in biomass between more or less productive sites smaller (Vasko et al., 2020). This can in turn make other features more important as to where bats choose to forage, i.e., forest structure, risk of predation and distance form roosts (Vasko et al., 2020).

I found that bat activity was affected by abiotic environmental variables such as day length and soil moisture. Bat activity decreased with daylength and soil moisture. The LRE bats showed the strongest negative response to day length, followed by the SRE bats, and the MRE bats showed the weakest response, although the difference was minimal. The relationship had a steeper decline for all guilds at sites with tall ground cover vegetation. Bat activity among temperate bats are highest during the summer when temperatures increase (Perks & Goodenough, 2020). Food availability for insectivorous bats is affected by temperature, as insects are ectotherms and many have a temperature threshold for when they are active around 6-10 C (Hope & Jones, 2013) (Jones et al., 1995) (Taylor, 1963). (Perks & Goodenough, 2020) found a weak positive correlation for temperature on overall bat activity. (Rojo Cruz et al., 2019) also found a positive influence of temperature on bat activity. Temperature was not included in my best model, but (Johns, 2021) found a positive effect of temperature at a wind facility.

5. Conclusion

I found that using automatic camera traps can be a useful method for quantifying food abundance for insectivorous forest-dwelling bats. However, for the method to work reliably, the camera must be deployed in open areas (gaps) in the forest to avoid insects being masked behind vegetation clutter.

6. Appendix

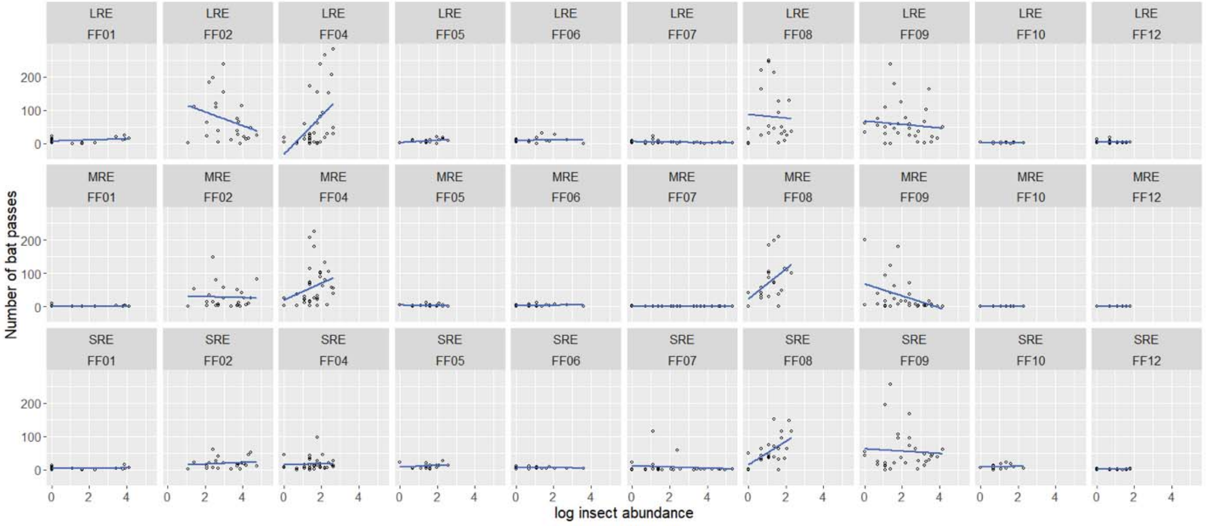

Figure A1. Observations of number of bat passes per night at 10 sites, for the guilds LRE, MRE and SRE, i.e., long, medium and short-range echolocators. Blue lines are fitted linear regression lines. Two sites (FF03 and FF11) are not shown because these sites were excluded from the analyses (only 4 and 5 nights of data recored, respectively). In addition, 9 outliers, i.e., observations with >300 bat passes per night are not shown as they were also excluded from the statistical analyses.

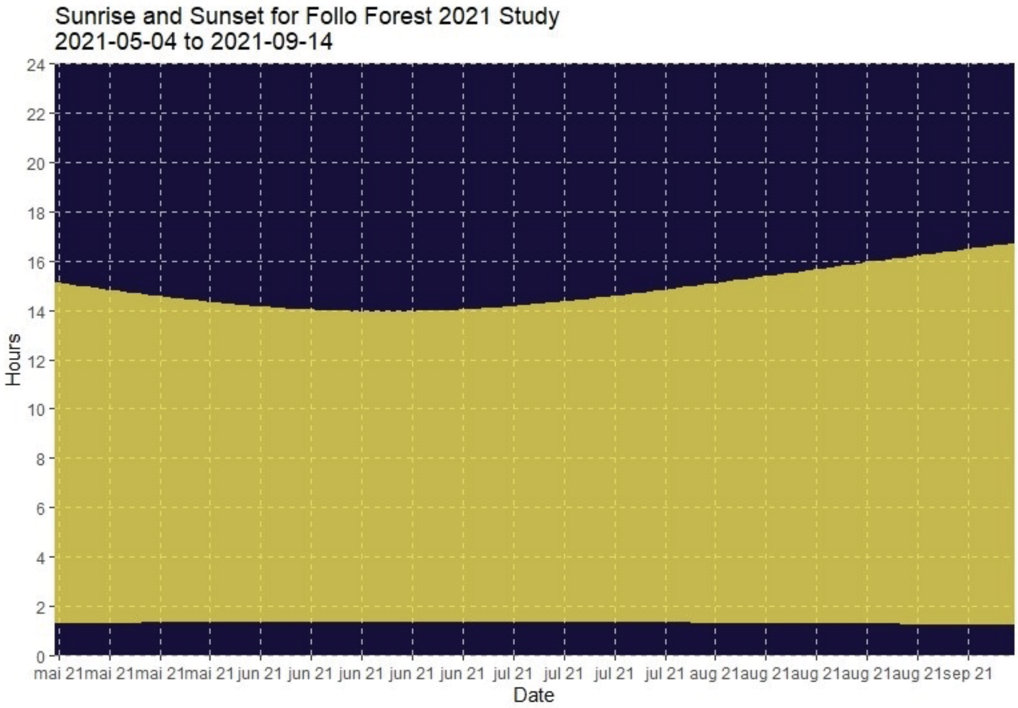

Figure A2. Daylength in hours in the study area (Follo region) from May 4th to September 14th of 2021.

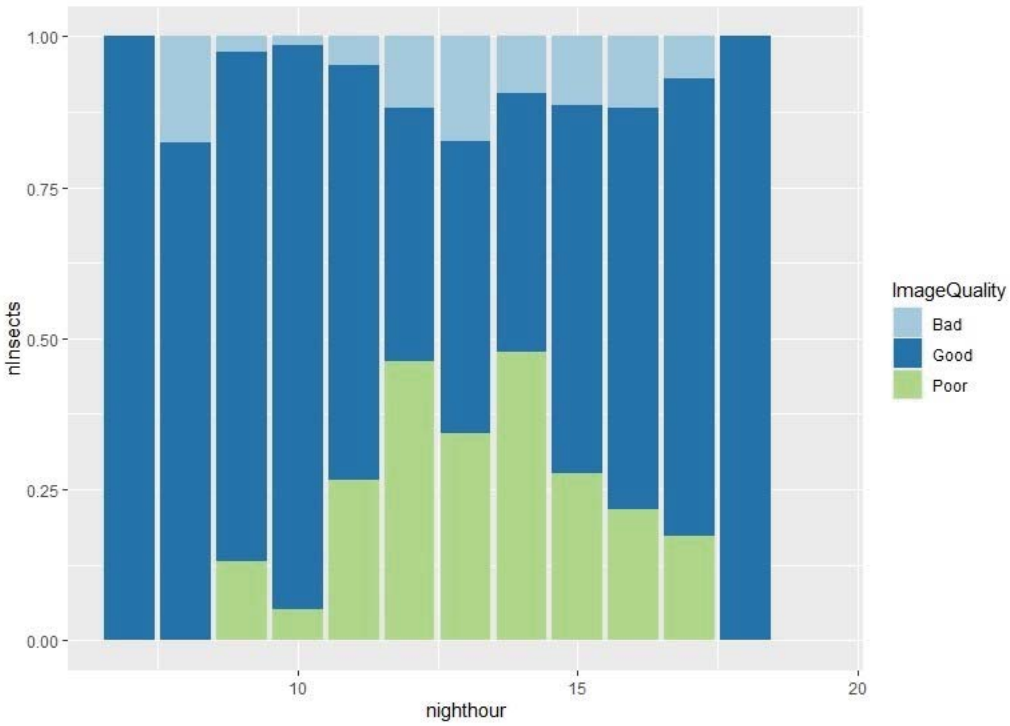

Figure A3. Image quality of nighttime images.

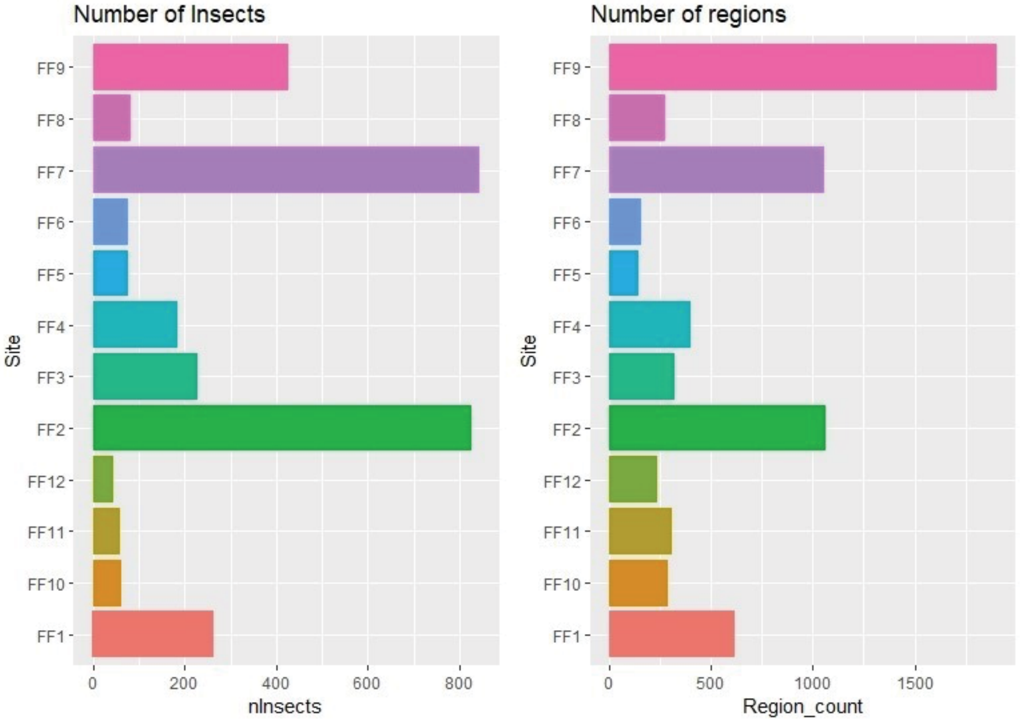

Figure A4: Number of insects and region counts on images from insect camera traps for the 12 forest sites.

Figure A5: Number of specimens, arthropods, sampled at each site divided by two daytime and one nighttime sampling events per site.

7. Literature

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