Ecosystem services of insectivorous bats in intensively managed arable land benefit from adjacent near-natural areas

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Abstract

Ecosystem services provided by insectivorous bats are an important yet underappreciated economic benefit of biodiversity. To investigate what is needed to maintain these services, we asked whether bat-mediated ecosystem services depend on near-natural areas adjacent to farmland. We used high-throughput tracking and genetic sequencing to determine the habitat use and diet of 128 common noctule bats (*Nyctalus noctula*). Common noctule bats spent an average of 55% of their foraging time over arable land, although arable land made up more than 95% of the area within their activity range, indicating avoidance. In contrast, bats foraged 14% of the time over water and wetlands, which constituted only 0.5% of the area, indicating a strong preference. Consequently, the overall diet consisted mainly of insects with aquatic larval stages. Of all insects consumed, 23% were pests, highlighting the ecological importance of noctule bats in both near-natural and human-altered ecosystems. Our data suggest that the ecosystem services provided by bats on farmland may depend strongly on adjacent near-natural areas where they can find sufficient insects to meet their energy demands. These findings highlight the need to maintain a high degree of habitat heterogeneity for the conservation of bat species and their contribution to sustainable agriculture.

Keywords: Trophic interaction, movement, high-throughput tracking, *Nyctalus noctula*, insect diversity, metabarcoding, agricultural landscape

Introduction

Predators exert selective pressure on prey populations, affecting their distribution and abundance, while prey availability and quality directly affect the fitness and spatial distribution of predators [1, 2]. Such trophic interactions are particularly dynamic in human-modified landscapes, where disturbance and habitat alterations can disrupt the stability of food web structures [3]. Yet, insects are key players in ecosystems and food webs providing an important source of energy and nutrients for many predators [4]. However, recent studies confirm an alarming decline in insect biomass in many anthropogenic landscapes around the world [5-9]. As total insect biomass declines, the composition of insect communities changes, with specialised taxa disappearing and generalist taxa, including many pest species, increasing in abundance [10]. These pests can have a major impact on crop yields, putting economic pressure on the agricultural sector [11-14]. As a result, farmers attempt to control pests by applying insecticides, often with disastrous effects on non-target insect species as well [15]. In combination, land use intensification and pesticide use can have complex consequences for insect-mediated trophic networks on agricultural land [3, 10].

There are more than 1,400 bat species worldwide, the majority of which are insectivorous [16]. Bats play an important role in modifying insect communities and trophic networks in both natural and anthropogenic ecosystems worldwide [17-19], including ecosystem services provided by the consumption of pests across latitudes from tropical to temperate [20-22]. The advent of molecular genetic tools, namely metabarcoding, has allowed a more detailed assessment of insect consumption by bats [23, 24] particularly of insect pests [25-28]. Simultaneously, technologies have been developed to track bats at landscape scale with high temporal resolution and spatial accuracy [29]. Here, we used the combination of both to shed light on the ecosystem services and spatial use of a highly mobile aerial-hawking species, the common noctule bat (*Nyctalus noctula*). As a typical aerial-hawking bat species, common noctule bats forage in open spaces, i.e. above pastures, arable land, lakes and urban areas [30-34]. They are known to feed on a wide variety of insects, including Coleoptera, Lepidoptera, Diptera, Trichoptera, Ephemeroptera, Hemiptera, and Neuroptera [25, 35-40].

To better understand the ecosystem services provided by insectivorous bats, we investigated the habitat preference and diet of common noctule bats in an intensively managed agricultural landscape in Central Europe. Specifically, we studied the seasonal and inter-annual variation in their diet in general and their consumption of pests. We expected the intensively managed farmland to be depleted of flying insects, as has been observed in similar landscapes [e.g. 41]. Accordingly, we predicted that bats would avoid arable land and prefer near-natural habitats such as water bodies or wetlands. We expected that the insect species composition would reflect their preference for near-natural areas, therefore predicting that the majority of the insect species would be from the near-natural habitats rather than the cultivated areas. In our study, we explore the adaptability of common noctules to agricultural landscapes and their ecological importance, but also the limitations and challenges for bats and their ecosystem services when exposed to areas with intensive agricultural practices.

Results

Habitat preferences of common noctule bats

Foraging area of the local population of common noctule bats averaged 12 ± 4.7 km^2 (median of kernel density estimator (KDE) with 95% confidence interval (CI) ± median absolute deviation) per seasons, ranging from 6.7 km^2 to 16.0 km^2, but did not differ between spring and summer (Wilcoxon rank test, $p = 0.2$). On average, foraging area overlapped between seasons by 71 ± 17% (min 39%, max 98%) for 95% KDE.

Tracked noctule bats ($n = 128$) mainly used arable land for foraging (mean of the population across all seasons: 55% of the total area within the minimum convex polygon of the population), followed by water bodies (14%), settlements (14%), grassland (10%) and forest (7%) (Fig 4B, seasonal details in Table S1). Arable land was most dominant in the activity rang of the bats (95.8%), followed by grassland under agricultural use (2.8%) including pastures, meadows and other permanent grasslands. In addition, settlements (0.50%), forests (0.49%) and water bodies (e.g. lakes, ponds, streams and wetlands) (0.47%) were also available within the populations activity range (Fig. 1A).

Looking at habitat selection by analysing used foraging habitats against available habitats with setting their roost habitat “forest” as reference, bats preferred foraging over aquatic habitats most (Fig. 2). Although noctule bats spent most of their foraging on arable land, the most dominate landscape category, they showed a negative selection towards this habitat category in all but one season (spring 2020; Fig. S1). Bats were attracted by grassland and showed a neutral response to settlements (Fig. 2; for seasonal and annual variation see Fig. S1 and Table S2).

Diet of common noctule bats

We identified 315 unique insect species belonging to 12 insect orders in the diet of noctule bats (Fig. S2, overview in Table S3, full list with taxa and seasonal information in Table S4). On average, we found 11 insect species per sample (min = 1, max = 44), with a total of 268 samples analysed. Diptera, Coleoptera, Lepidoptera and Hemiptera contributed with the highest species number (species richness) and detections (presence/absence counts across all samples) (Fig. S2, Table S3). Species richness ($q = 1$, rarfaction) of insects was higher in summer than spring (Fig. S3A). Despite the large number of samples, the plateau of the rarefaction curves were only reached for Shannon and for Simpson diversity, but not for species richness (Fig. S3A).

The ten most detected insect species (in descending order) were *Glyptotendipes tokunagai, Melolontha melolontha, Tipula paludosa, Cloeon dipterum, Dicranomyia modesta, Tanypus punctipennis, Symplecta hybrid, Chironomus plumosus, Amphimallon solstitiale* and *Chrysoperla carnea*, mostly insects from aquatic habitats, except *A. solstitiale, M. melolontha* and *Tipula paludosa* living on agricultural fields or grasslandand *Chrysoperla carnea* occurring in multiple habitats.

Species-level prey composition varied significantly between seasons and years (Fig. 3), with strong interannual variation in the diet of bats (Table 2). To a smaller extent, methodological factors (e.g., primer choice, sample type) is shaping insect community composition outputs, as for example we additionally used the primer 16S in year 2022 and 2023 only (Table 2). However, a substantial proportion of the variation in insect composition remains unexplained by the included factors.

Linking foraging and insect habitats

Most prey insects detected in faecal samples of common noctule bats live in aquatic habitats, forest or grassland (Figure 4C). In contrast, the bat population used arable land most frequently for foraging (Fig. 4B).

Pest insect species in the diet of common noctule bats

Seventy-one of the 315 insect taxa consumed were pest insects, representing 23% of the total taxa identified. Pests were categorised into three types depending on their field of economically damage or nuisance with disease transmission potential: agricultural (28 species) and silvicultural (22 species) pest insects in addition to nuisance insects (21 species) (Fig. S3B). Presence of pest insects in faecal samples was higher in summer (mean = 1.3 ± 1.6, min = 0, max = 6) than in spring (mean = 0.7 ± 1.1, min = 0, max = 5) (Wilcoxon rank sum test, $p < 0.005$) and further highest in the first study year (see rarefaction curve, Fig. S4). We detected significantly more agricultural pests than silvicultural pests or nuisance insects, on average 1.96, 0.32 and 0.97 pests per sample accordingly (Kruskal-Wallis rank sum test $\chi^2 = 157$, $p < 0.005$; post-hoc pairwise Wilcoxon rank sum test, all $p < 0.005$; Fig. 5). In addition, 54% of the total number of insects found living on arable land are considered as pests (Fig. 4D). Out of the ten most frequent detected insects, the larvae of common cockchafer (*Melolontha melolontha*), European crane fly (*Tipula paludosa*) and summer chafer (*Amphimallon solstitiale*) are agricultural pest species.

Discussion

Ecosystem services provided by predators, such as those mediated by aerial-hawking bats and birds feeding on pest insects, contribute to sustainable crop production worldwide, and e.g. was quantified as saving annually 570 to 730 USD/ha on plantations or over 1 billion USD globally on corn crops [12-14, 42]. Despite the indisputable contributions of these ecosystem services of bats, they remain widely underappreciated, with exception to organic farming practices [43]. Beyond the provision of roosting structures [44], little guidance exists on maintaining and enhancing the ecosystem services provided by bats. To address this gap in intensively farmed areas, we investigated the habitat preference and diet of a European insectivorous bat using high-throughput tracking and genetic sequencing. We chose the common noctule bat as our study species because of its habit of foraging above arable land [32, 45, 46] and its known predation on pest insects [25, 35].

In line with our expectation, common noctules showed opportunistic feeding behaviour, foraging mainly in arable land. This is consistent with previous studies describing noctule bats as open-space foragers that are able to exploit intensively managed landscapes [31, 47, 48]. Although common noctule bats avoided arable land in all but the first season compared to its availability, they still foraged mostly on arable land due to its dominance in the landscape, and therefore provided important services for agricultural pest control. Similar findings are reported from England [46]. Nevertheless, bats preferred aquatic habitats and showed a positive association with agricultural grassland. This result suggests that although arable land provides foraging opportunities, the structurally poor landscape may lead to low insect richness and abundance [6, 41, 49-51].

Despite the limited availability of water bodies (<0.5% within the population activity range), common noctule bats foraged around 14% over aquatic habitats, highlighting their preference and the importance as high quality foraging sites, as reported in previous studies [39, 47, 52]. Aquatic ecosystems likely support a high abundance of nutrient-rich insects, especially dipterans; particularly non-biting midges (Chironomidae), mosquitoes (Culicidae) and Limoniidae, the largest crane fly family, represented a major prey in the diet of common noctules. The observed seasonal and annual consistency in the size of the populations foraging activity range (12km²) suggests that habitat resources in the study area were sufficient to meet energetic demands across seasons, despite the high level of agricultural management and therefore expected low levels of insect abundances as known from Dietzer, Keicher [41]. Overlap between seasonal activity ranges (71% on average) further indicates a consistent habitat use by the local population of common noctule bats, possibly linked to the predictability of resources at foraging sites like water bodies. This finding contrasts with studies on other bat species that suggest seasonal changes in the foraging behaviour and habitat use [e. g. 53].

Our metabarcoding analysis revealed a diverse diet for common noctule bats. We detected 315 prey insect species from 12 orders. This diversity aligns with previous findings that noctule bats exhibit a generalist feeding strategy and facilitates their persistence in human-dominated landscapes, including highly urbanised areas [25, 34]. Diptera, Coleoptera, Lepidoptera, and Hemiptera were the most prevalent insect orders, going in line with previous metabarcoding studies on noctule bats [25, 35, 38]. Others studies found mainly sclerotic remains of Trichoptera and Coleoptera in faecal pellets of common noctules [36, 39], however visual inspection of bat pellets might yield data that underestimate the proportion of small insects, such as small Diptera. The dominance of prey associated with aquatic habitats, mainly dipterans such as non-biting midges of the genus *Glyptotendipes* and *Chironomus,* but also aquatic coleopterans such as the genus *Enochrus* is consistent with our tracking data suggesting that common noctules favour aquatic habitats for foraging.

The significant increase in insect species diversity and swarming probability during summer may indicate a seasonal peak in prey availability, as reported by previous studies [5, 10, 54]. Notably, prey composition varied across seasons and years, similar to observation from noctule bats [37] and other European bat species [55]. The high interannual variation suggests that seasonal patterns are not consistent across years, emphasising the complexity of ecological dynamics in insect communities. In particular, insect numbers in lakes highly fluctuate [54]. Irrespective of the annual variation in prey composition, common noctules fed consistently on pest insects. In particular, 71 out of 315 identified taxa consumed by common noctule bats were either agricultural and silvicultural pest insects or nuisance insects, such as mosquitoes. Agricultural pests, such as common cockchafer (*Melolontha melolontha*), European crane fly (*Tipula paludosa*) and summer chafer (*Amphimallon solstitiale*) were particularly frequent. These findings provide strong evidence for the role of common noctule bats as natural pest regulators, which is consistent with findings from other aerial-hawking bats in Europe and North America [13, 56, 57] and Asia [58]. The higher number of detected pest insects in summer goes in line with findings from other bat species [24]. This pattern might be best explained by the higher biomass production in summer [54], and the specific life-histories of these insects which often start with a soil or ground-based herbivorous larvae in spring and a high abundance of flying imago in summer. As aerial-hawking insectivores, common noctules prey exclusively on the airborne imago, which is also the reproductively active life stage. Therefore, noctule bats interfere with the imago's ability to reproduce and disperse from which a new generation of herbivorous larvae can hatch. As a result, insectivorous bats can limit crop damage from insect pests in the following season, which is particularly beneficial if the larvae live in the soil and damage the roots, e.g. *Melolontha melolontha* and *Amphimallon solstitiale*. The feeding of nuisance insects also contributes to the ecosystem services of bats since mosquitoes and biting midges are transmitter of diseases for humans, e.g. West Nile Virus, and livestock, e.g. bluetongue disease [59]. The observed interannual variation in pest insect consumption, with the highest detections in 2020 and the lowest in 2023, may be caused by fluctuations in pest insect populations driven by environmental or climatic factors [5, 60], or by inter-annual variation in the application of insecticides. Such temporal variability highlights the need for long-term monitoring to better understand the dynamics of bat-mediated pest suppression.

Linking foraging habitat preference and avoidance from high temporal resolution movement data to detailed dietary information on noctule bats collected during the spring and summer seasons over three study years has been an important contribution to combining study approaches and shows how even small proportions of aquatic habitats in intensive cultivated areas are important to bats. To our knowledge, Stidsholt, Scholz [34] is the only other study linking movement and diet information, it their case prey size and feeding success but no taxonomic details. Most previous studies either focused on the movement of bats [e.g. 31] or analysed prey composition without information on the movements [e.g. 25]. While our combination of state-of-the-art methods allows robust conclusions about habitat preferences and prey selection, we acknowledge limitations. For example, in insect diversity, primer bias and the reference database are known to alter the outcome of metabarcoding studies [61]. To reduce this bias, we followed a dual primer approach, targeting the classical COI region, which is commonly used as a brought amplifier, in addition the 16S region, which is more stable and showed satisfying results for insect taxa [61, 62]. While metabarcoding technique provides detailed data on prey diversity, it does not quantify the biomass of consumed prey [63], which limits our ability to assess the amount of insects consumed. Instead, we assumed that patterns from similar field sites would be comparable to our site [e.g. 41]. Capturing the spatial and temporal dynamics of flying insects above agricultural land is particular challenging in the context of our study since common noctule bats forage at altitudes ranging between 20 m to several hundred meters above ground [32, 33]. Given the logistical and technical challenges of quantifying arthropod diversity and abundance across this range of altitudes, we refrained from exploring comparisons between insect taxa consumed and insect taxa available.

Conclusion

Our study provides important insights into the habitat selection and diet of common noctule bats in an intensively managed agricultural landscape. By combining high-resolution tracking data with prey identification via metabarcoding, we revealed a consistent preference of this bat species for aquatic habitats as feeding grounds across seasons and years. Irrespective of the fact that bats avoided arable land as foraging ground compared to its availability in most seasons, they spend 55% foraging above arable land. In total, nearly a quarter of the consumed insects were pest insects, the majority of which represented agricultural pests. For insects living on arable land, this proportions more than doubles and over 54% of insects detected are considered pests compared to non-pest living on arable land. Our study demonstrates that common noctule bats are able to adapt to a landscape that is heavily altered by humans for crop production. We argue that populations of common noctule bats may only be resilient to intensive agricultural practices if near-natural areas adjacent to farmland provide foraging hotspots for bats to meet their energetic requirements. Even though common noctule bats are highly mobile and take advantage of group hunting [64], they may only survive in agricultural landscapes that include near-natural areas or structurally rich farmland [2]. In the case of common noctule bats, and most likely other bat species, water bodies are critical resource habitats in an otherwise resource-poor landscape. Protection of these key habitats is therefore essential to maintain the ecosystem services provided by noctule bats. These findings have important implications for bat conservation and sustainable agricultural management, emphasising the need to maintain habitat heterogeneity to support bat populations and their associated services.

Methods

Study area

We conducted our study in the northeast of Germany (53°23'29.7"N 13°46'17.2"E, Fig. 1A). Here, the landscape is characterised by large areas of arable land (>95%) and some patches of grassland (3%), interspersed with numerous small water bodies, known as kettle holes, which are post-glacial depressions that fill with water temporarily or permanently. The landscape includes also small woodlands, lakes and settlements (<0.5% each).

Tracking movements of bats

To study bat movements, we used custom-made radio transmitters programmed to record spatial positions at 8 s intervals (transmitter mass 1.1 to 1.4 g, equivalent to < 5% body mass) using the ATLAS system (Tel Aviv University, Tel Aviv, Israel). ATLAS is a remote access automated radio telemetry system that can collect very high frequency and automated telemetry data, using the time difference of signal arrival at a known antenna position to calculate the position of the tag [further details see 65]. Our system operated with 11 to 13 stationary antennas covering an area of approximately 80 km², including the roosting and main foraging habitats known from previous studies [31]. Signals from bats leaving the area became noisy or disappeared until the bats re-entered the covered area.

In 2020, 2022 and 2023, we tagged 128 common noctule bats, mostly adult females (Table 1). We conducted our study in spring (May) and summer (July/August). In each season, we tagged 16 to 31 individuals from the same colony in a small forest patch each with a transmitter. The bats were accessed during the morning hours by checking artificial bat roosts, called bat boxes. All bats were removed from their boxes and returned to the same box after all bats had been handled (approximately 2 hours). Tags were attached with medical skin adhesive (Sauer Hautkleber, Manfred Sauer GmbH) to the fur below the interscapular region of the bats. Handling took approximately 15 min per bat, after which the animal was individually placed in a bag until all bats had been processed. Tags remained until they fell off after approximately one week (mean tracking duration 7 days, min = 1 day, max = 24 days). The work was carried out under the Animal Welfare Licences 2347-6-2020 and 2347-16-2022-14-G and the Nature Conservation Licenses 4732/132+11#40472/2020 and 4730/22+18#164717/2022.

Table 1 Number of common noctule bats tagged per season and date of tracking period. Date and duration represents the maximum runtime of tags in a given season.

Year	Season	Number of tagged bats	Date	Duration in days
2020	Spring	18	10.05.2020 - 23.05.2020	14
	Summer	18	23.07.2020 - 06.08.2020	15
2022	Spring	19	15.05.2022 - 01.06.2022	18
	Summer	26	20.07.2022 - 12.08.2022	24
2023	Spring	16	13.05.2023 - 27.05.2023	15
	Summer	31	22.07.2023 - 08.08.2023	18

Collection of faecal samples

We collected 268 faecal samples over 76 sampling days, 36 samples from individual bats during the tagging process and 232 mixed samples from collection plates placed under the bat boxes during the corresponding tracking period, resulting in multiple samples where multiple boxes were used. Samples were collected in the early hours of the morning to avoid contamination and minimise DNA degradation. Fresh pellets were transferred with a pair of tweezers to 5 to 50 ml plastic tubes filled one-third with desiccated silica beads and stored at -20°C until processed in the laboratory.

Processing of samples

DNA extraction, amplification of marker gene sequences, and sequencing

DNA was extracted from 268 individual samples using the NucleoSpin DNA Stool Mini Kit (Macherey-Nagel GmbH & KG, Düren, Germany) according to the manufacturer's protocol using up to 220 µl dissolved or 180-220 ng dry sample. Sample size varied from a single pellet to multiple pellets completely filling the 50ml tubes. In most cases, when sample amount was large enough, we extracted an original and a biological replicate and later reunited in the analysis to increase robustness. Samples were dissolved in PBS buffered solution or nucleoase-free water and homogenised using a Unidrive X 1000D disperser or ceramic beads in the Precellys® 24 at 6,000 x g, 2 × 15 s duration and 10 s pause. Quantification of DNA reads was verified using a Qubit 2.0 Fluorometer (Thermo Fisher Scientific Inc., USA). If necessary, extracted DNA was purified using Zymo-Kit (Zymo Research, 17062 Murphy Ave, Irvine, USA) to remove PCR inhibitors. To control for contamination, the DNA extraction and PCR procedure was regularly checked with negative and positive controls in all steps. After each PCR, the concentration of PCR products was checked using agarose gel images. After indexing, each product was measured by fluorometric quantification (Quant-iT™ dsDNA Assay Kit, high sensitivity, ThermoFisher Scientific, Walham, USA) in a Tecan plate reader (infinite M200, Tecan, Switzerland), and samples were spiked or diluted before pooling to meet the required standards of the BeGenDiv, a consortium high-throughput sequencing facility in Berlin (Königin-Luise-Straße 6-8, 14195 Berlin, Germany). Prior to pooling, two cleaning steps were performed using magnetic beads (CleanNGS, GC biotech, Waddinxveen, The Netherlands). To increase the robustness of the data and availability of detection, we amplified two target regions, COI (cytochrome oxidase subunit I, ~133bp), which is known for its high resolution and common bat diet [62], and 16S (~155bp), a more stable region and therefore useful for identifying insects to species level [66]. DNA was identified from pooled samples at the BeGenDiv, with the CO1 and 16S regions placed in separate cartons to avoid compromising quality due to differences in product length.

Taxonomic assignment

Sequencing reads were filtered and assigned in R Studio [R version 4.2.0; 67] using the 'dada2' package [68]. After a quality check, sequencing reads (forward and reverse) were trimmed at 180 bp and primers were removed. An error model was developed and de-replicated reads were filtered before applying a core sequence variant inference algorithm. Dereplicated forward and reverse paired reads were merged if they overlapped exactly. In the next step, chimeras were removed. Where possible, taxonomy was assigned to the inferred amplified sequence variants (ASVs) down to the species level using the reference library for COI by Heller et al. [69] and a custom library for 16S created in-house [see 25 for details]. Taxonomic level assignment was based on the single best hit or last common ancestor (in the case of multiple best hits), with 50 out of 100 bootstrap replicates as the minimum bootstrap confidence.

For post-sequencing cleaning steps, we compared the number of reads to blank samples (negative controls) and afterwards to technical replicates for each ASV within the sample to remove contaminations during lab procedures using the R package “microDecon” [70] and created a presence-absence matrix for further analysis.

Data analysis

We used RStudio [R Version 4.3.0; 67] for all data filtering steps, statistical analysis, visualizations and tables of results. If not reported otherwise, visualisations were created in R package “ggplot2” [71] and tables in R package “gt” [72].

Tracking data

After visual inspection, movement data from six bats with malfunctioning tags were excluded from the analysis due to poor quality or missing flight paths. We deleted locations recorded during daylight hours (between sunrise and 1 h before sunset), removed low accuracy estimates of spatial position (>40 m), unrealistically fast speeds (>20 m/s), excluded the forest patch of the roost and a 200 m buffer, and split data into individual trips when missing locations for >5 min to obtain individual flight paths. To filter for foraging behaviour, we classified movement into three behavioural states using revisits analysed with the R package “recurse” [73], firstly separating between area-restricted searching (revisits >2) and commuting (revisits <=2), secondly separating foraging and resting behaviour by residence time (<30 min and >=30 min) per trip. Commuting and resting behaviour was excluded, and all further analysis was based on foraging data only.

Activity range and overlap per season were calculated on population level in the R package “amt” [74] using the 95% Kernel Density Utilisation (KDE) estimate. We tested for seasonal and annual variation via Kruskal-Wallis rank sum test and post-hoc pairwise Wilcoxon rank sum test. To analyse habitat composition of habitats available to the bats, we created a minimum convex polygon (MCP) of the whole population in R package “amt” [74] and extracted landscape types based on CORINE land cover 2018 [CLC; GeoBasis-DE / 75] using R package “sf” [76]. We simplified the CLC categories from 16 to five habitat categories (arable land, grassland, forest, settlements and water bodies) by grouping different forest types to forest and different urban structures or degree of intensity to settlements. Due to the low proportion of wetlands in the study area, they were combined with other water bodies such as lakes, streams and ponds in the category ‘water bodies’. Habitats used for foraging were extracted separately per year and season at population level and visualised as percentages.

We used a binomial generalised mixed model to analyse habitat selection, the attraction and avoidance response to the habitats available, by comparing land use of foraging locations with random points within the 100% MCP. Because the tracked bats roost in forests and emerge from forest into their nightly flight trips, the intercept was set to this land use category. Results were plotted using coefficient models in package “ggstats” [77].

Metabarcoding data

We collected 268 faecal samples, after blank correction we removed 19 empty samples. From the remaining 249 samples, we identified 345 insects to species level. Species were checked using Google searches, GBIF.org [78] and Red List Centre [79] to determine pest status, larval and imago habitat, range and conservation status. A total of 315 insects were retained for further analysis after removing 30 taxa with distributions outside Europe where misidentification at the genus level was likely.

Habitat of imagines was classified into the same five simple habitat categories used for movement analysis (arable land, grassland, forest, settlements and water bodies), with the addition of the category 'multiple' for generalists. For larval habitat, the categories 'parasitic' and 'soil' were added. Insects were marked as pests if they were known to cause economic or ecological damage, or as non-pest insects with potentially submitting diseases; we categorised pest insects into "agricultural", "silvicultural" and "nuisance".

We used the species richness of the insects detected in the faeces samples of common noctule bats to assess prey diversity in both seasons and across years. We estimated species richness, Shannon diversity and Simpson diversity [80] in a rarefaction analysis using the R package iNEXT [81] to identify richness and diversity of the bats food spectrum and for completeness of sample collection. We tested for seasonal and annual variation of pest insects in the diet of common noctule bats and the variation of pest type via Kruskal-Wallis rank sum test and post-hoc pairwise Wilcoxon rank sum test. To test diet composition variation at the species level across dates, we computed a dissimilarity matrix with Nonmetric Multidimensional Scaling (NMDS) using package “vegan”[82].

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Data availability

Data will be made accessible upon request once the article has been accepted for publication.

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Authors contributions

CCV and MK designed the study; CCV and FJ acquired the funding, CCV, FJ and CS advised students; MK, TB, CS, MR and JP collected data in the field; MK and CS contributed to the metabarcoding analyses in the laboratory and performed subsequent analysis; MK analysed the movement data; RN, ST and JP operated the tracking system; MK and CCV lead the writing of the manuscript; all authors edited the manuscript and made valuable scientific contributions throughout the writing process.

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Figures and tables

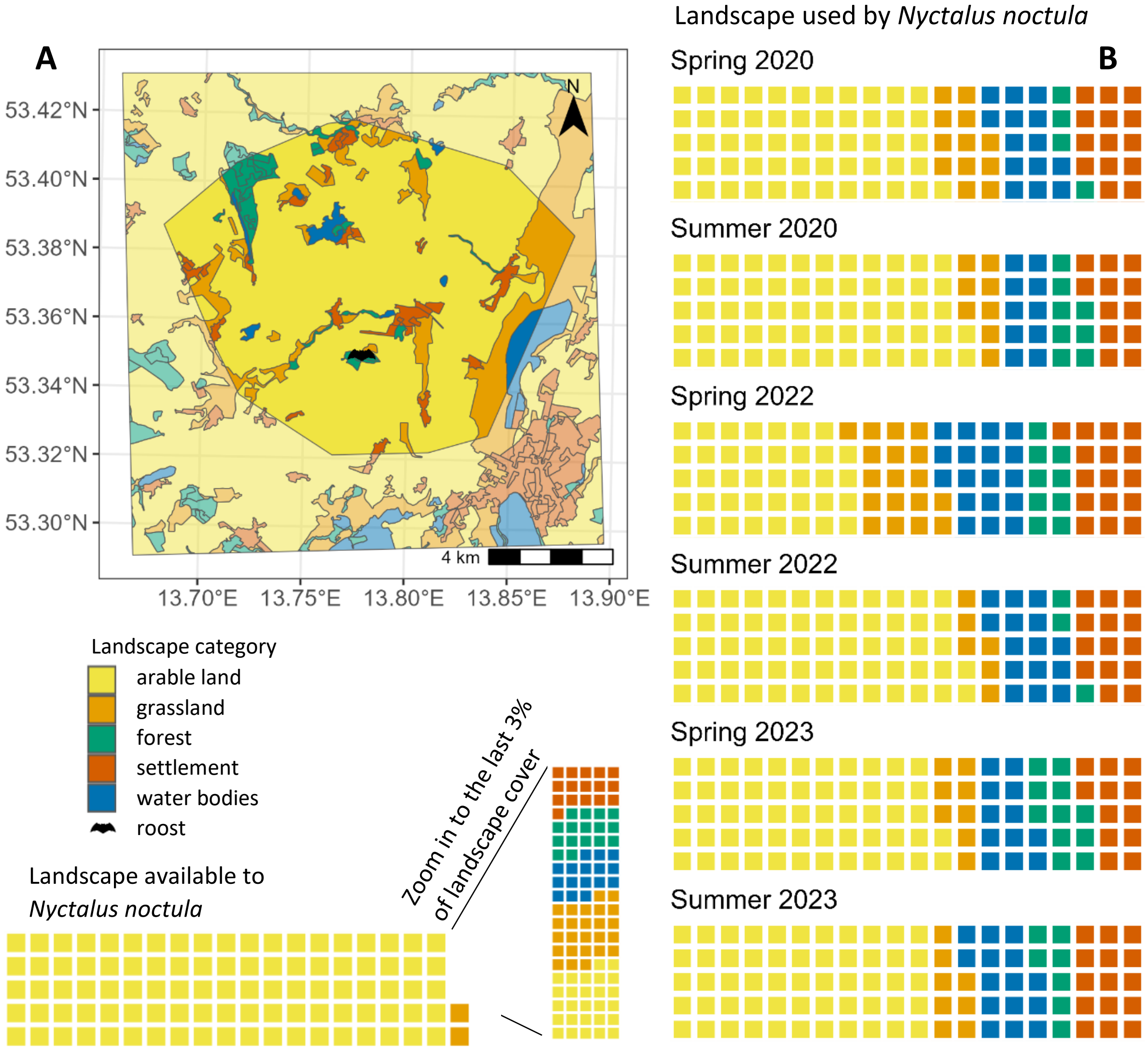

Figure 1 Habitat composition of landscape available within the 100% minimum convex polygon of the bat population (black lined polygon) showing over 95% arable land as most available habitat **(A)** and seasonal foraging activity of noctule bats with increased proportions of used landscape categories compares to availability for all but arable land (percentage of localisation points of foraging) **(B).** Data based on CORINE land cover 2018 with customized simplified categories. The silhouette of the bat shows the main roosting location (location of tag application).

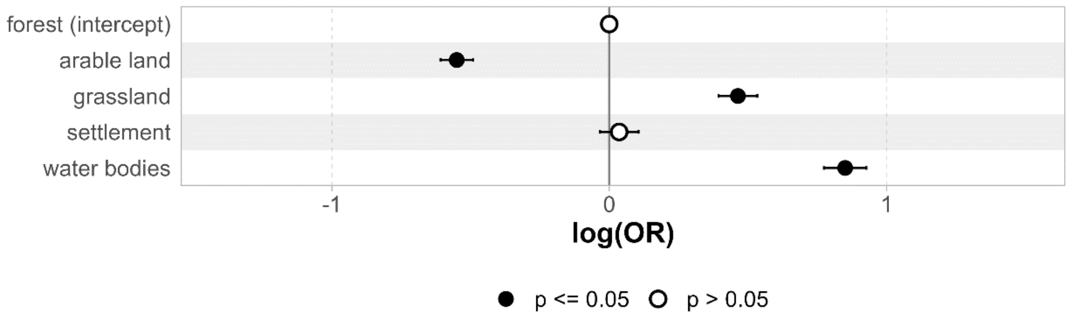

Figure 2 Model coefficients as odd ratio (OR) of habitat selection model across all seasons and years with forest as reference habitat (vertical line) on logarithmic scale. Common noctule bats significantly preferred water bodies while showing avoidance towards arable land. Filled dots represent significant, unfilled dots non-significant results. Horizontal lines show confidence interval.

Table 2 Permutational Multivariate Analysis of Variance using Jaccard dissimilarity matrix of presence/absence data of insect species per sample. Each term explains variation after accounting for the terms before it.

Term	Degree of freedom	Sum of squares	R^2	F-value	p-value
season (spring | summer)	1	4.49	0.06	13.86	0.001
year (2020 | 2022 | 2023)	2	8.80	0.11	13.57	0.001
primer (COI | 16S)	2	2.07	0.03	3.19	0.001
sample type (individual | roost)	1	2.33	0.03	7.18	0.001
day of the year	1	1.48	0.02	4.57	0.001
season:year	2	4.40	0.05	6.79	0.001
Residual	178	57.71	0.71	–	–
Total	187	81.28	1.00	–	–

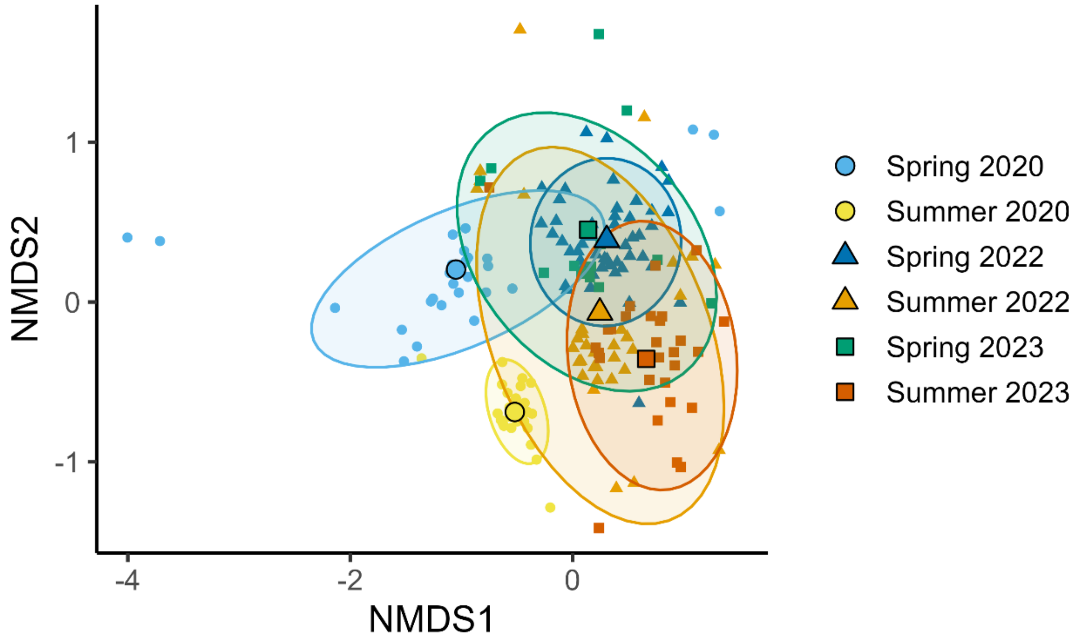

Figure 3 Non-Metric Multidimensional Scaling (NMDS) Analysis based on Jaccard dissimilarity matrix of presence-absence data of insect species per sample highlighting seasonal and interannual variation of prey detected in faecal samples of common noctule bats.

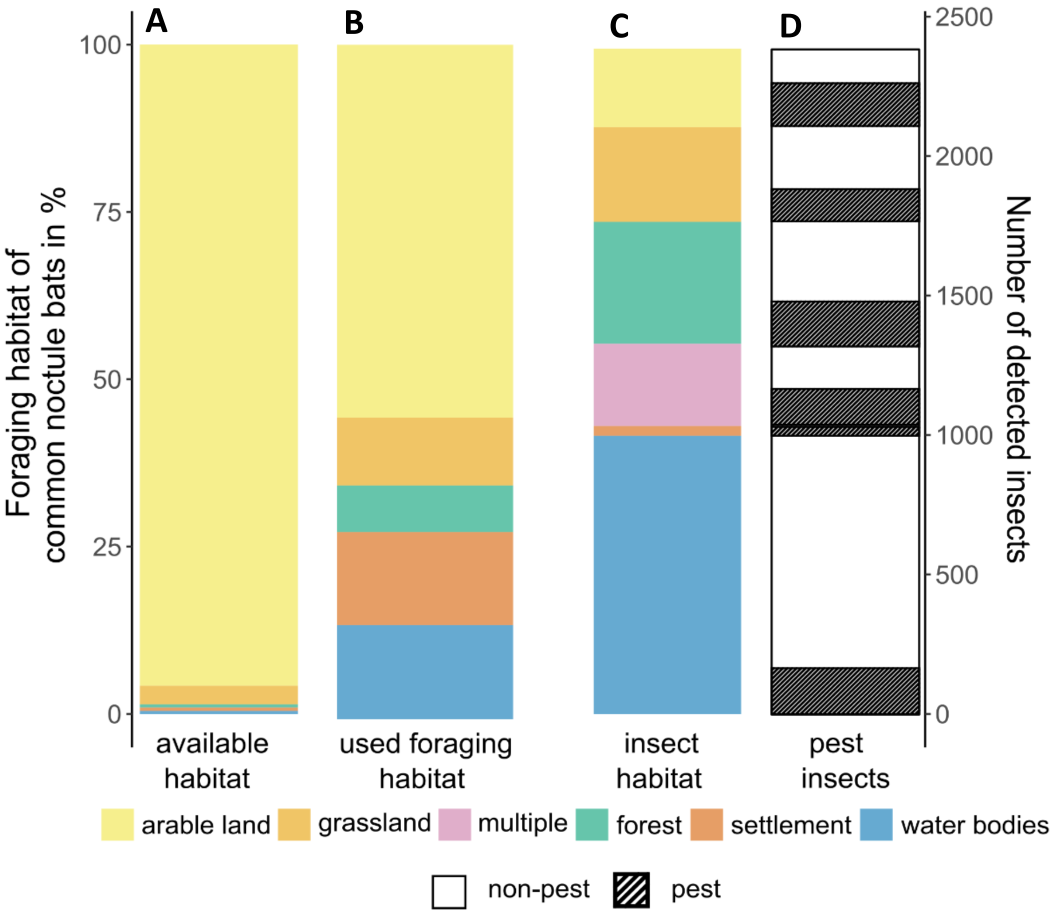

Figure 4 The two columns on the left side show the habitat proportion available within the populations 100% MCP **(A)** and habitat proportion used for foraging (mean across season and year) **(B)** by the common noctules populations in percentage. Common noctule bats forage less over arable land compared to the availability while preferring habitats such as water bodies. The right columns show the number of detected insects per habitat **(C)** and number of pest verses non-pest insects per habitat **(D)**. While bats used arable land most frequently for foraging, most prey insects detected in their faecal samples live in aquatic habitats. Highest proportion of pest insects were detected in insects living in arable land.

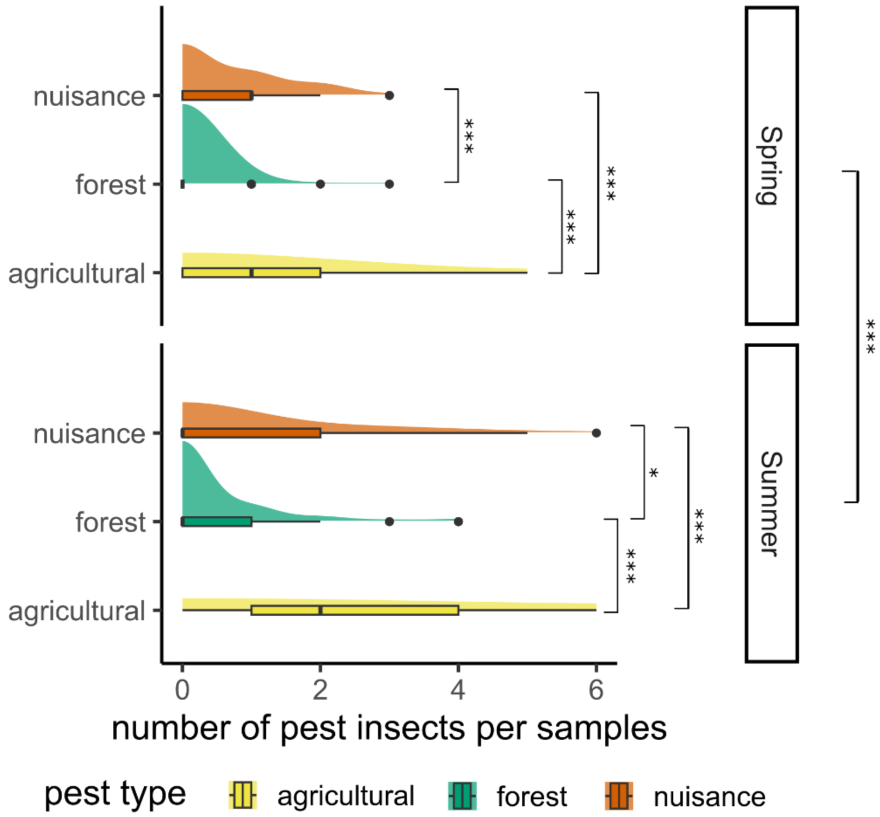

Figure 5 Number of pest insects detected in common noctule bats diet with significant differences between spring and summer season (Wilcoxon rank sum test, p < 0.01) and significant differences between all pest types (pairwise Wilcoxon rank sum test, significance codes: '***' <0.001, '**' <0.01, '*' <0.05).

Supplement

Table S1:

Habitat composition of available land cover within the 100% minimum convex polygon of the bat population and the proportion of used habitats per season. All values in %.

category	available	spring 2020	summer 2020	spring 2022	summer 2022	spring 2023	summer 2023
arable land	95.78	55.77	61.98	39.26	61.88	57.48	55.34
grassland	2.76	12.26	7.92	18.21	5.63	8.41	8.01
forest	0.49	3.72	8.08	8.48	3.35	10.95	6.80
settlement	0.50	14.10	12.34	15.61	14.23	11.79	14.59
water bodies	0.47	14.15	9.69	18.45	14.91	11.38	15.26

Table S2:

Results of generalised linear model analysis of habitat selection in relation to forest (intercept) with significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Term	**Estimate**	**Standard Error**	**Statistic**	**P-value**	
Spring 2020					
forest (Intercept)	-14.054	0.061	-228.788	0.000	***
arable land	0.146	0.064	2.281	0.023	*
grassland	1.075	0.073	14.731	0.000	***
settlement	0.085	0.079	1.077	0.281	
water bodies	0.817	0.095	8.618	0.000	***
Summer 2020					
forest (Intercept)	-13.410	0.063	-213.303	0.000	***
arable land	-0.612	0.066	-9.246	0.000	***
grassland	0.299	0.080	3.757	0.000	***
settlement	-0.115	0.083	-1.393	0.164	
water bodies	1.111	0.095	11.639	0.000	***
Spring 2022					
forest (Intercept)	-13.390	0.079	-169.378	0.000	***
arable land	-0.961	0.086	-11.127	0.000	***
grassland	0.315	0.095	3.306	0.001	***
settlement	0.287	0.095	3.023	0.003	**
water bodies	0.874	0.104	8.445	0.000	***
Summer 2022					
forest (Intercept)	-13.816	0.095	-144.899	0.000	***
arable land	-0.247	0.098	-2.516	0.012	*
grassland	0.699	0.115	6.086	0.000	***
settlement	0.448	0.109	4.114	0.000	***
water bodies	1.279	0.109	11.736	0.000	***
Spring 2023					
forest (Intercept)	-13.116	0.080	-163.818	0.000	***
arable land	-0.928	0.089	-10.436	0.000	***
grassland	-0.054	0.123	-0.441	0.659	
settlement	-0.784	0.121	-6.459	0.000	***
water bodies	0.035	0.131	0.267	0.790	
Summer 2023					
forest (Intercept)	-12.960	0.057	-228.916	0.000	***
arable land	-1.255	0.061	-20.522	0.000	***
grassland	-0.027	0.078	-0.342	0.732	
settlement	-0.128	0.070	-1.820	0.069	.
water bodies	0.521	0.080	6.533	0.000	***

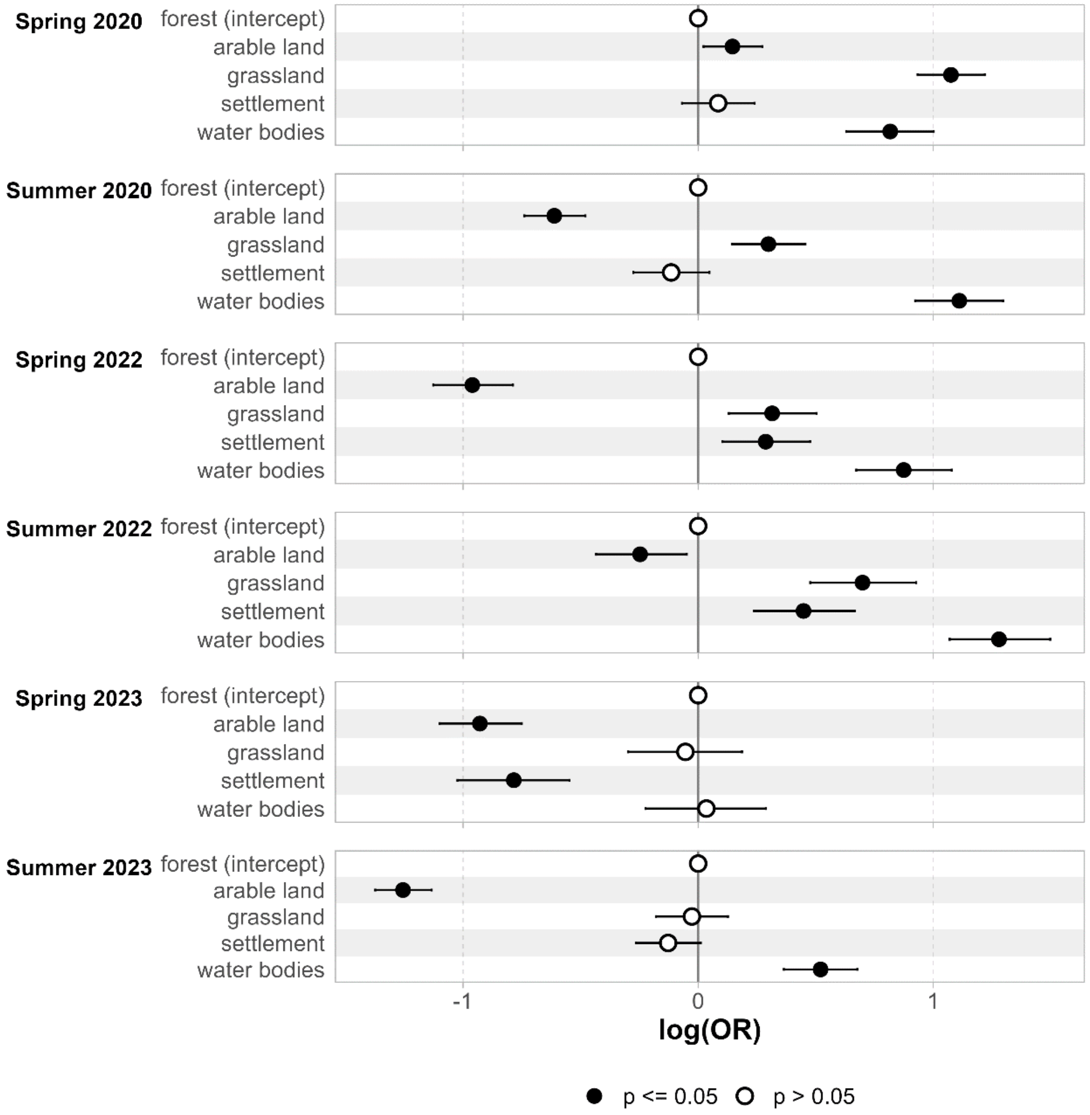

Figure S1

Model coefficients as odd ratio (OR) of habitat selection model per season with forest as reference habitat (vertical line) on logarithmic scale. Common noctule bats significantly preferred water bodies most seasons while showing avoidance towards arable land in all but the first spring season. Filled dots represent significant, unfilled dots non-significant results. Horizontal lines show confidence interval.

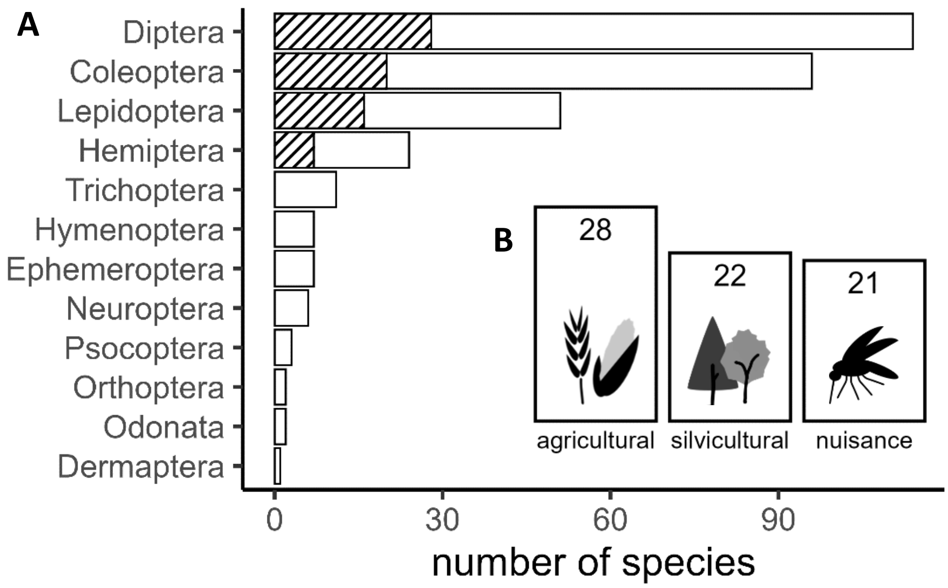

Figure S2

Number of unique insect species per order detected in common noctule faeces collected over three study years **(A)**. Stripped pattern represents the number of unique pest species, which are known to cause economical damage or potentially transmit diseases. Number of pest species per pest type **(B).**

Table S3:

Number of detected insects in 268 faecal pellets on order level.

Order	**Total**	**Number of families**	**Number of species**
Coleoptera	644	22	96
Dermaptera	2	1	1
Diptera	1085	33	114
Ephemeroptera	107	4	7
Hemiptera	140	10	24
Hymenoptera	24	2	7
Lepidoptera	130	19	51
Neuroptera	56	2	6
Odonata	2	2	2
Orthoptera	7	1	2
Psocoptera	4	3	3
Trichoptera	85	4	11

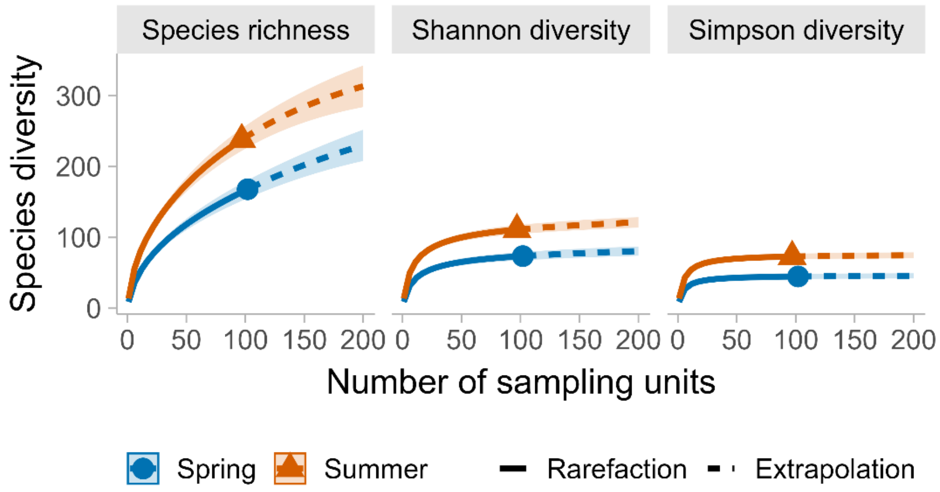

Figure S3

Species diversity

Sample-based rarefaction (solid line) and extrapolation (dotted line) curve with 95% confidence intervals (shaded areas) with species diversity per number of samples of common noctule faeces collected over three years. Samples collected in spring (blue) or summer (orange). Plots shown separately by diversity order, hill numbers: q = 0 species richness, q = 1 Shannon diversity, q = 2 Simpsons diversity. Dots (spring) and triangles (summer) represent reference samples.

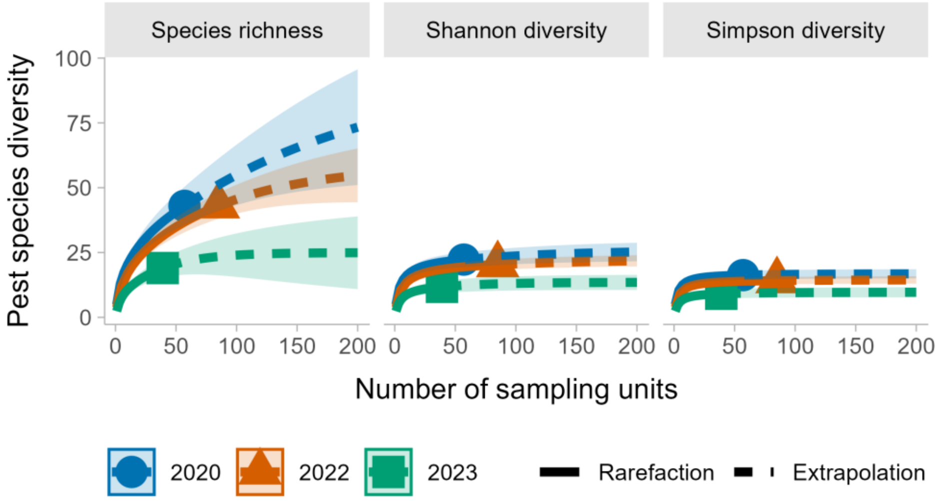

Figure S4

Pest species diversity

Sample-based rarefaction (solid line) and extrapolation (dotted line) curve with 95% confidence intervals (shaded areas) with species diversity per number of samples of common noctule faeces collected over three years. Samples collected in 2020 (blue), 2022 (orange) or 2023 (green). Plots shown separately by diversity order, hill numbers: q = 0 species richness, q = 1 Shannon diversity, q = 2 Simpsons diversity. Dots (2020), triangles (2022) and square (2023) represent reference samples.

Table S4:

Taxon detection in faecal pellets on species level. The frequency refers to the number of times a species was detected in all samples or the number of times it was detected in each sampling season. Only taxa with a resolution to species level were included in the analysis.

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
Coleoptera								
Anobiidae	*Dryophilus pusillus*	1	1	0	0	0	0	0
	Priobium carpini	1	0	0	0	1	0	0
Brachyceridae	*Dorytomus longimanus*	1	1	0	0	0	0	0
	Notaris scirpi	2	0	0	0	2	0	0
Cantharidae	*Cantharis decipiens*	1	1	0	0	0	0	0
Carabidae	*Acupalpus parvulus*	1	0	0	0	1	0	0
	Amara apricaria	23	0	0	0	17	6	0
	Amara aulica	12	0	0	0	9	2	1
	Amara bifrons	18	0	0	0	17	1	0
	Amara consularis	17	0	0	0	14	3	0
	Amara majuscula	5	0	0	0	5	0	0
	Blethisa multipunctata	1	0	0	0	0	1	0
	Bradycellus verbasci	2	0	0	0	1	1	0
	Calathus ambiguus	6	0	0	0	6	0	0
	Calathus cinctus	8	0	0	0	8	0	0
	Calathus fuscipes	1	0	0	0	1	0	0
	Calathus melanocephalus	6	0	0	0	0	6	0
	Carabus nemoralis	1	1	0	0	0	0	0
	Dolichus halensis	18	0	0	0	0	15	3
	Dromius quadrimaculatus	1	0	0	0	1	0	0
	Harpalus froelichii	13	0	0	0	8	5	0
	Harpalus griseus	10	0	0	0	10	0	0
	Harpalus herbivagus	19	0	0	0	0	15	4
	Harpalus rufipes	24	0	0	0	20	2	2
	Harpalus smaragdinus	1	0	0	0	0	1	0
	Lesticus magnus	1	0	0	1	0	0	0
	Loricera pilicornis	1	0	0	0	0	1	0
	Ophonus ardosiacus	2	0	0	0	0	2	0
	Ophonus puncticeps	14	0	0	0	14	0	0
	Ophonus rufibarbis	1	0	0	0	1	0	0
	Stenolophus mixtus	4	0	0	0	4	0	0
	Trechus quadristriatus	13	1	0	0	3	8	1
	Zabrus tenebrioides	1	1	0	0	0	0	0
Cerambycidae	*Arhopalus rusticus*	7	1	0	0	3	1	2

Family	**Species**	**Total**	**Spring 2020**	**Spring 2022**	**Spring 2023**	**Summer 2020**	**Summer 2022**	**Summer 2023**
	Cortodera humeralis	1	0	1	0	0	0	0
	Exocentrus punctipennis	1	0	0	0	1	0	0
	Prionus coriarius	2	2	0	0	0	0	0
	Spondylis buprestoides	19	5	0	0	3	8	3
Cleridae	*Opilo mollis*	1	0	0	1	0	0	0
Coccinellidae	*Harmonia axyridis*	21	0	1	0	5	10	5
	Harmonia quadripunctata	2	0	0	0	0	1	1
Curculionidae	*Brachyderes incanus*	5	0	0	0	0	5	0
	Ceutorhynchus pallidactylus	2	0	0	0	0	2	0
	Curculio elephas	1	0	0	0	0	1	0
	Curculio glandium	21	0	0	0	19	2	0
	Curculio venosus	1	0	0	0	1	0	0
	Gasterocercus depressirostris	5	0	0	0	0	3	2
	Hylobius abietis	2	1	1	0	0	0	0
	Phyllobius argentatus	1	1	0	0	0	0	0
	Pityophthorus pubescens	1	0	1	0	0	0	0
	Polygraphus poligraphus	1	0	0	0	1	0	0
	Strophosoma capitatum	7	1	0	0	0	6	0
Dermestidae	*Ctesias serra*	1	0	1	0	0	0	0
Dytiscidae	*Colymbetes fuscus*	2	0	0	0	0	2	0
	Colymbetes striatus	1	0	0	0	1	0	0
	Copelatus aruensis	1	0	0	0	0	0	1
	Cybister lateralimarginalis	1	0	0	0	1	0	0
	Dytiscus dimidiatus	3	0	0	0	0	1	2
	Graphoderus austriacus	2	0	2	0	0	0	0
	Hygrotus impressopunctatus	4	0	1	0	0	3	0
	Rhantus frontalis	2	0	0	0	1	1	0
	Rhantus suturalis	5	0	3	0	0	2	0
Elateridae	*Agriotes stabilis*	3	0	3	0	0	0	0
	Ampedus sinuatus	1	0	1	0	0	0	0
	Athous haemorrhoidalis	1	0	1	0	0	0	0
	Athous subfuscus	3	0	2	0	0	1	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
	Athous vittatus	1	0	1	0	0	0	0
	Dalopius marginatus	1	0	1	0	0	0	0
	Denticollis linearis	7	0	7	0	0	0	0
	Melanotus villosus	6	0	6	0	0	0	0
	Stenagostus rhombeus	47	0	0	0	19	24	4
Heteroceridae	*Heterocerus fenestratus*	1	0	0	0	1	0	0
Histeridae	*Carcinops pumilio*	1	0	1	0	0	0	0
Hydrophilidae	*Enochrus bicolor*	29	0	1	5	2	16	5
	Enochrus melanocephalus	1	0	0	0	1	0	0
	Enochrus quadripunctatus	7	0	3	1	0	3	0
	Enochrus testaceus	14	0	2	2	1	7	2
	Helochares obscurus	1	0	0	0	0	1	0
	Hydrobius fuscipes	19	0	1	2	0	14	2
	Hydrophilus acuminatus	2	0	2	0	0	0	0
Latridiidae	*Enicmus brevicornis*	1	0	0	0	1	0	0
Lucanidae	*Dorcus parallelipipedus*	1	0	1	0	0	0	0
Melyridae	*Hypebaeus flavipes*	1	0	0	0	1	0	0
Mycetophagidae	*Litargus connexus*	1	0	0	0	1	0	0
Ptinidae	*Ptinus rufipes*	4	0	4	0	0	0	0
Scarabaeidae	*Amphimallon solstitiale*	51	3	0	0	15	18	15
	Aphodius rufipes	2	0	0	0	2	0	0
	Maladera holosericea	1	0	1	0	0	0	0
	Melolontha hippocastani	1	0	0	0	0	1	0
	Melolontha melolontha	63	17	19	13	0	12	2
	Serica brunnea	11	0	0	0	1	5	5
Staphylinidae	*Bisnius subuliformis*	3	2	0	0	0	0	1
	Lathrobium brunnipes	1	0	1	0	0	0	0
	Philonthus quisquiliarius	1	0	0	0	1	0	0
Tenebrionidae	*Gonodera luperus*	2	2	0	0	0	0	0
	Tenebrio molitor	2	0	0	0	0	2	0
Dermaptera								
Forficulidae	*Forficula auricularia*	2	0	0	0	0	2	0
Diptera								

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
Anisopodidae	*Sylvicola fenestralis*	3	0	2	0	0	0	1
	Sylvicola punctatus	23	0	20	2	0	1	0
Anthomyiidae	*Botanophila fugax*	2	0	0	0	2	0	0
	Delia platura	37	0	8	3	7	8	11
	Delia radicum	1	1	0	0	0	0	0
	Emmesomyia grisea	1	0	1	0	0	0	0
	Paregle audacula	1	0	0	0	0	0	1
	Zaphne divisa	5	0	2	0	1	0	2
Asilidae	*Neoitamus cyanurus*	1	0	0	0	0	0	1
Bibionidae	*Bibio marci*	1	0	1	0	0	0	0
Calliphoridae	*Pollenia pediculata*	2	1	0	0	1	0	0
Ceratopogonidae	*Forcipomyia tenuis*	1	0	1	0	0	0	0
Chironomidae	*Chironomus dilutus*	12	9	1	0	2	0	0
	Chironomus melanescens	2	0	0	0	2	0	0
	Chironomus plumosus	44	20	0	0	24	0	0
	Chironomus riparius	11	0	6	2	0	3	0
	Chironomus tepperi	85	0	36	9	0	21	19
	Cryptochironomus supplicans	1	0	1	0	0	0	0
	Einfeldia dissidens	5	0	0	0	0	5	0
	Endochironomus nigricans	20	4	0	0	16	0	0
	Glyptotendipes tokunagai	71	0	25	9	0	19	18
	Macropelopia notata	1	1	0	0	0	0	0
	Micropsectra atrofasciata	1	1	0	0	0	0	0
	Micropsectra contracta	1	0	1	0	0	0	0
	Polypedilum nubifer	1	0	1	0	0	0	0
	Prodiamesa olivacea	1	0	1	0	0	0	0
	Tanypus punctipennis	48	1	23	6	1	14	3
Clusiidae	*Clusiodes ruficollis*	1	0	1	0	0	0	0
Culicidae	*Aedes cinereus*	2	0	0	0	2	0	0
	Aedes esoensis	1	0	1	0	0	0	0
	Aedes vexans	24	0	0	0	24	0	0
	Anopheles atroparvus	2	0	1	0	0	1	0
	Anopheles claviger	3	2	0	0	1	0	0
	Anopheles maculipennis	2	0	0	0	2	0	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
	Anopheles messeae	1	0	0	0	1	0	0
	Anopheles sacharovi	36	0	26	0	0	8	2
	Coquillettidia richiardii	1	0	0	0	1	0	0
	Culex modestus	1	0	0	0	1	0	0
	Culex quinquefasciatus	30	0	2	0	25	2	1
	Culex tritaeniorhynchus	7	0	7	0	0	0	0
	Culiseta annulata	29	3	0	0	26	0	0
	Culiseta morsitans	6	2	0	0	4	0	0
	Ochlerotatus annulipes	9	9	0	0	0	0	0
	Ochlerotatus excrucians	26	3	20	0	2	0	1
	Ochlerotatus flavescens	12	2	8	1	0	1	0
	Ochlerotatus scapularis	45	0	40	5	0	0	0
Dolichopodidae	*Dolichopus bigeniculatus*	3	0	0	0	2	1	0
	Dolichopus latilimbatus	10	0	2	0	0	6	2
	Dolichopus nitidus	1	0	0	0	0	1	0
	Dolichopus nubilus	1	0	0	0	0	1	0
	Dolichopus plumipes	11	1	5	0	0	4	1
	Neurigona quadrifasciata	4	0	4	0	0	0	0
Drosophilidae	*Drosophila funebris*	3	0	0	0	0	0	3
	Drosophila subobscura	1	0	1	0	0	0	0
	Scaptomyza flava	1	0	0	0	1	0	0
	Scaptomyza pallida	3	0	0	0	3	0	0
Empididae	*Hilara maura*	3	0	3	0	0	0	0
Ephydridae	*Ephydra packardi*	1	0	0	0	0	1	0
	Hydrellia modesta	1	0	0	0	0	1	0
Heleomyzidae	*Suillia bicolor*	2	0	2	0	0	0	0
Lauxaniidae	*Calliopum aeneum*	4	0	1	0	0	2	1
	Calliopum simillimum	1	0	0	0	0	1	0
	Pseudolyciella pallidiventris	21	0	1	0	0	15	5
Limoniidae	*Dicranomyia danica*	2	0	0	0	1	1	0
	Dicranomyia modesta	50	0	24	0	0	17	9
	Epiphragma mediale	9	0	7	1	0	1	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
	Pseudolimnophila brunneinota	3	0	0	0	0	1	2
	Rhipidia chenwenyoungi	8	0	8	0	0	0	0
	Rhipidia maculata	1	1	0	0	0	0	0
	Symplecta hybrida	47	0	17	0	8	18	4
Muscidae	*Gymnodia humilis*	1	0	0	0	0	0	1
	Hebecnema nigra	2	0	0	0	2	0	0
	Helina depuncta	2	0	0	0	2	0	0
	Helina evecta	1	0	0	0	1	0	0
	Helina impuncta	8	0	7	0	0	0	1
	Hydrotaea ignava	2	0	1	0	0	1	0
	Potamia littoralis	27	0	5	0	8	8	6
Mycetophilidae	*Allodia pyxidiiformis*	1	0	1	0	0	0	0
	Exechia frigida	1	0	0	0	0	0	1
	Exechia fusca	4	0	4	0	0	0	0
	Mycetophila alea	1	0	1	0	0	0	0
	Mycomya trivittata	1	0	1	0	0	0	0
	Phronia strenua	1	0	1	0	0	0	0
	Platurocypta testata	1	0	0	0	0	0	1
Opomyzidae	*Opomyza florum*	3	0	0	0	0	3	0
Pediciidae	*Pedicia albivitta*	4	0	4	0	0	0	0
Polleniidae	*Pollenia rudis*	1	0	0	0	0	1	0
Psychodidae	*Psychomora mycophila*	1	0	0	0	0	1	0
Sarcophagidae	*Sarcophaga sexpunctata*	7	0	0	0	7	0	0
Scathophagidae	*Scathophaga stercoraria*	33	0	24	2	2	2	3
	Scathophaga taeniopa	3	0	3	0	0	0	0
Sciaridae	*Schwenckfeldina carbonaria*	1	0	1	0	0	0	0
Sciomyzidae	*Anticheta analis*	1	0	0	0	0	1	0
	Anticheta melanosoma	1	0	0	0	0	0	1
	Pherbellia argyra	1	0	0	0	0	1	0
	Pherbellia dorsata	2	0	0	1	0	1	0
	Pherbina coryleti	2	0	0	0	0	2	0
	Sciomyza simplex	3	0	1	0	0	2	0
Syrphidae	*Episyrphus balteatus*	1	0	1	0	0	0	0
	Melanostoma scalare	1	0	1	0	0	0	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
	Merodon equestris	1	0	0	0	0	1	0
Tabanidae	*Haematopota subcylindrica*	7	0	5	1	0	1	0
Tachinidae	*Blondelia nigripes*	1	0	1	0	0	0	0
	Pales pavida	1	0	0	0	0	0	1
Tephritidae	*Campiglossa bidentis*	1	0	0	0	0	1	0
Therevidae	*Dialineura lyneborgi*	1	0	1	0	0	0	0
Tipulidae	*Nephrotoma quadrifaria*	19	0	18	0	0	1	0
	Nephrotoma tenuipes	1	0	1	0	0	0	0
	Nigrotipula nigra	2	0	0	0	0	2	0
	Tipula flavolineata	1	0	1	0	0	0	0
	Tipula oleracea	30	16	7	2	0	5	0
	Tipula paludosa	54	0	37	7	0	1	9
Ulidiidae	*Ceroxys urticae*	36	0	0	0	25	8	3
	Melieria omissa	1	0	0	0	0	1	0
Ephemeroptera								
Baetidae	*Baetis canariensis*	1	0	0	0	0	1	0
	Cloeon dipterum	50	1	18	1	25	3	2
Caenidae	*Caenis horaria*	35	0	16	5	0	10	4
	Caenis robusta	1	0	1	0	0	0	0
Ephemeridae	*Ephemera danica*	13	0	11	1	0	0	1
	Ephemera vulgata	1	0	1	0	0	0	0
Heptageniidae	*Heptagenia sulphurea*	6	0	6	0	0	0	0
Hemiptera								
Acanthosomatidae	*Elasmostethus interstinctus*	11	0	8	2	0	1	0
	Elasmucha grisea	4	0	0	0	0	4	0
Alydidae	*Leptocorisa chinensis*	1	0	1	0	0	0	0
Aphididae	*Rhopalosiphum padi*	8	1	4	1	0	2	0
	Sitobion avenae	3	0	1	1	0	1	0
	Symydobius kabae	4	0	4	0	0	0	0
Cicadellidae	*Idiocerus stigmaticalis*	3	0	0	0	3	0	0
Cimicidae	*Cimex pipistrelli*	5	0	1	0	0	3	1
Corixidae	*Corixa dentipes*	4	0	0	0	0	4	0
	Corixa punctata	1	0	0	0	1	0	0
	Glaenocorisa propinqua	19	0	1	0	0	12	6
Lygaeidae	*Kleidocerys resedae*	11	0	4	4	1	2	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
Miridae	*Adelphocoris lineolatus*	1	0	0	0	0	1	0
	Lygus pratensis	39	0	3	0	0	22	14
	Phytocoris intricatus	2	0	0	0	0	2	0
	Phytocoris pini	1	1	0	0	0	0	0
	Phytocoris tiliae	1	0	0	0	1	0	0
	Plagiognathus laricicola	1	0	1	0	0	0	0
	Stenodema calcarata	2	0	0	0	1	1	0
	Stenodema rubrinerve	2	0	0	0	0	2	0
Nabidae	*Nabis ferus*	11	0	0	0	1	9	1
Pentatomidae	*Aelia acuminata*	2	0	1	0	0	1	0
	Holcostethus vernalis	1	0	0	0	0	0	1
	Piezodorus lituratus	3	0	0	0	3	0	0
Hymenoptera								
Formicidae	*Cephalotes eduarduli*	8	0	3	3	0	1	1
	Lasius fuliginosus	6	1	0	0	5	0	0
	Lasius grandis	3	0	2	0	0	1	0
	Myrmica ruginodis	4	0	0	0	1	2	1
Ichneumonidae	*Meloboris collector*	1	0	0	0	1	0	0
	Ophion luteus	1	0	1	0	0	0	0
	Promethes sulcator	1	0	0	0	1	0	0
Lepidoptera								
Batrachedridae	*Batrachedra praeangusta*	1	0	0	0	1	0	0
Blastobasidae	*Blastobasis glandulella*	1	0	0	0	1	0	0
Cosmopterigidae	*Limnaecia phragmitella*	1	0	0	0	1	0	0
Crambidae	*Acentria ephemerella*	2	0	0	0	0	2	0
	Agriphila straminella	3	0	0	0	3	0	0
	Cataclysta lemnata	3	0	0	0	0	3	0
Elachistidae	*Elachista argentella*	1	0	1	0	0	0	0
Erebidae	*Phragmatobia fuliginosa*	1	0	0	0	0	1	0
Gelechiidae	*Bryotropha terrella*	16	0	0	0	15	1	0
	Caryocolum fischerella	1	0	0	0	1	0	0
	Dichomeris alacella	1	0	0	0	1	0	0
Geometridae	*Chlorissa obliterata*	1	0	1	0	0	0	0
	Eupithecia abbreviata	1	0	1	0	0	0	0

Family	**Species**	**Total**	**Spring 2020**	**Spring 2022**	**Spring 2023**	**Summer 2020**	**Summer 2022**	**Summer 2023**
	Macaria notata	2	0	2	0	0	0	0
	Omiza lycoraria	3	0	1	0	0	2	0
	Perizoma alchemillatum	1	0	0	0	0	0	1
	Thera britannica	1	0	1	0	0	0	0
Gracillariidae	*Cameraria ohridella*	1	0	0	0	1	0	0
	Phyllonorycter klemannella	1	0	0	0	1	0	0
	Phyllonorycter quercifoliella	1	0	0	0	1	0	0
Lasiocampidae	*Dendrolimus pini*	3	2	0	0	1	0	0
	Dendrolimus superans	4	0	0	2	0	1	1
Momphidae	*Mompha epilobiella*	1	0	0	0	1	0	0
Noctuidae	*Abrostola triplasia*	1	0	1	0	0	0	0
	Agrotis puta	3	0	2	1	0	0	0
	Agrotis segetum	3	1	1	0	0	1	0
	Apamea monoglypha	1	1	0	0	0	0	0
	Mesapamea secalis	1	0	0	0	0	1	0
	Mythimna albipuncta	4	0	0	0	3	1	0
	Mythimna impura	2	0	0	0	0	2	0
	Oligia strigilis	1	1	0	0	0	0	0
Notodontidae	*Notodonta ziczac*	3	0	0	1	0	2	0
	Pheosia rimosa	1	0	1	0	0	0	0
Oecophoridae	*Harpella forficella*	2	0	0	0	2	0	0
Plutellidae	*Plutella xylostella*	26	0	0	0	26	0	0
Pyralidae	*Aphomia zelleri*	1	0	0	0	1	0	0
	Endotricha flammealis	9	0	0	0	9	0	0
	Hypsopygia costalis	1	0	0	0	1	0	0
	Pyralis farinalis	1	0	0	0	0	1	0
Sphingidae	*Laothoe populi*	1	0	0	0	0	1	0
	Mimas tiliae	1	0	1	0	0	0	0
	Sphinx morio	1	0	0	0	0	1	0
Tortricidae	*Agapeta hamana*	1	0	0	0	1	0	0
	Cochylis posterana	1	0	0	0	1	0	0
	Cydia fagiglandana	3	0	0	0	3	0	0
	Cydia strobilella	1	0	0	1	0	0	0
	Gypsonoma aceriana	4	0	0	0	4	0	0
	Notocelia uddmanniana	3	0	0	0	0	3	0

Family	Species	Total	Spring 2020	Spring 2022	Spring 2023	Summer 2020	Summer 2022	Summer 2023
	Rhyacionia pinicolana	1	0	0	0	1	0	0
	Spilonota laricana	1	0	0	0	1	0	0
Yponomeutidae	*Cedestis subfasciella*	1	1	0	0	0	0	0
Neuroptera								
Chrysopidae	*Chrysoperla carnea*	41	0	15	2	0	16	8
	Chrysoperla lucasina	1	0	1	0	0	0	0
Hemerobiidae	*Drepanepteryx phalaenoides*	3	0	1	0	0	2	0
	Hemerobius stigma	5	0	2	1	0	0	2
	Micromus angulatus	2	0	0	0	1	1	0
	Wesmaelius subnebulosus	4	0	3	0	0	0	1
Odonata								
Aeshnidae	*Anax parthenope*	1	0	1	0	0	0	0
Coenagrionidae	*Enallagma cyathigerum*	1	0	0	0	0	1	0
Orthoptera								
Tettigoniidae	*Euconocephalus pallidus*	6	0	5	0	0	1	0
	Nipponomeconema sinica	1	0	0	0	0	0	1
Psocoptera								
Ectopsocidae	*Ectopsocus meridionalis*	2	0	0	0	1	1	0
Lachesillidae	*Lachesilla pedicularia*	1	0	0	0	1	0	0
Peripsocidae	*Peripsocus subfasciatus*	1	0	0	0	1	0	0
Trichoptera								
Hydropsychidae	*Hydropsyche pellucidula*	14	4	4	0	6	0	0
	Hydropsyche siltalai	5	0	3	0	1	1	0
Leptoceridae	*Leptocerus tineiformis*	5	0	0	0	4	1	0
	Oecetis lacustris	1	0	0	0	1	0	0
	Oecetis ochracea	8	5	0	0	3	0	0
	Triaenodes bicolor	2	0	0	0	2	0	0
Limnephilidae	*Limnephilus flavicornis*	33	2	28	0	1	2	0
	Limnephilus germanus	1	0	0	0	0	1	0
Phryganeidae	*Agrypnia deflata*	4	0	2	0	0	1	1
	Agrypnia pagetana	10	0	7	0	2	1	0
	Phryganea grandis	2	0	0	0	2	0	0