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A home for the many? Beaver lodges as hotspots for bird and mammal diversity

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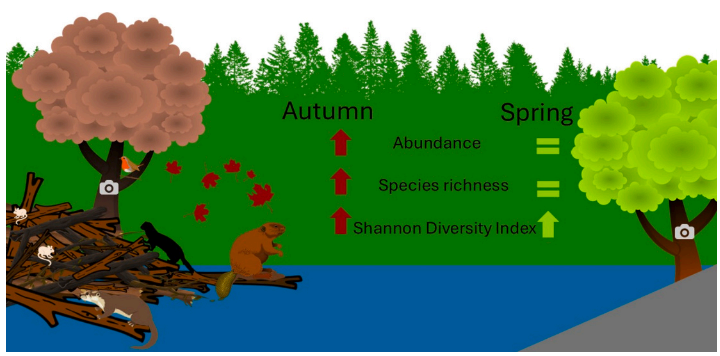
HIGHLIGHTS

- Ecosystem engineers play a crucial role in maintaining and enhancing diversity.
- Higher species abundance, richness and diversity were found at beaver lodges in autumn.
- Beaver lodges were hotspots for six species/genus, i.e. two birds and four mammals.
- Beavers create resources such as food, shelter and warm microclimates on the lodge exterior.
- Beaver lodges are diversity hotspots and show the role of beavers as an ecosystem engineer.

GRAPHICAL ABSTRACT



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ABSTRACT

Diversity loss is a growing global concern. Keystone species and ecosystem engineers play a crucial role in maintaining and enhancing diversity. The Eurasian beaver (*Castor fiber*) is one such species, impacting the landscape through activities such as felling trees, digging tunnels, building dams, and constructing lodges. Numerous studies have shown that beavers increase diversity especially related to their dams. However, the relationship between beaver lodges and diversity is rarely studied. Therefore, we have mapped the diversity of birds and mammals at active beaver lodges in south-eastern Norway. The study was carried out in three large rivers without beaver dams. We installed wildlife cameras at 18 active beaver lodges in the autumn and 17 in the spring, matched with an equal number of paired control sites across the river. Beaver lodges had higher abundance, species richness and Shannon Diversity Index of animals (birds and mammals) than control sites in autumn, but the differences were less pronounced in spring. We found that six species were especially attracted to the beaver lodges. Our results support the concept of beaver lodges as local diversity hotspots for animals particularly in autumn, most likely due to the availability of resources such as food, shelter and warm microclimates on the lodge. Our findings also illustrate the role of beavers as ecosystem engineers beyond the impacts of dam construction. This knowledge may help to increase the diversity of both birds and mammals in habitats across the northern hemisphere.

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1. Introduction

Terrestrial- and freshwater diversity is being reduced on a rapid scale across the globe (Di Marco et al., 2019; Spiller et al., 2025). Invasive species, overexploitation, pollution, climate change, habitat loss and degradation of ecosystems there leads to diversity loss including extinction of species (Bellard et al., 2022; Bradford and Warren, 2014). Fortunately, there are species that can counteract some of these human-induced negative effects, known as keystone species (Mills et al., 1993). Keystone species are pivotal organisms with a disproportionately large impact on their ecosystems relative to their abundance (Mishra, 2024). Keystone species have a significant ability to regulate populations and maintain diversity and are therefore crucial for the structure and stability of an ecosystem (Kau et al., 2025). An example, from the aquatic ecosystem, is the sea otter (*Enhydra lutris*) who maintain kelp forest by preying on sea urchins and thus reduce the intensity of herbivory (Konar, 2000). Some keystone species are ecosystem engineers that shape the biotic or abiotic material in their habitat, creating access to resources and habitats for other species (Wright et al., 2002). Muskrats (*Ondatra zibethicus*) are semiaquatic ecosystem engineers that construct houses and feeding/resting platforms, i.e. natural island habitats in wetlands that are used by many different birds and mammals (Kiviat, 1978; Mittman et al., 2023). It is important to understand how keystone species and ecosystem engineers impact diversity through their activity and presence (Sanders and Frago, 2024).

The Eurasian beaver (*Castor fiber*) and the North American beaver (*C. canadensis*) are territorial keystone species and ecosystem engineers that significantly impacts the landscapes they inhabit and the animals living there (Rosell et al., 2005; Rosell and Campbell-Palmer, 2022; Stringer and Gaywood, 2016). They live in monogamous pairs (Rosell and Campbell-Palmer, 2022) that are part of family groups of 2–12 individuals (Mayer et al., 2020). Beavers may drastically alter the surrounding landscape by damming water bodies, building lodges, digging tunnels, and felling trees (Rosell and Campbell-Palmer, 2022). Felling of trees create heterogeneity in the landscape by increasing the amount of deadwood and gaps in the tree canopies (Donkor and Fryxell, 1999). The beaver diet and behaviour shape freshwater habitats and can contribute to increased diversity in the areas by altering the interactions in food webs through indirect and direct effects on the ecosystem (Wright et al., 2002). Where beavers build dams, the water level rises, often altering and flooding the local area upstream of the dam, creating wetlands and retaining water during both floods and drought (Pollock et al., 2003). This allows animals such as aquatic invertebrates (Grudzinski et al., 2022; Mazza et al., 2024; Nummi et al., 2021; Washko et al., 2022), terrestrial invertebrates (Washko et al., 2022), amphibians (Feldman et al., 2023; Wilson and Bremner-Harrison, 2024), reptiles (see review by Wilsson (1971)), fish (see review by Rosell and Campbell-Palmer (2022) and Wilson and Bremner-Harrison (2024)), birds (Fedyń et al., 2023, 2024) and mammals (Fedyń et al., 2022; Hooker et al., 2024; Nummi et al., 2019; Wikar et al., 2024) to thrive there. Most research into the impacts of beavers have focused on beaver dams and their effect on hydrology, carbon storage and diversity (Rosell and Campbell-Palmer, 2022). However, dams are not the only construction that beavers contributes, as they also construct lodges in the interface between land and water (Rosell and Campbell-Palmer, 2022).

Beaver lodges are constructed from debarked sticks and logs that the beavers pile up, as well as mud and stones. The entrance is submerged and protects beavers from predators, but tunnels may be dug out and extending far onto land (Wilsson, 1971). Beavers often construct several of these lodges within a territory but mostly occupy one main lodge, especially during autumn to spring (Rosell and Campbell-Palmer, 2022). As central-place foragers, the lodge can be defined as their central place in which they transport some food resources that are eaten inside or close to the lodge (Fryxell and Doucet, 1991; Hood and Bayley, 2008; Rosell and Campbell-Palmer, 2022). During late autumn at northern latitudes, beavers may also construct a food cache outside the lodge to give access to food around the lodge (Busher et al., 2020). These beaver lodges are a significant feature along waterways, but the effect of lodges on species diversity has received limited research attention (Wilson and Bremner-Harrison, 2024).

Previous studies of beaver lodges as hotspots for species diversity have used methods such as live trapping of small rodents, or camera traps, which indicated that beaver lodges are used by a wide range of different species (Orazi et al., 2022; Tye et al., 2021; Viviano et al., 2022; Wikar et al., 2024). In their recent review, Wilson and Bremner-Harrison (2024) found that only six (of 35) articles were classified as key articles investigating the impacts of beaver lodges on species diversity but only two of these focused on the Eurasian beavers and sampled only small mammals using lethal snap traps (Samas and Ulevičius, 2015; Ulevičius and Janulaitis, 2007). Wilson and Bremner-Harrison (2024) recommended that future studies should use videographic methodology as a monitoring method, and that there is a clear scope for further projects to investigate the relationship between diversity and Eurasian beaver lodges. After Wilson and Bremner-Harrison (2024) was published, a study on the Eurasian beaver has been conducted in central Italy with camera trap methodology (Viviano et al., 2022). However, neither of the Eurasian beaver studies mentioned above included a proper control area or statistically test whether beaver lodges had higher diversity than surrounding areas, which makes it difficult to conclude whether diversity is higher on lodge locations or if it simply reflects an overall high diversity around the edge of the water.

In this study, we investigated the diversity of birds and mammals at active beaver lodges in large rivers, without beaver dams, using camera traps. We included a relatively large sample of beaver lodges and an equal number of control areas that we monitored across two distinct seasons (autumn and spring). We hypothesized that beaver lodges will influence the abundance, species richness and diversity of species. We predicted a higher number of individual animals (1), species (2) and Shannon Diversity Index (3) at beaver lodges compared to the control areas. In addition, we predicted that certain species will be especially attracted to beaver lodges, while others either avoid or are neutral to beaver lodges. We also controlled the effects of shrub- and canopy cover, river, and season.

2. Material and methods

2.1. Study area and animals

The study was conducted from August 30 to October 24, 2023 (autumn), and from March 11 to May 8 (spring), 2024, in Midt-Telemark and Nome municipalities in Telemark County, southeastern Norway (59°N, 60°W). The study is part of a long-term beaver study that has been ongoing since 1997, carried out by the Norwegian Beaver Project (NBP). NBP focuses primarily on the three rivers Sauer, Gvarvelva in Midt-Telemark municipality, and Straumen in Nome municipality. The width of the rivers varies between 10 and 150 m, and all eventually flow into lake Norsjø (Haarberg and Rosell, 2006; Lodberg-Holm et al., 2022). None of the main rivers have beaver dams, providing a clearer understanding of the lodges as local hotspots for diversity. The rivers traverse various rural landscapes, including agricultural areas and forests with significant human activity such as agriculture, forestry and villages. The rivers are surrounded by vegetation dominated by mixed and deciduous forests, with substantial agricultural influence (Haarberg and Rosell, 2006; Lodberg-Holm et al., 2022). The most common tree species along the rivers are black and grey alder (*Alnus glutinosa*, *A. incana*), birch (*Betula pubescens*), spruce (*Picea abies*), pine (*Pinus sylvestris*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and willow (*Salix* spp.) (Haarberg and Rosell, 2006). In the study area, the average beaver family size is 4.0 ± 1.9 SD individuals. The size of beaver territories averages 3.3 ± 1.5 SD km along the riverbanks but can vary between 1.5 and 6.5 km (Mayer et al., 2020). The beaver predators in the study area includes the species that are common in the rest of southeastern Norway, with red fox (*Vulpes vulpes*), American mink (*Neovison vison*), Eurasian otter (*Lutra lutra*), and lynx (*Lynx lynx*) (other larger predators are not present) (Aulagnier et al., 2025).

The average temperature remained relatively stable at an average of 15.3 °C in August before dropping to around 5.4 °C in October 2023, while in the spring average varied between 2.6 in March to 15.1 °C in May 2024. The measurements were taken at the nearest weather station, Gvarv - Nes Bioforsk, which is relatively central to the study area (Yr, 2025).

2.2. Field work

We monitored 18 active beaver lodges in autumn and 17 during spring, which matched up with an equal number of paired control areas in each of the two study periods. We aimed to monitor the same beaver lodges again during spring, but on one of the lodges the landowner was actively hunting beavers and did not grant us permission to monitor the lodge in spring. In two other cases the active lodge was washed away by flooding and the beavers relocated to a new lodge, which we monitored instead. The beaver lodges are all monitored as part of the NBP, and their locations were therefore known previously. At each active beaver lodge, we selected a control area on the opposite side of the river to compare the diversity in an area without a beaver lodge and other significant beaver activities (i.e., no lodge, dam or trail and only old tree cuttings), i.e. unmodified by beavers. Beavers have been in the rivers since the 1920s (Olstad, 1937) and it was therefore impossible to find a control area without old tree cuttings made by beavers. The control area on the opposite side of the river was part of the same beaver territory as the monitored lodge. We avoided placing the control area in densely vegetated areas to ensure that the camera traps (Browning Spec Ops Advantage model: BTC - 8A (12 units) and Browning Spec Ops Elite HP4 model: BTC - 8E - HP4 (4 units)) could monitor an area of similar size to the beaver lodge. Therefore, the control area was sometimes placed slightly upstream or downstream from the beaver lodge on the opposite riverbank. We recorded a general habitat description, including an estimation of canopy- and shrub cover as percentage of vegetation cover, and noted the habitat type by visual estimation at both the lodges and control locations. Additionally, we recorded the slope of the riverbank as steep, flat or medium.

We conducted a pilot test using five camera traps on the same beaver lodge to determine which angles worked best to capture the most birds and mammals. Results from this pilot test indicated that two cameras per location could cover the area well. Camera 1 was placed at the rear of the beaver lodge and focused on the water covering the length of the lodge. Camera 2 was set up between 0.5 and 9 m besides the lodge and focused along the water's edge and over the lodge. We attached the cameras to trees or stakes with a line of sight over the lodge at a height varying between 0 m - 2.5 m. Monitoring of the control areas was done using the same camera types and set-up as the beaver lodges. These areas lacked a specific focal point, so we selected a more open area to focus on. We placed one camera focusing on the river and one focusing on the area along the water's edge, to mimic the placement at the lodge. Date and time were set on the cameras prior to placement, and they were set to the trail-cam function "photos". Photos were taken at 20 MP quality, with a 1-s photo delay, 24 m motion sensor, fast photo trigger, and economical IR light strength. The cameras were equipped with 8 AA 1.5 V batteries and a SD card of 16 or 32 GB. All cameras within the same territory had the same storage capacity on the SD card and were of the same model. The cameras were placed on the lodges and control areas using a motorboat and were left out for one week in each territory before being recollected. As we captured photos and not videos, we could not determine the behaviour of the animals and make any conclusions on what attracted them to the area, and we only used cameras to record the presence of species.

2.3. Data analysis

The image analysis from the camera traps was done manually by counting the number of individuals in the pictures as well as the data and time of each observation. Every observation of an animal was recorded with a threshold of 30 min before identifying a new observation to avoid multiple observations of the same individual (Tye et al., 2021). Animals that were picked up by both cameras at the same time were recorded as one observation, but if more than one individual was seen at the same time these were recorded as multiple individuals. We did not manage to identify all small mammals (mice, voles and shrews) to the species level, and species like Wood mouse (*Apodemus sylvaticus*) and Yellow-necked mouse (*A. flavicollis*), were therefore pooled into the genus *Apodemus* spp. (Aulagnier et al., 2025). In most cases, we managed to distinguish Bank voles (*Clethrionomys glareolus*) and Grey-sided voles (*Craseomys rufocanus*) but in some cases they were pooled into the group "Bank- or Grey-sided voles" since Red vole (*Clethrionomys rutilus*) is not found at our location (Aulagnier et al., 2025). We also identified Field vole (*Microtus agrestis*) to the species level but shrews only to genus (*Sorex* spp.) (Aulagnier et al., 2025). We identified other blurred images of other small mammals as "Rodentia" without recording the species. All other animals were identified to the species level, while those that could not be identified due to the quality of the photos were excluded from the analysis. We summarized the number of individuals and the number of species in each area during the monitored week. Additionally, we recorded the river, territory, type of area (lodge or control), spatial coordinates, and the location ID of each lodge or control area. For visualization purposes, we assigned the mammals into three groups based on size, i.e. small- medium- and large mammals and birds as a separate category (Table S1).

Our statistical analysis was divided into two parts. First, we investigated which variables influenced the abundance of individual animals, species richness and Shannon Diversity Index using generalized mixed effects models (GLMM), and secondly, we explored the driver of individual species occurrence using Generalized Linear Latent Variable Models (GLLVM). For each type of area, we counted the number of observed individuals of each species (species count), the total number of individuals across all species (abundance), and the number of species (species richness) during each monitoring week within each season. Additionally, we calculated Shannon Diversity Index using the *vegan* package in R for every location in each season (Oksanen et al., 2025). We followed the steps described by Zuur et al. (2010) and Zuur and Ieno (2016) for data exploration including checking all the potential numerical explanatory variables for collinearity using a Pearson correlation matrix with a cut-off of 0.7 and variance inflation factors (VIF) to check collinearity between all the explanatory variables (Harrison et al., 2018; Zuur et al., 2010; Zuur and Ieno, 2016). Habitat type was highly collinear with other habitat characteristics such as canopy- and shrub cover and was therefore dropped from the analysis. We also investigated the relationship between all potential explanatory variables and the response variables and found that slope to be unimportant, and we therefore excluded it from the analysis to reduce the number of explanatory variables. Thus, only canopy cover, shrub cover, season, river and area (lodge/control) were retained. We also explored a potential interaction effect between season and area.

In the first analysis, we fitted GLMM candidate models using the glmmTMB package (Brooks et al., 2017) for each of our three response variables (abundance, species richness and Shannon Diversity Index). We included territory and location ID as nested random effects on the intercept (Harrison et al., 2018). We modelled abundance and species richness using Poisson distribution and modelled Shannon Diversity Index using a Gaussian distribution (Zuur et al., 2010). Due to convergence issues, we only included one random variable (territory) in the models predicting Shannon Diversity Index. For each response variable, we created 14 candidate models with different combinations of the explanatory variables including a null model with only the random variables. We applied Akaike Information Criterion with correction for a small sample size (AICc) (Burnham and Anderson, 2004) using the model.sel function from the MuMIn package (Barton, 2013) to select the top models within a ΔAICc <2. Among these, we selected the most parsimonious (simplest) model to avoid pretending variables with limited statistical importance (Arnold, 2010; Leroux, 2019). Any variables included in the final model in which 95 % confidence overlapped with zero was considered uninformative (Arnold, 2010).

For our second analysis, we explored the importance of our explanatory variables as drivers of the abundance of each species. We used GLLVM models to fit multiple response variables (species counts) and possible dependencies between them. To be able to model individual species and potential underlying latent variables, we only selected those species that were observed at more than five locations, which left us with 22 species. We conducted the same steps of data exploration as described by Zuur and Ieno (2025). We provided starting values for the optimization algorithm using the control.start argument to initialize the model five times using different starting values and introduced some random noise by setting jitter.var to 0.1 to increase the robustness (Zuur and Ieno, 2025). To ensure model convergence, we only used territory as a random variable, and included area, season, canopy and shrub cover as fixed explanatory variables without any interactions. First, we fitted the GLLVM model using Poisson distribution, but after issues with overdispersion, we refitted the models using negative binomial distribution. We created four candidate models that we compared using AICs and the model.sel function from the MuMIn package with different structures in terms of the latent variables. The most supported model was used to visualize the impact of the explanatory variables on the total count of the 22 most observed species.

We checked model fit of all our models containing all explanatory variables by simulating residuals using the R package DHARMa (Hartig et al., 2024). We plotted model residuals against expected and fitted values to observe deviations from the expected distribution and against each explanatory variable to check for non-linear patterns. We also checked the models for issues with overdispersion, zero-inflation, spatial correlation or outliers with a large impact on the results (Zuur and Ieno, 2016). All statistical analyses were conducted in RStudio with R version 4.3.3 (RStudio., 2025).

3. Results

3.1. Diversity of animals

We registered 869 individual observations of animals from the camera traps across all locations. This included 51 species in addition to three mammal groups that could not be identified to the species level (bat, *Apodemus* spp. and Bank- or Grey-sided vole). Additionally, we had 41 observations of small mammals that could not be identified by species or genus. Across all areas, small mammals were the most observed group (41 %), followed by birds (38 %), medium sized mammals (18 %), and finally large mammals (3 %). Mice species *Apodemus* spp. were observed most often, followed by American mink and beavers, which were all most common on beaver lodges (Fig. 1). On the beaver lodges, we identified 40 species and 643 observations of individuals, while the control areas had a total of 39 species and 226 individuals. Beaver lodges and control areas therefore had a very similar number of species, but beaver lodges had almost triple the abundance of animals compared to the control areas. On beaver lodges, small mammals were the most common, followed by birds, medium mammals and very few large mammals (Fig. S1). In total, 11 species were observed on beaver lodges that were never found in the control areas (Table S1). Among these, 19 field voles were observed on six lodges and 19 Grey-sided voles on three lodges, while the rest were never observed >1–2 times (Table S1). Birds were the most common group in the control areas, followed by medium sized animals, small mammals and large mammals (Fig. S1). The control areas had 11 species that were never observed on beaver lodges and the most common was Mute swan (*Cygnus olor*) with 18 observations in one control area, while the rest were rarely observed (Table S1). Beaver lodges had a slightly higher percentage of omnivores and control areas had more herbivores, while the distribution of carnivores and

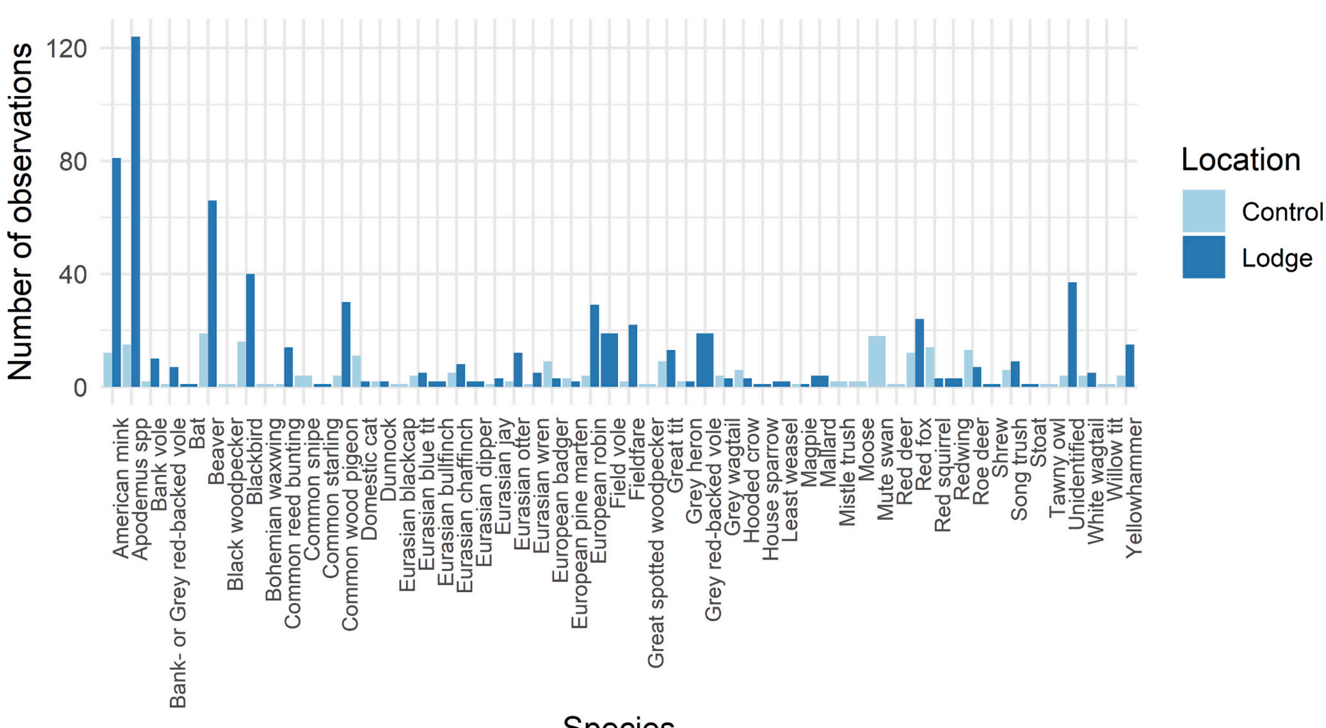

Fig. 1. Total number of observations of different species or species groups across beaver lodges and control areas within the study area in southeastern Norway for spring and autumn combined (2023–2024).

insectivores was more similar across the two areas (Fig. S1). Overall, the beaver lodges had a slightly higher mean Shannon Diversity Index (1.09) compared to the control areas (0.77).

3.2. Circadian activity patterns

We also registered the time of day of all animal observations from the camera traps. The beaver lodges and control areas differed in their circadian patterns of animal observations. On the beaver lodges there were high levels of animal activity during night from 18:00, but overall highest from midnight until 08:00, but also with a slight peak around noon. In the control areas, however, there was much less activity at night, but with some distinct peaks at 07:00, 10:00, 13:00, and 20:00 (Fig. 2).

3.3. Abundance, species richness and Shannon Diversity Index

The first statistical analysis explored abundance of animal observations, species richness and Shannon Diversity Index with three sets of candidate models. The most parsimonious candidate models to predict animal abundance included the explanatory variables season, area, and river, as well as an interaction between season and area (Table S2). The model predicted a higher abundance of animals on beaver lodges compared to control areas in autumn, but a much weaker difference during spring when the abundance of animals was high on both beaver lodges and control areas (Table S3 & Fig. 3). The same explanatory variables were important to predict species richness (Table S2). Again, the beaver lodges had a higher predicted species richness in autumn, but there was a much weaker difference during spring when species richness overall was higher across beaver lodges and control areas (Fig. 3). For the third response variable, Shannon Diversity Index, three candidate models were among the top models both containing season, area, canopy cover, and river, but the most parsimonious model did not include canopy cover or the interaction between season and area (Table S2). For both seasons, the model predicted that beaver lodges had a higher Shannon Diversity Index than the control areas (Table S3 & Fig. 3). The variable river was important in the most parsimonious models for all three response variables (Table S3), and this indicated that the Saua river had a lower abundance, species richness, and Shannon Diversity Index compared to the two other rivers that were more similar to each other (Fig. S2). Canopy and shrub density were not included in any of the most parsimonious models for any of the response variables (Table S2).

3.4. Species counts

The second analysis using GLLVM to investigate drivers of individual species on the beaver lodges and control areas indicated that the first model including the explanatory variables and the random effect, but without any latent effects were the most supported model (Table S4). We visualized the predicted effect of each of the explanatory variables on the count of each of the included species (Fig. 4). A total of six species/genus besides beavers had a higher occurrence on beaver lodges compared to control areas. This included the invasive American mink, *Apodemus* spp., Common reed bunting (*Emberiza schoeniclus*), Eurasian otter, European robin (*Erithacus rubecula*) and Field vole. Other species did not display a statistically important impact of beaver lodges (Table S5 & Fig. 4). The model also indicated that several species were estimated to have a higher occurrence in spring than autumn including Field vole, Yellowhammer (*Emberiza citronella*), and Song trush (*Turdus philomelos*) (Table S5 & Fig. 4). Canopy cover was unimportant for most species and only had a statistically important effect on Common wood pigeon (*Columba palumbus*) and *Apodemus* spp., while shrub cover had a positive impact on the abundance of Eurasian otters (Table S5 & Fig. 4).

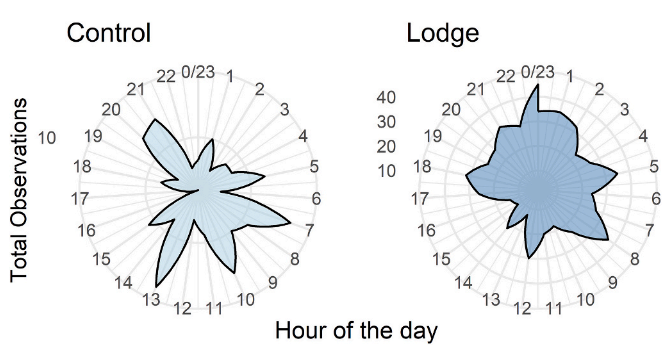

Fig. 2. Observations of animal activity in relation to the hour of the day on beaver lodges or control areas within the study area in southeastern Norway during autumn and spring (2023–2024).

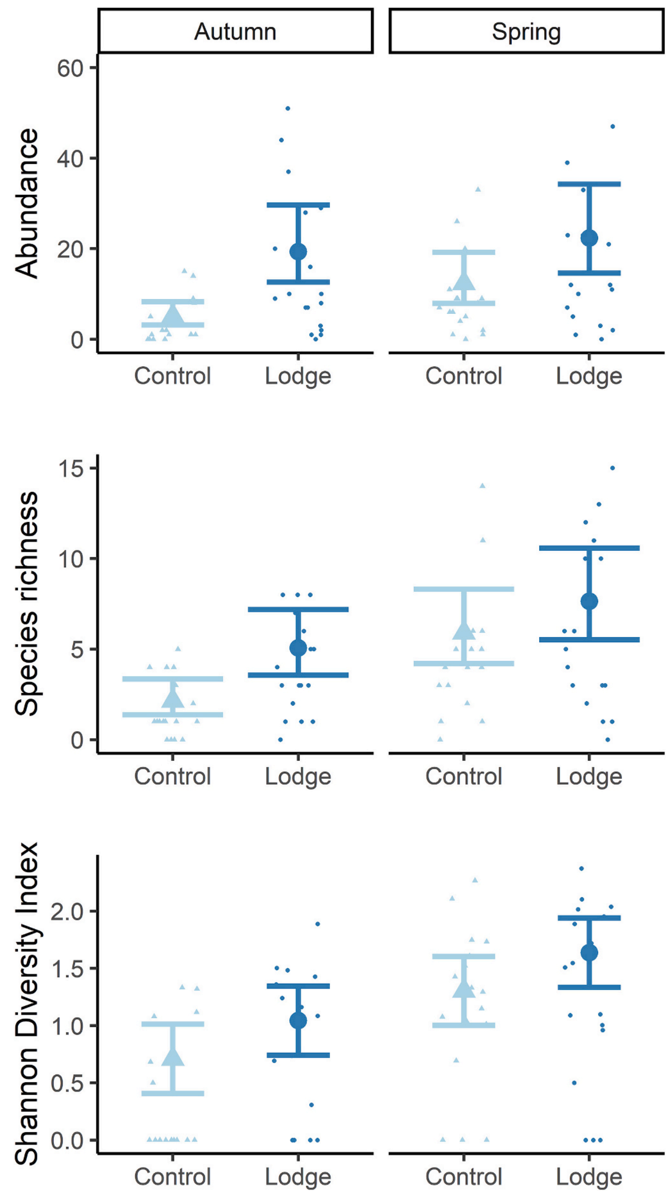

Fig. 3. Model estimates from the most supported models investigating the abundance of animals, species richness and Shannon Diversity Index on beaver lodges and control areas across autumn and spring (2023–2024) in southeastern Norway.

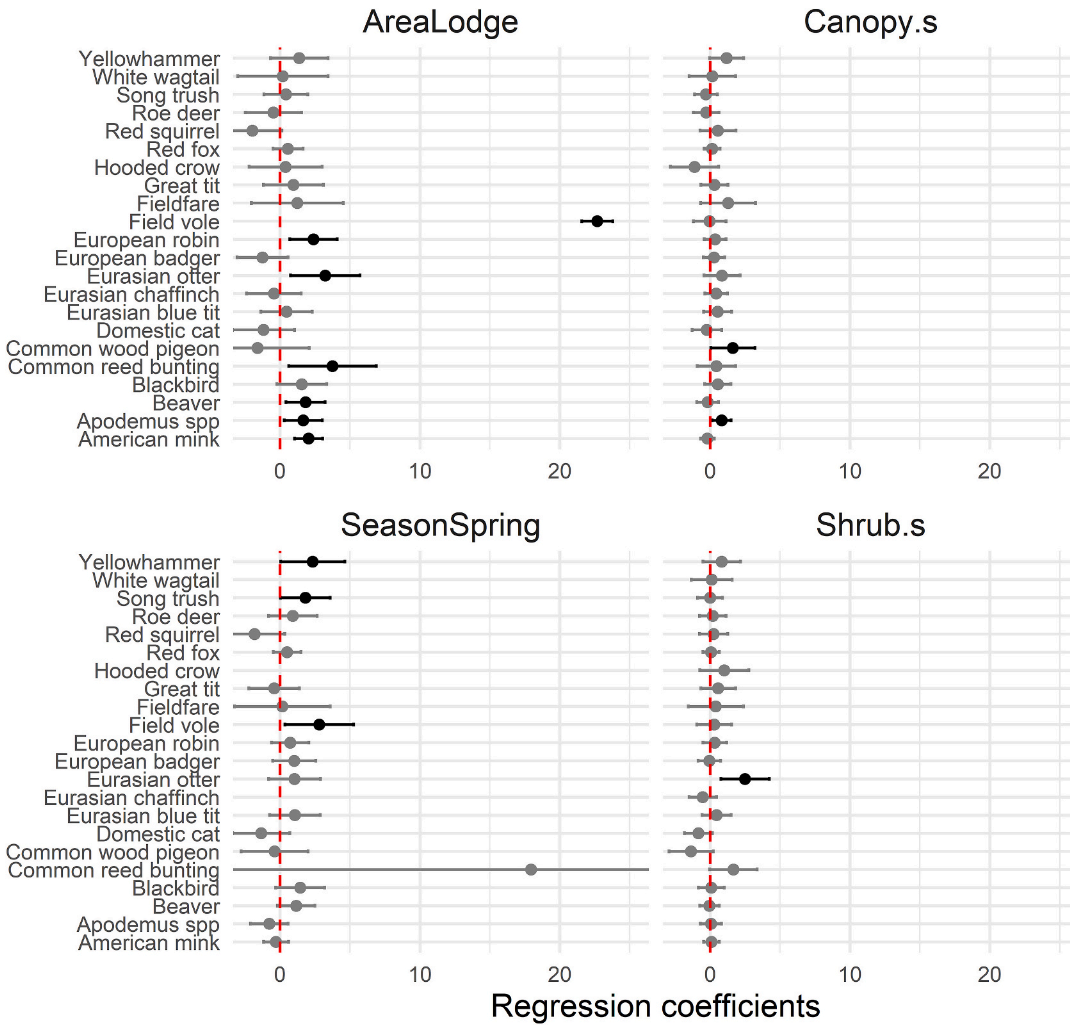

Fig. 4. Regression coefficients for each explanatory variable included in the most supported Generalized Linear Latent Variable Model (GLLVM), illustrating the effect sizes of area (beaver lodge and control area), season, canopy, and shrub cover on the 22 most commonly observed species on beaver lodges versus control areas in southeastern Norway during autumn and spring (2023–2024). The control areas and autumn season serve as the baseline in the intercept. Estimates to the right of the vertical line indicate a positive effect of the parameter on species counts, while those to the left indicate a negative effect. Estimates for species with standard errors overlapping zero, marked in grey, denote a non-significant effect on those species. Canopy and shrub cover variables have been standardized to ensure model convergence.

4. Discussion

Our results showed that beaver lodges do act as hotspots for numerous birds and mammals. Across both seasons, the number of species observed on beaver lodges and the control areas were similar, but the abundance of individual animals was almost three times as high on beaver lodges as the control areas. Circadian activity patterns suggested that there were many high levels of animal activity on beaver lodges during the night, compared to control areas that had a few distinct activity peaks throughout the day. Our statistical models predicted a higher abundance and species richness of animals at the beaver lodge compared to the control areas in autumn, which partly supports our hypothesis and predictions. However, we did not find the same effect in spring when both abundance and species diversity was higher overall and similar between beaver lodges and control areas. Shannon Diversity Index, however, indicated higher diversity and evenness on beaver lodges throughout both seasons. Focusing in on specific species revealed that beaver lodges were important hotspots for two mammalian carnivores (American mink and Eurasian otter), and the herbivorous Field vole, omnivorous Wood mouse and Yellow-necked mouse (i.e., *Apodemus* spp.) and two omnivorous birds (Common reed bunting and European robin), besides the beavers themselves. This supports our prediction that certain species are attracted by beaver lodges, and there was no statistical support to suggest that any species avoided beaver lodges.

4.1. *Beaver lodges affect the abundance, species richness and Shannon Diversity Index of animals*

Our results showed a higher abundance (643 observations) and species richness (40 species recorded) of animals at the beaver lodges compared to the control areas in autumn, while the Shannon Diversity Index indicated more diversity and evenness on beaver lodges throughout both seasons. In their recent review of the association between diversity and beaver lodges, Wilson and Bremner-Harrison (2024) found that 86 species were recorded on beaver lodges, i.e. 28 mammal species, 33 bird species, at least three reptile species and five amphibian species, five fish species and 12 macroinvertebrate families. In Nebraska, USA, 57 species of vertebrates (amphibians, reptiles, birds and mammals) were found on muskrat island houses and on feeding platforms (Mittman et al., 2023), and Kiviat (1978) found that >60 vertebrate species used these structures that are similar to beaver lodges but much smaller. Animal behaviours on these structures included basking, copulating, displaying, foraging, grooming, perching, preening, raising young, resting, and vocalizing (Mittman et al., 2023). Also, beaver lodges are used as breeding- and foraging areas by a diversity of vertebrates (Tye et al., 2021; Viviano et al., 2022). Our results are therefore in accordance with other studies that found richer and more abundant assemblages of animals on beaver modified areas than in unmodified areas (Fedyń et al., 2024; Orazi et al., 2022). As we relied on photos and not videos, we could not draw conclusions on the behaviour of the animals, and whether they were just passing through, foraging, hunting, or resting. However, if animals observed on the beaver lodges were just moving along the waterways, we would expect to see the same abundances and diversity on the control locations, which was not the case. Still, some of the most rarely observed species may just be moving through the area and not especially attracted by beaver lodges. The overall higher abundance and diversity, as well as those species observed in much higher abundance on the lodges compared to the control areas, however, suggest that beaver lodges contain certain attractants for these species.

4.2. Beaver lodges importance for specific species

Our study revealed that beaver lodges were important hotspots for especially small mammals such as herbivorous Field voles, omnivorous Wood mouse, and Yellow-necked mouse that were attracted to beaver lodges more than control areas. Herbivores Grey-sided voles were also only observed on beaver lodges, but only on a few lodges, which is probably the reason why we did not find a clear statistical difference between the beaver lodges and the control areas. Surprisingly, we only recorded one shrew on a beaver lodge. Sundell et al. (2021) trapped small mammals (mice, voles and shrews) in ten beaver-modified habitats and the non-beaver habitats and found a difference in species composition. Grass-eating Field voles and invertebrate-eating shrews (*S. araneus* and *Neomys fodiens*) tended to be common in beaver sites while forest-dwelling Wood lemmings (*Myopus schisticolor*) and Yellow-necked mice were only captured in control sites. Wikar et al. (2024), similarly to our results, found that the abundance and species richness of small mammals were highest near beaver dams and declined with distance. The structure of a dam, especially its downstream side, resembles the roof and walls of a lodge, thus one may expect a similar finding on beaver lodges. The structure of a beaver lodge with gnawed branches and the warm microclimate for resting and food for small rodents and shrews (Viviano et al., 2022). The warm microclimate both on the lodge exteriors and interior may also encourage denning and nesting by small rodents and shrews (McKinstry et al., 1997; Ulevičius and Janulaitis, 2007). Studies in Poland and central Italy support this and showed large diversity of species and high activity levels of small rodents in both beaver dams and on lodges, claiming this is due to the shelter, protection, and warmth in the beaver lodge (Viviano et al., 2022; Wikar et al., 2024). Small rodents and shrews likely also benefit from the resources beavers bring back to the lodge, such as twigs, fresh bark, leaves and deadwood, including coarse debris (Busher, 1996; Lodberg-Holm et al., 2022; Rosell and Campbell-Palmer, 2022). Also, beavers bring back grain to both the lodge and the food cache in late summer and autumn (Busher, 1996; Lodberg-Holm et al., 2022; Rosell and Campbell-Palmer, 2022). In Lithuania and Italy, the Wood mouse and the Yellow-necked mouse were suggested to use beaver lodges as shelter/refuge for resting and reproduction, protection from predators and to search for food (Samas and Ulevičius, 2015; Viviano et al., 2022). In accordance with our findings, two studies from Lithuania also caught more small mammals on beaver lodges during autumn (Samas and Ulevičius, 2015; Ulevičius and Janulaitis, 2007). Autumn is the season where beavers initiate their food cache- and lodge repair behaviour with fresh twigs that can be a good food source for small mammals (Rosell and Campbell-Palmer, 2022).

Our study revealed that beaver lodges were also important hotspots for American mink and Eurasian otters. The invasive American mink, and stoats, least weasel and red foxes, commonly hunts small mammals, birds and invertebrates (Sundell et al., 2021). Prey availability is therefore the most likely the reason why these predators are visiting the lodge (Razik and Sagot, 2020) as they do in other beaver-affected areas (Fedyń et al., 2022). American mink, Eurasian mink (*M. lutreola*), red fox and Eurasian otters have also been known to use lodges as shelters/denning and scent mark here (Mott et al., 2013; Nummi et al., 2019; Rosell et al., 2005; Sidorovich and Macdonald, 2001). Eurasian otters and American minks (and red foxes) have also been documented hunting young beavers at lodges, which also may attract them to these areas (Kile et al., 1996; Rosell and Campbell-Palmer, 2022). We observed in our camera trap images of American minks swimming outside the lodge and moved up and down the lodge to the water, which is consistent with hunting behaviour to catch small fish and amphibians. These species may occur at higher densities close to the lodge due to the branches and coarse wood debris that provide important habitats and hiding spaces (France, 1997). The American minks' diet mainly consists of fish in the colder months at northern latitudes (Zschille et al., 2014), which may make beaver lodges an important hunting area during autumn. Fish may again be attracted to the beaver lodge by the increased number of aquatic invertebrates that can provide a valuable food resource for the fish (Andersen et al., 2024; France, 1997). This was illustrated in Chile where brown trout (*Salmo trutta*) benefited from both fish and macroinvertebrates found near beaver lodges (Arismendi et al., 2020). The water surrounding the beaver lodges may thus serves as a "buffet" for carnivores such as American mink and Eurasian otters.

Beaver lodges were also important hotspots for European robins together with Common reed bunting. These may also be attracted to beaver lodges to find food. Both species feed on ground-dwelling invertebrates and plant seeds (Orłowski and Czarnecka, 2007; Stringer and Gaywood, 2016). Unfortunately, little is known about terrestrial- or aquatic invertebrates on or near Eurasian beaver lodges compared to control areas, but it is likely to assume that the abundance and richness of some invertebrate species are higher here. In addition to aquatic invertebrates, the beaver lodge offers shelter for terrestrial invertebrates among twigs and other woody debris used for lodge construction (Rosell and Campbell-Palmer, 2022). It is known that beavers have a positive effect on terrestrial arthropods such as for example true bugs (Heteroptera), beetles (Coleoptera) and spiders (Arachnida) (Orazi et al. (2022); see also review by Andersen et al. (2024)). In Montana, USA, wolf spiders (Lycosidae) occurred in a 60 % higher density around beaver-impounded sites than near lotic section of streams (McCaffery and Eby, 2016). Heat from inside active lodges creates a milder microclimate, and saproxylic invertebrates and their larvae may thrive on the lodges due to all the dead wood (Mourant et al., 2018). In Italy, the protected saproxylic longhorn beetles (*Morimus asper* and *Aegosoma scabricorne*) were found on beaver lodges and were attracted by the damaged trees and recently cut wood (Viviano et al., 2022). A North American study showed that the number of aquatic invertebrates also increased near beaver lodges (France, 1997). However, future studies are necessary to show if more terrestrial- and aquatic invertebrates are found at the beaver lodge compared to control areas.

In the control areas, birds were the most common group and, in general, the rivers attract a lot of birds during spring, which were observed both on the beaver lodges and control areas. Our study was conducted outside the birds nesting period and few insects had emerged when we ended our study and may therefore be the reason why the beaver lodges were only important for the European robin and Common reed bunting. For example, in south-eastern Germany, Orazi et al. (2022) found that species as Gray wagtail, Eurasian siskin, Common snipe and Common crane benefit from beaver-induced habitat modifications.

5. Conclusions

We conclude that the abundance and species richness of animals are higher at the beaver lodge compared to the control areas in autumn, while the Shannon Diversity Index indicated more diversity and evenness on beaver lodges throughout both seasons. Beaver lodges have multiple uses and fitness benefits for many animals, and function as local diversity hotspots. Resources such as warmth, shelter, and food most likely attract them (Andersen et al., 2024; Viviano et al., 2022). We know less about invertebrates and fish diversity around the lodges, and therefore the diversity of the species on and near Eurasian beaver lodges, especially at northern latitudes, should be further researched. For example, through electrofishing, aquatic- and terrestrial invertebrate sampling. This can further provide answers to what attracts birds, small rodents like mice and voles, shrews, and mammals to the beaver lodge. The knowledge gained from this study will hopefully contribute to a better understanding of beavers as a nature-based agent in the restoration of freshwater and riparian ecosystems (Brazier et al., 2021; Thompson et al., 2021), and its potential role in bird and mammal conservation. Beavers are important ecosystem engineers that create habitats for other species, not only by damming areas and felling trees, but building lodges that create important structures in the transitional zone between land and water utilized by a multitude of species.

CRediT authorship contribution statement

Frank Rosell: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Hanna Kavli Lodberg-Holm:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Floris Meijer:** Writing – review & editing, Methodology, Investigation, Data curation. **Martin Midbøe:** Writing – review & editing, Methodology, Investigation, Data curation.

Ethical statement

The study was performed in accordance with Norwegian law.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179898.

Data availability

Data will be made available on request from the corresponding author.

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