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Effects of beaver presence and forestry on mammal diversity
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Abstract

Ecosystem engineers, such as beavers, enhance ecological functioning and biodiversity by modifying habitats, especially in areas impacted by human activity. Through damming and selective foraging, beavers expand wetlands and increase resource availability for other taxa in riparian areas. This study examines the influence of beaver presence on mammal communities in a forestry-impacted region in Southern Norway. We compared mammal diversity and relative abundances of carnivores and herbivores between sites with (n=16) and without (n=18) beaver presence. Presence sites were located by beaver lodges, while absence ones were selected based on environmental similarities with presence sites. Environmental features (number of deciduous trees, human footprint index, proportion of clear cuts, and percentage cover of graminoids and of mosses) were recorded using maps and vegetation plots, while mammals were surveyed using camera traps. We compared differences in environmental features between beaver presence and absence sites, and tested the effect of beaver presence and environmental features on mammal diversity and abundances. We found significant differences in forest cover and varying habitat and groundcover types between beaver presence and absence sites. Beaver-modified habitats had higher mammal diversity, and particularly benefited carnivore relative abundances. The number of deciduous trees and graminoid cover in beaver presence sites positively influenced herbivore relative abundances. The increased mammal diversity was likely linked to the environmental changes beavers induce, including the promotion of deciduous tree growth and the expansion of graminoids for herbivores. Our findings suggest that beavers can increase ecological functions and biodiversity in ecosystems impacted by forestry. Reintroducing beavers to degraded landscapes could enhance habitat complexity and support the recovery of biodiversity and ecosystem services.

Zusammenfassung

Ökosystemingenieure wie der Biber verbessern das ökologische Funktionieren und die Artenvielfalt, indem sie Lebensräume verändern, insbesondere in Gebieten, die durch menschliche Aktivitäten beeinträchtigt werden. Durch Aufstauen und selektive Nahrungssuche vergrößern Biber Feuchtgebiete und erhöhen die Verfügbarkeit von Ressourcen für andere Tierarten in Uferbereichen. In dieser Studie wird der Einfluss des Bibers auf Säugetiergemeinschaften in einer forstwirtschaftlich geprägten Region in Südnorwegen untersucht. Wir verglichen die Säugetiervielfalt und die relativen Häufigkeiten von Fleisch- und Pflanzenfressern in Gebieten mit ($n=16$) und ohne ($n=18$) Bibervorkommen. Die Standorte mit Bibervorkommen wurden anhand von Biberburgen ermittelt, während die Standorte ohne Bibervorkommen aufgrund von Umweltähnlichkeiten mit den Standorten mit Bibervorkommen ausgewählt wurden. Umweltmerkmale (Anzahl der Laubbäume, Index des menschlichen Fußabdrucks, Anteil der Kahlschläge und prozentuale Bedeckung mit Graminoiden und Moosen) wurden anhand von Karten und Vegetationsplots erfasst, während die Säugetiere mit Hilfe von Kamerafallen untersucht wurden. Wir verglichen die Unterschiede in den Umweltmerkmalen zwischen Standorten mit und ohne Biber und untersuchten die Auswirkungen der Biberpräsenz und der Umweltmerkmale auf die Vielfalt und Häufigkeit von Säugetieren. Wir fanden signifikante Unterschiede in der Waldbedeckung und in den verschiedenen Lebensraum- und Bodendeckertypen zwischen den Standorten mit und ohne Biber. Durch Biber veränderte Lebensräume wiesen eine höhere Säugetiervielfalt auf, was insbesondere der relativen Häufigkeit von Fleischfressern zugutekam. Die Anzahl der Laubbäume und der Bewuchs mit Graminoiden in Bibergebieten wirkte sich positiv auf die relative Häufigkeit von Pflanzenfressern aus. Die erhöhte Säugetiervielfalt stand wahrscheinlich im Zusammenhang mit den Umweltveränderungen, die der Biber hervorruft, einschließlich der Förderung des Wachstums von Laubbäumen und

der Ausbreitung von Graminoiden für Pflanzenfresser. Unsere Ergebnisse deuten darauf hin, dass Biber die ökologischen Funktionen und die Artenvielfalt in forstwirtschaftlich genutzten Ökosystemen erhöhen können. Die Wiederansiedlung von Bibern in geschädigten Landschaften könnte die Komplexität der Lebensräume verbessern und die Wiederherstellung der biologischen Vielfalt und der Ökosystemleistungen unterstützen.

Introduction

Ecosystem engineers modify habitats, enhancing resource availability and reducing stress for other organisms (Nummi & Holopainen, 2014). By altering the environment, they improve resources for foraging, protection, and hunting to other organisms (Wright *et al.*, 2002; Wilby, 2002; Romero *et al.*, 2015). In low-productivity environments, these modifications promote biodiversity through facilitation (Wright & Jones, 2004), which is crucial given the global biodiversity decline (Tilman *et al.*, 1994; IPBES, 2019; WWF, 2024).

Beavers (*Castor* spp.) are notable ecosystem engineers, reshaping aquatic habitats through dam and channel building, which alters physical, chemical, and biological properties of water systems (Naiman *et al.*, 1986; Novak, 1987; Sun *et al.*, 2000; Collen & Gibson, 2001). Dams raise water levels, prevent freezing, protect against predators, and enhance food supply by modifying nearby vegetation (Rosell *et al.*, 2005, 2022). They also improve water quality, retain sediment, and increase soil moisture and nutrients (Naiman *et al.*, 1994; Rosell *et al.*, 2005).

Beavers are central place foragers, typically foraging up to 40-50 m from shorelines, thus strongly impact riverine vegetation (Fryxell *et al.*, 1991; Graf *et al.*, 2016). As long-lived (approx. 20 years), territorial rodents, their effects are lasting (Rosell *et al.*, 2005). Burrowing, damming and cutting create wetlands, and result in a shift to riparian and aquatic vegetation dominated by deciduous species, such as *Salix* spp. and *Alnus* spp. This provides beavers with woody vegetation required for dam building and as food. Their primary winter food consists of twigs, bark and leaves of deciduous trees, while in spring and summer they also consume aquatic and non-woody vegetation (Rosell & Campbell-Palmer, 2022). By regulating plant communities and increasing complexity through browsing and selective foraging, beavers support greater ecological connectivity and diversity, particularly in

degraded areas (Naiman *et al.*, 1986; Rosell *et al.*, 2005; Pollock *et al.*, 2023). Through abiotic and biotic changes to riparian environments, they favour ecosystem processes and support greater species richness, for example of woody species (Lawton & Jones, 1995; Nummi & Holopainen, 2014). Their disturbances also increase light availability for small-statured plants proximal to beaver dams (Naiman *et al.* 1994). This benefits a range of animal species, including carnivores (LeBlanc *et al.*, 2007; Sundell *et al.* 2020; Fedyń *et al.* 2022), bats (Ciechanowski *et al.*, 2011) and ungulates (Nummi *et al.*, 2019). Although certain amphibious and bird species have declined following beaver stream occupation (Suzuki *et al.*, 2004; Elmeros *et al.*, 2003), generally beavers augment diversity in their surroundings (Wright *et al.* 2002; Rosell *et al.*, 2005; Sundell *et al.*, 2021; Wikar *et al.*, 2024), especially in wetland habitats (Law *et al.*, 2017; Brazier *et al.*, 2021).

Eurasian beaver (*Castor fiber*) populations, once decimated by trapping, are recovering and expanding, now occupying about 25% of their original range (Halley *et al.*, 2020). Much of their current range lies in Northern Hemisphere forests, including boreal ecosystems (Vehkaoja *et al.*, 2017). These coniferous-dominated forests, encompassing 27% of the world's forested land, provide critical ecological functions and services (FAO, 2020). Through climate regulation via carbon storage and water purification, and by providing resources, they support human societies worldwide, and contribute to global biodiversity by giving habitats to specialised and ecologically relevant species (Angelstam & Kuuluvainen, 2004; UN Forum on Forests, 2017). However, commercial forestry is degrading these forests by reducing structural and biological diversity (Brandt *et al.*, 2013; UN Forum on Forests, 2017; Wei *et al.*, 2022). Therefore, re-establishing ecosystem engineers, such as beavers, is a proposed approach to restore ecological interactions and services (Albert and Trimble, 2000). Beaver-induced habitat modifications in the boreal forest are believed to increase resilience to anthropogenic change (Dittbrenner *et al.*, 2018; Stoll & Westbrook, 2020), by maintaining

wetlands that ensure water availability and provide resources for other species (Hood & Bayley, 2008).

Various mammal species rely on riparian areas, where their taxonomic richness, diversity, and evenness are higher than in other forest areas (Kaufmann *et al.*, 2001; Anthony *et al.*, 2003). Mammal community composition varies spatially based on resource availability, body size, niche complementarity, and human influence (Marcot *et al.*, 2003; Anthony *et al.*, 2003; Wolff, 2003; Fisher & Wilkinson, 2005). Hence, understanding how beaver presence influences mammal communities in areas characterised by low-productivity and varying degrees of human influence can reveal facilitation processes of this ecosystem engineer for co-existing mammals.

Beaver presence in human-altered habitats has been shown to increase habitat structure and species richness (Law *et al.*, 2017). For example, Nelner *et al.* (2011) observed an increase in mammal diversity across habitats altered by agricultural land-use. However, the effects of beavers in forestry-impacted areas are less clear (Pejstrup *et al.*, 2023). Boreal forests in Fennoscandia, which represent approx. 5% of total boreal forests, are intensively managed for silviculture (Burton *et al.*, 2010). Moreover, beavers inhabit the area and interact with ongoing forestry. This study will examine how beaver habitat modifications influence mammal diversity and abundance in a forestry-impacted boreal region in Southern Norway. We hypothesized that beaver presence will increase mammal diversity in forestry-impacted areas by enhancing resource availability. We expected effects of species on mammals to be species-specific due to idiosyncratic interspecific interactions, resulting in differences in species abundances between sites with and without beavers. Finally, we expected that both carnivore and herbivore abundances will increase from the enhanced resources in beaver-modified habitats.

Methods

Study Area

Surveys were carried out in the northern part of the Finnskogen County, in south-eastern Norway (60.95130 N, 12.10716 E, Fig. 1). The study area (approx. 1650 km²) ranges between elevations of 291 and 600 m a.s.l. and is classified as a boreal ecosystem. Two main roads delimit the study area to the south-west and to the north. To the east, the study area is bordered by Sweden, marking a change in wildlife management and policy. Hunting quotas differ between the two countries (Morellet *et al.*, 2011; NJFF, 2007; Svenska Jägarförbundet, 2005). It is the only area in Norway where four large carnivore species coexist: brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), lynx (*Lynx lynx*) and wolverine (*Gulo gulo*). Cervid species in this boreal area are moose (*Alces alces*), roe deer (*Capreolus capreolus*), and red deer (*Cervus elaphus*) (Bjørneraas, 2012; Bevinger, 2015). They are highly dependent on seasonal habitat and resource availability. In the dense moose population in the Finnskogen region, this leads to migrations between winter and summer sites for breeding and foraging (Andersen & Sæther, 1996). Of the smaller herbivore species, beavers have been increasing along the many principal waterbodies since their near extirpation in the mid-19th century (Nolet & Rosell, 1998; Parker & Rosell, 2003) (Fig.2), and were estimated at 80,000 individuals in Norway in 2020 (Halley *et al.*, 2021). In contrast, the populations of mountain hare (*Lepus timidus*) are declining in population size due to altered patterns in snow cover and to habitat fragmentation, which are aggravated by forestry and urbanisation (Pedersen, & Pedersen, 2012). Forest management is widespread and ongoing in the entire region, with large areas undergoing clear-cutting and selective logging (Hansen *et al.*, 2013; Breidenbach *et al.*, 2020; Astrup *et al.*, 2021). Managed forests mainly consist of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). As such, woodland habitats are often dominated by pine or spruce with varying age classes, and management levels (from clear-cuts to selective

logging, to natural reserves). Patches of deciduous forest (comprising mainly of birch *Betula* sp., willow *Salix* sp., alder *Alnus* sp., and rowan *Sorbus aucuparia*) can be found, as well as mixed stands (Astrup *et al.*, 2019). The dominating understorey species are shrubs and dwarf shrubs (*Calluna vulgaris*, *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Empetrum nigrum*, *Juniperus communis*). A large portion of the area is wetland, which is dominated by mosses, monocot species (*Carex* sp. and *Eriophorum* sp.) and shrubs such as *Salix* sp. and *Betula nana*. Despite the low human density, anthropogenic disturbances remain: low-level urbanisation, fishing, hunting, and, most importantly, silviculture affect the area and drive the expansion of road networks and forest fragmentation.

Site Selection

Along the shorelines of the main waterbodies in the study area, beaver presence was known through previous monitoring of signs of presence (lodges, dams, and old and new beaver cut stems with diameter >0.2 m at stump height). Among the observations, all active beaver lodges (n=16) were selected as sites of beaver presence for this study (here termed “presence” sites). A minimum of 2 km between sites was set to maintain spatial independence. This threshold was established to contain beaver activity in each surveyed location to one family group by considering typical beaver territory sizes between 1.5–3 km of shoreline (Vorel *et al.*, 2008; Graf *et al.*, 2016). To be able to distinguish the effect of beaver presence on mammal diversity and abundance, 18 reference sites were selected in areas without beaver lodges and/or habitat modifications by beavers (termed “absence” sites). Absence sites were located in areas with similar habitat and forest characteristics compared to corresponding presence sites. This was done to distinguish beaver presence effects on mammal populations by ensuring the same degree of habitat variation between beaver presence/absence sites. As a result, 34 sampling sites were investigated simultaneously during spring.

Using GIS software (QGIS.org, 2024), maps were used to distinguish environmental features of sites at a landscape-scale, in order to locate beaver absence sites which match the forest habitats of presence sites. The land cover attributes used for site selection were: dominant forest type (spruce, pine, deciduous), mean tree age (considering trees above 5 m height), percentage of tree cover per 1 km² (forest cover), and percentage of clear cuts and young forest stands, estimated from clearcuts conducted between the years 2000-2022. Forest type is indicative of habitat type, and was derived from maps obtained via remote sensing and national forest assessments at a 16 m² resolution in raster format (SR16, Breidenbach *et al.*, 2020; Astrup *et al.*, 2021), while forest age, cover and proportion of clearcuts spatially describe forestry intensity, and were derived from Landsat maps at a 30 m resolution (Hansen *et al.*, 2013). The sampling design, thus, consisted of matching sites of beaver presence and absence that accounted for forest disturbance histories on a landscape-level. With the same maps used for site selection, I created a 300 m buffer around each camera trap to extract land cover attributes. This radius was chosen based on the average minimum area affected by beavers (Remillard *et al.*, 1987). These were: tree crown cover (%), height (dm), base surface mean diameter (cm) for trees with diameter at breast height ≥ 8 cm, and tree abundance per hectare (Breidenbach *et al.*, 2020; Astrup *et al.*, 2021). Additionally, human disturbance, mainly associated to silviculture in the study area, was quantified using a 1 km resolution map of the Human Footprint Index (HFI), which is a metric for anthropogenic impact based on human density, infrastructure and transport ways (Wildlife Conservation Society, 2005).

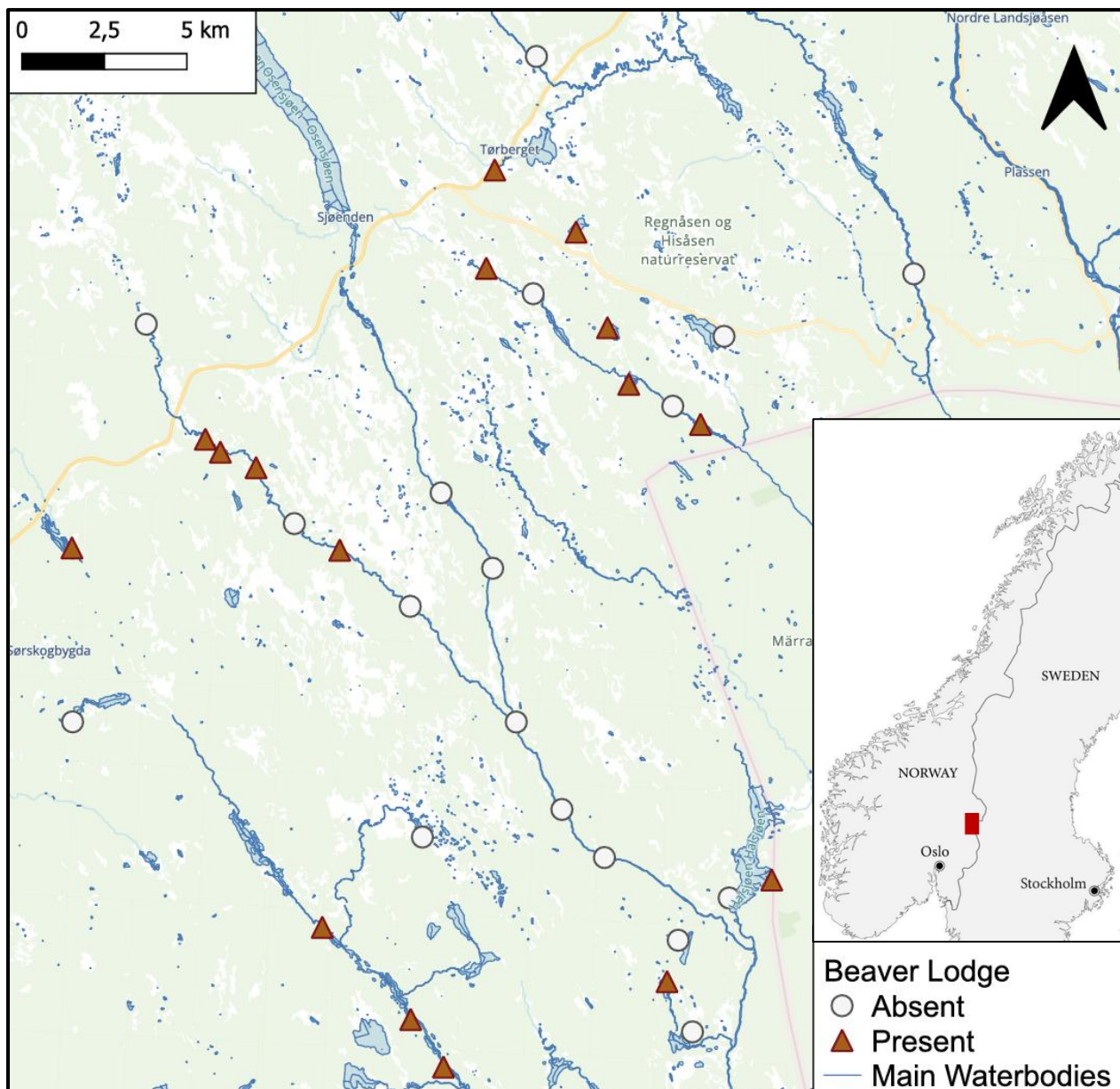


Figure 1 The study area, located in Northern Finnskogen (South-East Norway) (red box), where surveys were done. Camera traps ($n=34$) were deployed at 16 sites with active beaver lodges (brown triangles), and 18 absence sites (no or little beaver activity; white circles).

Field Surveys

i) Mammals

Mammals were monitored using camera traps because they are a cost-effective, non-invasive method to monitor animal activity across large areas and over long periods of time.

In this study, one camera trap was deployed at each site ($n = 34$) for a period of approx. 60 trap-nights (May 2024 – July 2024). Camera traps (“Zodiac Observer” and “Brecom CM4000 Hunting Camera”) were set to taking photos at 8 mpi, with no or 0.5 s delay (for Zodiac cameras). Detection sensibility was set to “High”, and trigger speed was 0.35 s with a 12 m to 20 m range of view. At the beaver presence sites, camera traps were positioned within 25 m of the beaver lodge. Cameras at both presence and absence sites were placed at approx. 0.50 m from the ground to capture the widest size range of mammal species, and with the most open range of view as possible, facing away from the water body. In some cases, obscuring vegetation was cleared around the camera. Camera traps were placed at a maximum distance of 25 m from the waterbodies because 87-95% of beaver cut stems are located within 50 m from the shore (England & Westbrook, 2021; Stoffyn-Egli & Willison, 2011; Pejstrup *et al.*, 2023).

ii) Habitat & Vegetation

Habitat, tree and groundcover vegetation sampling was done to get information on the local environment beyond those extracted from the forest maps, as well as to better understand the available resources for mammal species in the area (i.e. for protection and foraging). At each camera trap site, I surveyed tree and groundcover at 4 circular plots, one directly at the camera trap, and three located along a semi-circle 25 m from the camera trap (brown circles in Fig. 2). Each plot had an area of 29.6 m² (3 m radius), within which the main habitat types (bog, old = age >20 years, or young forest = age <20 years), the dominating groundcover (grasses, mosses, shrubs), and the number of available stems classified by tree species and by size were recorded. In addition, four rectangular vegetation plots (1 m x 0.5 m) were placed at random within the 25 m semi-circle (green box in Fig.2). All observed plant species within each plot were recorded. Vascular plants were determined to species level, while mosses and lichens were recorded as phyla. In addition, percentage cover by functional type (shrubs,

grasses, mosses, lichens, ferns/horsetail, forbs) was estimated. These plots were done to describe food availability for herbivorous mammal species, and to assess the impacts of beavers on local vegetation. In particular, the number, size and species of trees is relevant for beavers and ungulates (Baker & Hill, 2003), while understory plant diversity is an important food source for beavers and smaller herbivores in the warmer months (Hansson, 1969; Rosell & Campbell-Palmer, 2022).

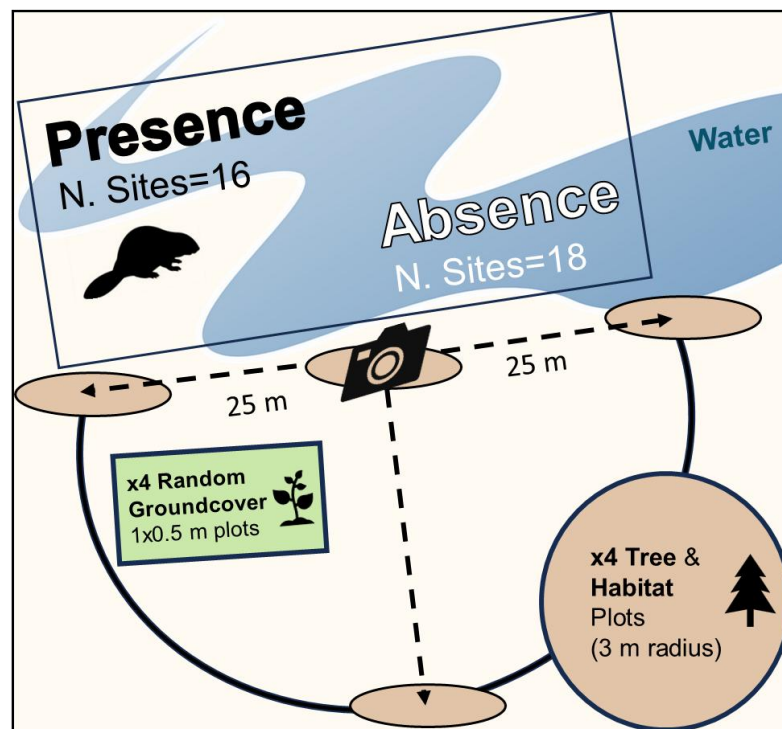


Figure 2: For both beaver presence and absence sites: stratified sampling to survey habitat and tree data using four circular plots with 3 m radius (brown circles): one around the camera trap, and three at right angles along a 25 m radius circle (black semicircle). Within this semicircle, four 1 x 0.5 m plots (green box) were placed randomly to survey groundcover vegetation.

Data Analysis

i) Mammals

Following retrieval, the camera trap data was loaded onto “Agouti.eu” (www.agouti.eu), an online platform that enables rapid processing and storage of camera trap images. Based on the image timestamps, the platform groups images into sequences. When no movement has been detected and the time difference between subsequent images exceeds 120 seconds, sequences are considered separate. Each sequence represents a single detection event, or the period of time in which animals trigger the camera traps. Combining bursts of images into sequences facilitates data processing and provides more accurate estimates of species abundances. Species identification was carried out manually, annotating each observation on the platform. The processed data was then exported as a Camera Trap Data Package, a community developed data exchange format for camera trap data, and loaded into R software (R Core Team, 2024) using the “camtrapdp” package (Bubnicki *et al.*, 2023). The Camtrap DP file contained files describing deployment sites, animal observations, and the species list. Each observation event featured taxonomic animal information, site name, GPS position, observation time, and deployment period. These were then used to calculate, for each site, species diversity metrics and relative abundances of the herbivore and carnivore functional groups (respectively, all herbivore species pooled, and all carnivore species pooled). Metrics used to measure mammals are (i) the number of species that occur (species richness) and two diversity metrics: (ii) Shannon Diversity Index, abundance-weighted range of species observed (Barnes *et al.*, 1998), and (iii) the Simpson Diversity Index, which accounts for their divergence in occurrence frequency (Simpson, 1949; Kiernan, 2014). Shannon diversity, calculated as $(H) = - \sum_{i=1}^S p_i \ln p_i$, is indicative of local ecological states assuming higher productivity with greater biodiversity. Simpson diversity ($D = - \sum_{i=1}^r p_i^2$), instead, weighs each species with its abundance, highlighting dominant species and habitat preferences based on

their occurrence likelihood under specific conditions. The relative abundances of herbivores and carnivores were calculated as the sum of the number of individuals observed per detection event at each site, grouped by functional group (herbivores and carnivores), and divided by the number of trapping days.

ii) *Habitat & Vegetation*

Multiple biotic and abiotic factors characterise each sampling site: elevation, habitat type, tree and groundcover vegetation, and anthropogenic disturbances. For each of these, the mean, standard deviation and 95% confidence intervals were calculated for sites with and without beavers (Appendix: Table 1). The normality was tested graphically using QQ plots. Subsequently, Kruskal-Wallis tests were done to statistically compare the environmental variables based on beaver activity (presence/absence), considering as the significance threshold $p = 0.05$. Among the environmental variables, six were chosen as the variables in the statistical models because they represented the food sources for beavers and other herbivores. These were: the number of deciduous trees (DT) counted within the habitat plots around camera traps, mean groundcover vegetation species richness (SR) and the relative cover by vegetation types (mosses M, and graminoids G), estimated by quadrat-sampling around the camera trap. Two additional parameters were selected because they are indicative of human impacts to forests: the human footprint index (HFI), and the proportion of clear cuts (L). A non-parametric Kendall correlation test was generated across these environmental factors to test for collinearity in the explanatory variables. Groundcover plant species richness, shrub and forb cover were correlated with other variables, with a correlation coefficient >0.6 or <-0.6 (Zuur & Ieno, 2016), thus were excluded from the analyses. Final environmental variables for modelling were DT, M, G, HFI, and L. All environmental variables were normally distributed, except for the mean percentage cover of the vegetation functional groups (mosses and graminoids), for which normality was obtained using log-transformations.

General Linear Models & Spatial Linear Mixed Models

I used general linear models (GLM) to investigate mammal species richness, Shannon diversity, Simpson diversity, and the relative mammal abundances (average number of observations per day) of carnivores and of herbivores (dependent variables in separate analyses; Table 1). Beaver presence/absence and the previously selected environmental variables were used as independent variables in a stepwise model selection process. Starting from the full model with all predictors, variables were removed by comparing the Akaike information criterion (AIC) (Burnham and Anderson, 2002), using the package “AICcmodavg” (Mazerolle, 2023). The top model was the one with lowest AIC (Akaike, 1973). The AIC method calculates model goodness of fit based on the number of parameters: the most parsimonious model is the one that best explains variation in the response variable with the fewest number of explanatory variables (Sober, 1981). A Gaussian distribution was used for all models except those with species richness as dependent variable, where a log-link Poisson distribution was used. For each of the best fitting models, spatial autocorrelation in the residuals of the GLMs was tested for using Moran's I test. For this, DHARMA residuals were simulated from each model, using the R packages “ape” (Paradis *et al.*, 2019) and “DHARMA” (Hartig, 2022), and tested for Moran's I, against the Euclidean distances between geographical coordinates (latitude and longitude). With significant p-values (≤ 0.05) for Moran's I, spatial dependence between model variables was assumed, thus the GLMs were discarded, and generalised linear mixed-effect models (GLMM) were adopted instead (using the “spaMM” package, by Rousset *et al.*, 2014). The spatial term was defined by a Matérn function where the sites' longitude and latitude are integrated to compute the auto-correlated random-slope term (Rousset, 2017, 2021). In this case the predictors are set as fixed effects, with latitude and longitude as the random effect. Analogous to before, Gaussian distributions were assumed for the diversity and relative abundance metrics, and a log-link Poisson

distribution was assumed for species richness. All models except for Shannon Diversity were non-significant to Moran's I test for spatial autocorrelation ($p > 0.05$). Shannon diversity, instead, minorly supported spatial autocorrelation ($p = 0.048$). Thus, I applied a spatial linear mixed model (SLMM) with the coordinates as the spatial terms (in the Matern function).

Finally, model assumptions were assessed for each best fitting model by graphically depicting the normality of residuals and the homoscedasticity of variables. Parameters that included zero within their 95% CI were considered uninformative (Arnold, 2010). The models accounting for spatial autocorrelation were checked with the DHARMA package.

Additional candidate models were run based on the models with $\Delta AIC < 2$ for the response variables, since this threshold indicates that models are equally well supported (Symonds *et al.*, 2011). The candidate models consisted of interactive combinations of the beaver presence/absence covariate (B) with the environmental variables (EV) selected in the best model for all response variables ($y \sim B \times EV$). The model with the lowest AIC was considered the best fit. These interactive models served the function to verify whether models were testing the true beaver effect.

Results

Habitat & Vegetation

Due to the systematic sampling approach, where absence sites were selected based on the replication of forest conditions at beaver sites, there were only minor differences in the overall habitat-type. Forest cover was lower at beaver presence sites than absence sites (Kruskal-Wallis test: $H=5.5$, $df=1$, $p=0.02$, difference= $10.62 \pm 0.7\%$). Statistical tests did not detect any significant differences between beaver presence/absence sites for the other forest variables used to select the beaver absence sites (Appendix: Table S1).

Differences between beaver presence and absence sites were observed at a smaller scale by analysing habitat features, trees and groundcover vegetation. Beaver presence determined significant differences in the mean percentages of groundcover of graminoids (Kruskal-Wallis test: $H=14.28$, $df=1$, $p<0.01$) and forbs (Kruskal-Wallis test: $H=38.65$, $df=1$, $p<0.01$), which were greater in beaver presence sites, and of shrubs (Kruskal-Wallis test: $H=6.05$, $df=1$, $p=0.01$), which were more abundant in absence sites (Appendix: Fig. S1E). Visual comparisons suggest that sites were mostly located in forested areas characterised by shrub understoreys, with more beaver presence sites proximal to older forests and in grassy habitats than beaver absence sites (Appendix: Fig. S1A-B). The number of deciduous trees and groundcover vegetation species richness did not differ between sites (Appendix: Fig. S1C-D). When beavers were present, species richness of groundcover vegetation was greater in old forests dominated by mosses, and did not differ between habitats when they were absent (Appendix: Fig. S2B). Presence sites with bogs had higher forest cover and number of deciduous trees than the respective absence sites, while forested and grass-dominated absence sites had greater forest cover but less deciduous trees than those of presence sites (Appendix: Fig. S2A-C).

Mammals

Among the 397 detection events, 12 mammal species were identified (11 at presence and 8 at absence sites). Mammal abundances were unequal between species across beaver presence/absence sites (Table 1, Fig. 3). Common herbivores (moose and roe deer) were similarly observed in both presence and absence sites, while detection rates differed for less frequently observed species: more mesocarnivores and smaller herbivores, but less red deer, were observed in presence sites relative to absence sites. Badgers, hares and beavers were only recorded at presence sites. Of the large carnivores in the area, bear, wolf and wolverine were observed, with one wolf at a presence site, one wolverine at an absence site, and bears

appearing at both. The mean number of total individuals detected per camera trap was slightly higher for beaver presence sites, but this difference was highly variable between cameras (presence sites: mean N. species/ camera trap = 13, N. individuals/ camera trap: mean = 13, range = 2-35; absence sites: mean N. species/ camera trap = 10, N. individuals/ camera trap: mean = 11, range = 1-39). Despite more cameras being placed in forested sites (Appendix: Fig. S1A), diversity of mammals was greater in bog habitats and where mosses dominated (Fig. 4).

Table 1 Total number of observations of each species across sites with beaver absence (N=18) and presence (with lodges, N=16) detected by camera-traps.

	Beaver Activity	
	Absent (18)	Present (16)
<i>Large carnivores</i>	3	4
Brown bear	2	3
Wolverine	1	0
Wolf	0	1
<i>Mesocarnivores</i>	8	30
Red fox	6	24
European pine marten	2	4
European badger	0	2
<i>Large herbivores</i>	168	157
Moose	64	51
Red deer	3	1
Roe deer	101	105
<i>Meso-/small herbivores</i>	10	17
Eurasian beaver	0	3
Mountain hare	10	13
Red squirrel	0	1
TOTAL	189	208

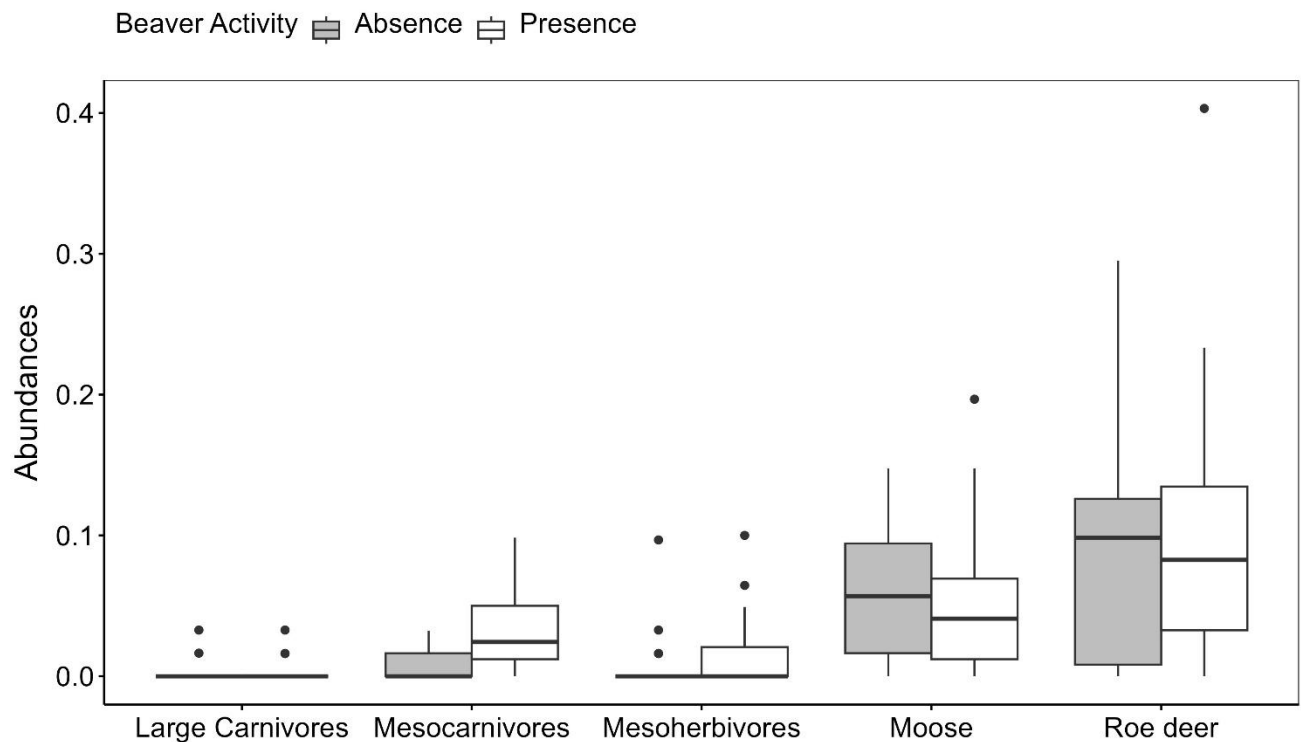


Figure 3 Mammal detections per day (count, y-axis) between beaver presence and absence sites. Boxplots represent the median and the 1st/3rd interquartile (bars).

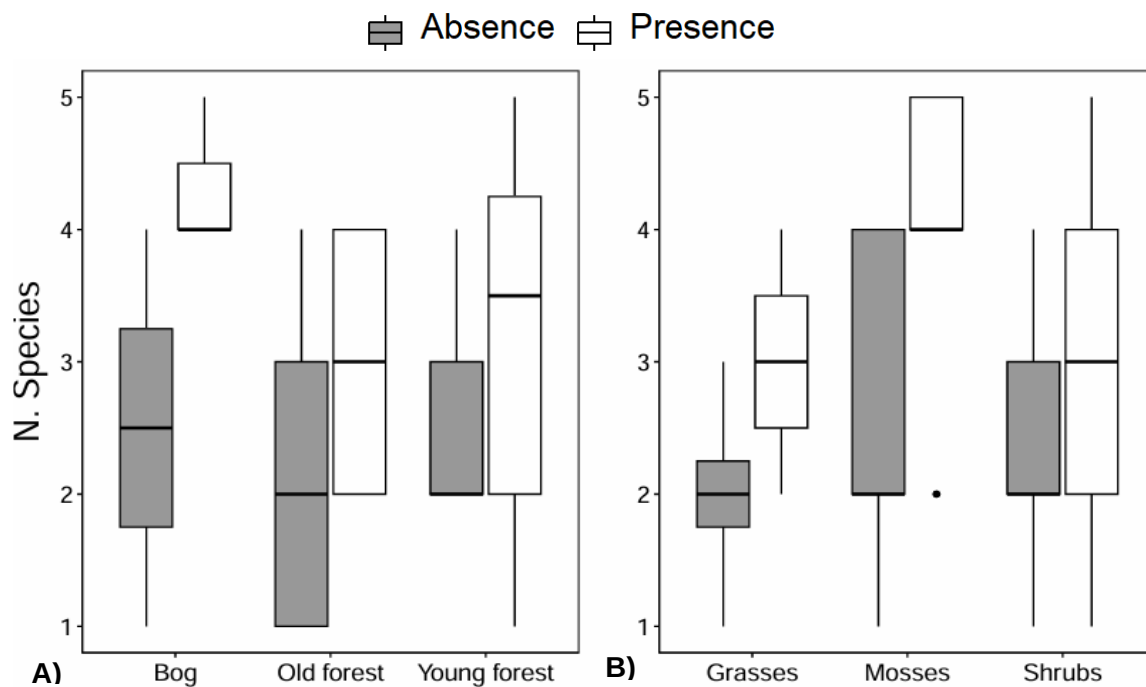


Figure 4 The number of mammal species detected across habitat types (A) and groundcover types (B) between beaver absence and presence sites. Boxplots represent the median and the 1st/3rd interquartile (bars).

Models

Beaver presence/absence best explained the variation in all diversity indices and in the relative abundance of carnivores (Table 2). Mammal Shannon Diversity and the relative abundance of carnivores was significantly higher at beaver presence sites than at absence sites (Table 3, Fig. 5B & 6D). The best fitting models for these measures were $< 2 \Delta AIC$ from the intercept-only model, meaning that the independent variables do indeed explain a proportion of the variation in the data. Based on the top model for herbivore relative abundance, deciduous trees and graminoid groundcover, but not beaver presence, best explained the observed variation in the data (Table 2), through a positive relationship (Table 3, Fig. 6A-C). However, the AIC decreased when including the interaction of beaver presence in the top model selected for the relative abundance of herbivores and of carnivores. In these models, positive coefficients suggest that beaver presence had a positive effect on herbivore and carnivore abundances when interactive with deciduous trees (Table 3, Fig. 6A-B). Independent variables had no significant impact on mammal Simpson diversity and species richness (Fig. 5A-C). The intercept-only model for these was within $\Delta AIC < 2$ from the best model, thus beaver presence did not explain the variation in the data.

Table 2 Criteria for the step-wise model selection process for each of the response variables, showing the full model (all the predictors variables), intercept-only and the best fit based on the lowest AICc of the non-interactive and interactive models. Interactive models are included in the table when they performed better than the non-interactive model.

Response	Model	K	AIC _c	ΔAIC
Shannon Diversity (spatial LMM)	Full Model	8	49.39	9.36
	Intercept	2	42.33	2.30
	Best Fit: Beavers	3	39.23	0
Species Richness	Full Model	7	128.08	11.56
	Intercept	1	117.51	0.99
	Best Fit: Beavers	2	116.52	0
Simpson Diversity	Full Model	8	8.34	9.17

	Intercept	2	-0.22	0.6
	Best Fit: Beavers	3	-0.83	0
Relative Abundance of Carnivores	Full Model	8	-146.57	12.19
	Intercept	2	-147.07	11.70
	Best Fit non-interactive: Beavers	3	-157.13	1.64
	Best Fit interactive: Beavers* N. Deciduous Trees	5	-158.77	0
Relative Abundance of Herbivores	Full Model	8	-41.94	11.46
	Intercept	2	-45.17	8.22
	Best Fit non-interactive: Graminoids + N. Deciduous Trees	4	-53.40	3.2
	Best Fit interactive: Beavers* Graminoids + Beavers* N. Deciduous Trees	7	-56.63	0

Table 3 Coefficients of the best fitting models for each response variable. Significant effects are highlighted in bold.

Response Variable	Predictor Variable	Estimate (95% LCI – UCI)	p-value
Shannon Diversity	Beaver Presence	0.30 (0.03 – 0.57)	0.031
Species Richness	Beaver Presence	0.37 (-0.04 – 0.78)	0.07
Simpson Diversity	Beaver Presence	0.13 (-0.02 – 0.28)	0.09
Relative Abundance of Carnivores	Beaver Presence	0.029 (0.014 – 0.044)	<0.001
	Beaver Presence	-0.0023 (-0.032 – 0.027)	0.88
	Deciduous Trees	-0.001 (-0.002 – 0.001)	0.34
	Beaver Presence *	0.012 (0.004 – 0.020)	0.04
	Deciduous Trees		
Relative Abundance of Herbivores	Graminoid Cover (%)	0.003 (0.000 – 0.005)	0.008
	Deciduous Trees	0.004 (0.000 – 0.001)	0.027
	Beaver Activity	-0.148 (-0.281 – -0.015)	0.037
	Graminoid Cover (%)	0.005 (0.002 – 0.009)	0.002
	Beaver Presence *	0.012 (0.004 – 0.020)	0.004
	Deciduous Trees		

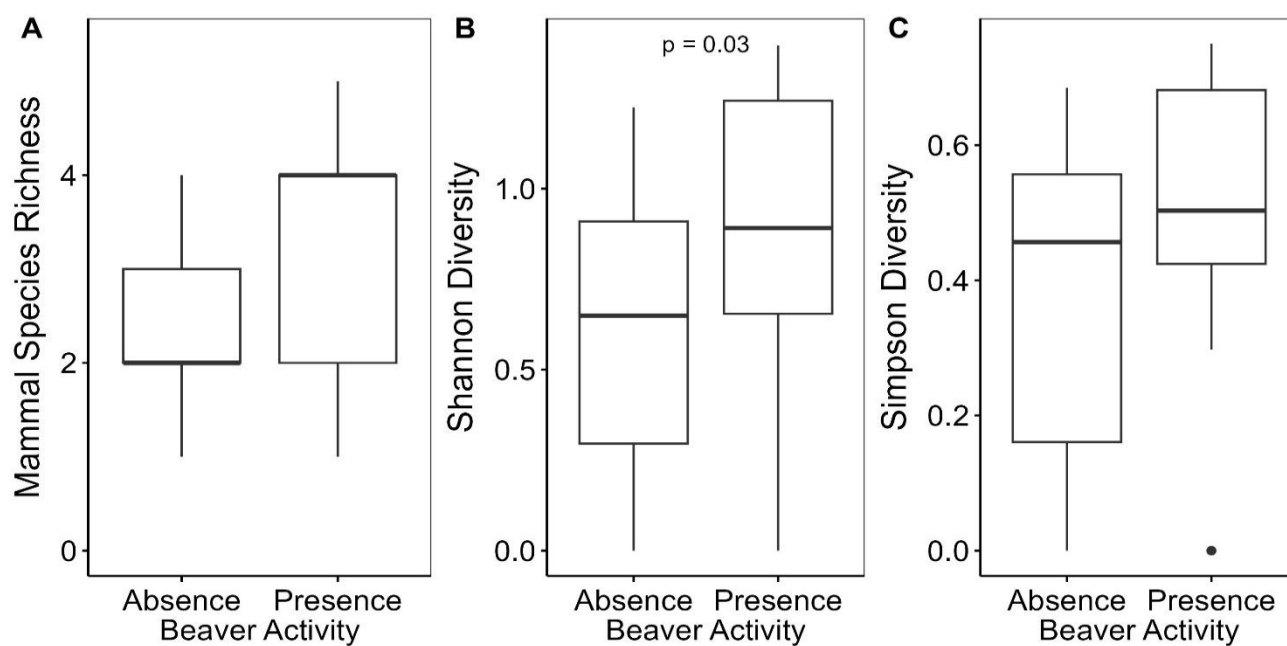


Figure 5 Differences in the estimated mammal (A) Shannon diversity, (B) species richness, and (C) Simpson diversity. Data were collected from 34 camera traps.

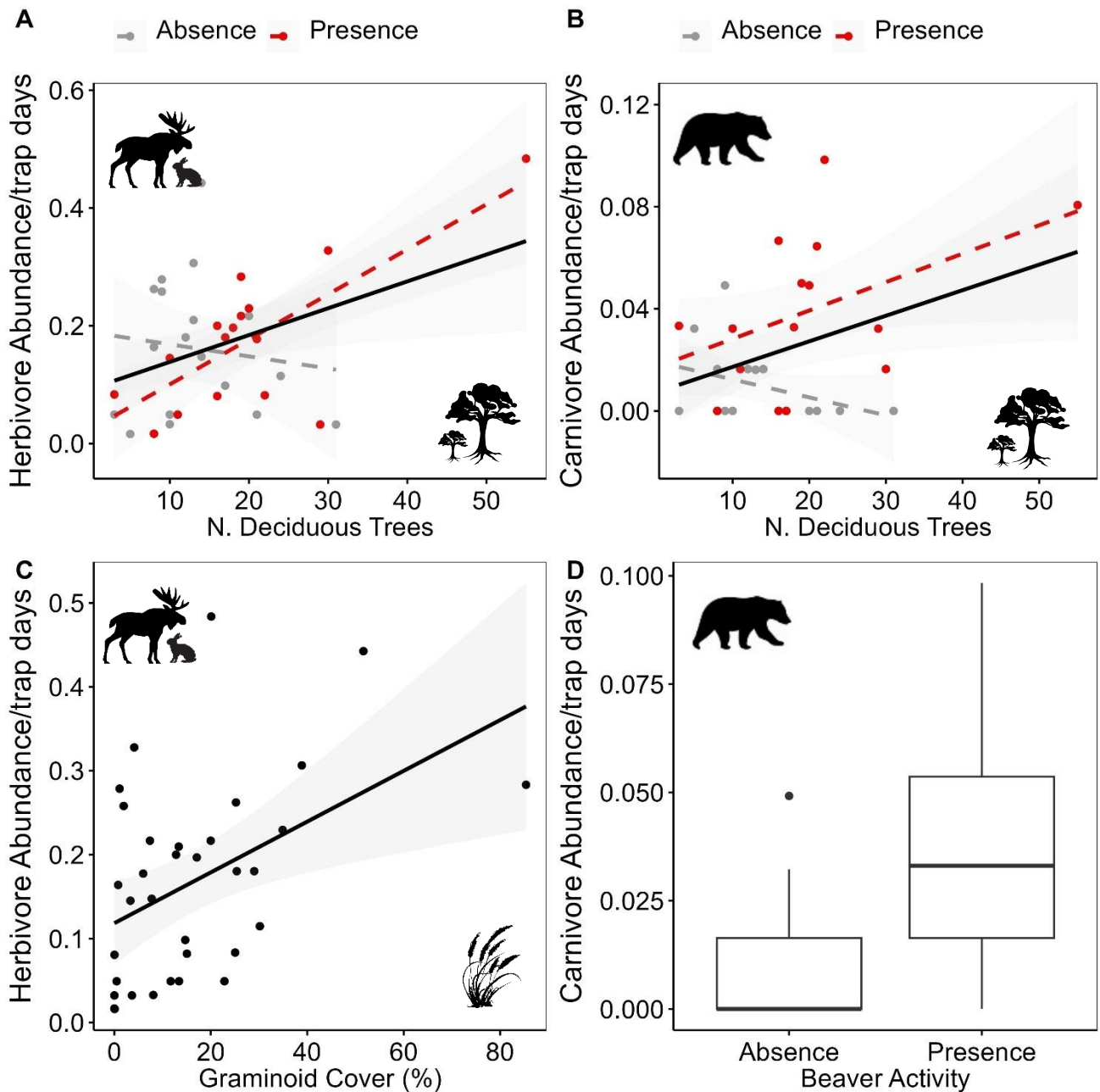


Figure 6 Scatterplots represent the significant relationships of (A) herbivore relative abundance and (B) carnivore relative abundance (y-axes) against the number of deciduous trees (x-axis). Line and dot colours represent the predicted relationships by the best fitting GLM of beaver presence (red) or absence (grey) associated to the number of deciduous trees on the estimated abundances. Black lines represent the overall relationship. In (C), the relative herbivore abundances show significant relationship (y-axis) with the % graminoid cover (x-axes), where the black line represents the predicted relationship by the GLM. In all

scatterplots, the 95% confidence intervals are shown as grey shading, and raw data as dots. Box plots (D) depict the significant difference in the relative abundance of carnivores (y axes) between beaver presence and absence sites (x axis). Bars represent the median and 1st/3rd interquartile.

Discussion

Our results indicate that beavers influence mammal communities in the boreal zone by increasing diversity and attracting specific functional groups. The higher mammal species richness and relative abundance of carnivores in beaver-modified areas indicate that beavers may facilitate survival in boreal forests by enhancing resources for foraging and protection. Beavers appear to promote carnivore but not herbivore relative abundances, and particularly increase mesocarnivore densities in beaver-modified areas. In areas where logging takes place, riparian strips act as ecological corridors for wildlife (Anthony *et al.*, 2003). Beaver-induced habitat modifications could support greater mammal diversity in such areas by improving resource availability and complexity. Thus, in areas where forestry reduces ecological integrity and environmental heterogeneity, beavers may help restore biodiversity.

Habitat & Vegetation

We aimed to compare sites with similar environmental conditions to isolate the effect of beaver presence. The few observed differences could be accounted for by beaver selection of certain habitat features and by beaver foraging impacts. Environmental data indicate that sites generally had wet, eutrophic soils, typical of boreal regions with deciduous-dominated vegetation (Sayer, 2006; Majasalmi *et al.*, 2020). Surveys revealed that forest canopy cover was lower near beaver lodges, likely due to foraging and damming activities that enlarge wetland areas and shift the forest structure to younger tree stems with less canopy cover.

This would explain the locally observed variation in forest and groundcover types. Around lodges, deciduous trees and moss cover were more abundant. Beavers select and shift the vegetation composition towards deciduous forest in their territory (Rosell & Campbell-Palmer, 2022). It is also likely that beavers selected bogs with sedge-moss cover, which facilitate channel digging (Rebertus, 1986). Through damming, beavers cause water level rise that likely promotes moss-covered wetlands (Rosell *et al.*, 2005; Bragina *et al.*, 2014). These play a fundamental role in carbon sequestration and water storage (Dise, 2009). They also contribute to increasing microbial diversity in the boreal ecosystem (Bragina *et al.*, 2014). Thus, beavers help regulate the global climate and promote biodiversity by increasing moss-dominated bogs.

Mammal Diversity

We detected a wide range of mammal species, with more abundant ungulates (moose and roe deer), which are well-suited to the boreal environment. Lower occurrence species, such as red deer, were also observed. Diversity indices accounted for the unequal distribution of rare and common species. Although sampling was limited to the spring and summer months, in this period of the year diversity indices, particularly Shannon Diversity, showed higher diversity near beaver lodges, possibly due to environmental modifications, including open forest and more deciduous trees. Studies have found that species' preference for different degrees of forest cover vary seasonally, in relation to snow cover and to food availability (Fox, 1990; Kie *et al.*, 2003; Ferretti *et al.*, 2023). Large mammals use open forest, such as clear cuts in harvested areas, to facilitate movement and increase hunting success in predators (Kie *et al.*, 2003; Jones *et al.*, 2024). Deciduous trees are food source to herbivores (Coughenour, 1985), and produce a nutrient rich litter layer that promotes soil fauna complexity (Nilsson *et al.*, 1999), increases arthropod diversity (Facelli, 1994), and provides additional temperature protection to herbivores (Garcia-Guzman & Benitez-Malvido, 2003).

Additionally, beaver felled trees lying on the floor host a multitude of insects (Andersen *et al.*, 2023). Thus, invertebrate and herbivorous communities in the areas affected by beavers may increase and further enhance diversity and provide abundant prey for omnivores and carnivores. Consequently, forest patches selected and modulated by beavers offer resources for multiple organisms.

In particular, we observed a significant difference in Shannon Diversity between beaver presence and absence sites, while species richness and Simpson Diversity did not vary significantly. Indeed, the small difference in AIC between the intercept-only and the best fitting models for the latter measures of diversity would imply that beaver presence had almost no effect on the species richness or on Simpson diversity. Shannon diversity responded positively to beaver presence, although the difference between the best fitting and the intercept-only models showed only a slight significant difference (Symonds *et al.*, 2011). Shannon diversity is an abundance weighted measure of diversity that accounts for both the number of species, its composition and their relative abundances (Shannon, 1948). It indicates dominance concentration while being highly sensitive to species rarity (Nagendra, 2002). In the highly homogenous boreal ecosystem, Shannon diversity more effectively captured the level of variation between communities compared to Simpson diversity, which was less sensitive to the rarer species that could have been drawn to beaver-modified habitats (Simpson, 1949). Vice-versa, species richness gives high leverage to rare species but is sensitive to sampling effort (Roswell *et al.*, 2021). Our study was limited in the sample size by time and technical constraints (lack of camera traps). Thus, inferences based on species richness could miss important variations in species abundances. Greater sampling effort could better capture the effect of beaver activity on mammal diversity. The higher Shannon diversity estimated at beaver presence sites alludes to their potential for attracting rarer or less detected mammal species. This metric also shows the relative differences in

abundance of specific species. Consequently, the difference in Shannon diversity could be attributed to the high number of moose, roe deer, hares and red foxes at sites with beavers, combined with the additional species observed exclusively here.

Relative Abundance of Carnivores

Our results suggest that beavers enhance carnivore abundance, especially of red foxes, but not herbivore abundance. The greater abundance of mesocarnivores relative to large carnivores in the complex beaver-modified habitats is likely due to the increased availability of prey and shelter from higher trophic levels (Mishin & Trenkov, 2016; Nummi *et al.*, 2019; Fedyń *et al.*, 2022). In particular, the interactive model shows that beavers' effect on deciduous forest raises carnivore abundance. Younger stands of abundant deciduous trees could attract prey species, thereby providing resources to both large and medium-sized carnivores, and may enhance habitat structure (Lyly *et al.*, 2014). The complex landscape derived from beaver habitat-modification may increase carnivores' predation success and provide refuge from competitors and larger predators for small and mid-sized carnivores (Thompson, 1988; Thompson *et al.*, 1989; Ferretti *et al.*, 2023). Beaver ponds attract amphibians and small mammals, providing additional food sources for mesopredators (Anderson *et al.*, 2015; Samas & Ulevičius, 2015; Wikar *et al.*, 2024). Furthermore, mesopredators also use beaver dams to cross water (Czajkowska & Janiszewski, 2021), and find shelter in lodges (Rosell *et al.*, 2005), while large carnivores use beaver-modified riparian strips as ecological corridors for their long-distance movements (Dickie *et al.*, 2020). Although large carnivore abundances did not differ much in this study, they could benefit from the increased abundance of fish and other prey at beaver sites (Nummi *et al.*, 2019).

Relative Abundance of Herbivores

Herbivore abundance did not differ significantly between beaver presence/absence sites, but was influenced by deciduous tree abundance and graminoid groundcover. The high fitness of the interactive model with beaver presence, the number of deciduous trees and graminoid cover indicates that beaver activity likely increased food resources for herbivores. Beaver habitat was characterised by more open forest cover, typical of early seral stages, where young seedlings, shrubs and grasses are most abundant and deciduous trees dominate. Herbivores prefer this for the greater food availability and lower visibility from predators (Coughenour, 1985; Collins *et al.*, 1998; Fisher *et al.*, 2005; Lyly *et al.*, 2014). Although commensurate with predation risks, moose and roe deer generally select areas with higher availability of deciduous tree species (Dussault *et al.*, 2005; Månsson *et al.*, 2015). Experiments also found that hares and voles consume birch shoots in winter because they grow faster than coniferous species and emerge earlier from the snow (Hjältén *et al.*, 2004). This would explain the higher abundance of herbivores in areas with frequent regrowth of deciduous trees.

Moreover, small to mid-size herbivores could benefit from greater cover of graminoid species in beaver-modified habitat, where they can hide from predators, find shelter, food, and favourable microclimates (Gray *et al.*, 2019). Eutrophic boreal soil types share the most variation in vertical vegetation fractionation than other types, often with moss-dominated ground layers and diverse upper understoreys consisting of shrubs, graminoids and herbs (Majasalmi *et al.*, 2020). Graminoids are also relevant food sources for ungulates. This plant group has co-evolved with grazers, so that moderate grazing increases vegetative production (Coughenour, 1985). In fertile soils, light competition determines the stature of graminoids. Thus, the correlation between beaver presence and reduced forest cover relative to areas

without beavers could enhance graminoid cover. With frequent beaver-induced disturbances more light can reach the nutrient-rich soils in beaver habitat, thereby encouraging the growth of graminoids, especially ruderals (Grime, 1977). Beaver-modified habitats may create more heterogeneous groundcover, fostering a favourable environment for herbivores.

Future Considerations

Our study supports the potential role of beavers in promoting mammal diversity in human-impacted areas. The higher diversity of species, particularly of carnivores at beaver sites, suggests that beavers play an important role in restoring trophic interactions and ecosystem functioning. With human activities fragmenting habitats and threatening biodiversity (Tilman et al., 1994), restoring natural processes through ecosystem engineers like beavers is essential to reversing ecological degradation (Hjältén *et al.*, 2023). In this study, beaver activity appears to increase local heterogeneity in the homogeneous forested landscape, where intensive forestry has reduced differences between forest stands. Forestry activities, such as harvesting (clear-cutting and thinning), ground scarification, road development, and soil fertilisation have led to replacement and homogenisation of tree stands, and the near extirpation of intact, old-growth forests from most boreal areas, thereby reducing biodiversity and ecological integrity (Burton *et al.*, 2003; Angelstam & Kuuluvainen, 2004). Beaver habitat modifications could compensate such damage by promoting structural complexity and wetland expansion. Rewilding practises that reintroduce beavers would help to re-establish trophic interactions, ensure ecological functioning and foster biodiversity (Svenning *et al.*, 2016).

Conclusion

Our study suggests that beaver presence increases mammal diversity by attracting species relative to areas without beavers, and enhancing the abundance of herbivores and carnivores. Beaver modifications may increase the availability of prey for carnivores, provide hunting advantage in the highly complex landscape, and maintain ecological connectivity along riparian strips. Additionally, herbivores benefit from greater abundance of deciduous trees and graminoid cover in beaver-modified areas. These findings highlight the potential for beavers to support ecological functioning and enhance biodiversity in boreal ecosystems impacted by human activities.

Appendix

Table S1 Descriptive statistics of the environmental variables compared between selected sites of beaver presence and absence ($n = 34$). LCI and UCI stand respectively for the 95% Lower and Upper confidence intervals around the mean. The asterisk (*) indicates a significant difference detected using between sites with and without beavers ($p \leq 0.05$).

Environmental Factors	Beaver Presence				Beaver Absence			
	Mean	SD	95% LCI	95% UCI	Mean	SD	95% LCI	95% UCI
<i>Elevation</i>	440.4	98.8	242.8	638	439.1	80.3	278.5	599.7
<i>N. Trees/ha</i>	900	250	399	1401	840	155	530	1150
<i>Above Ground Biomass</i>	70.3	16.3	37.7	102.9	78.4	20.8	36.8	120
<i>Volume with Bark</i>	112.5	28.1	56.3	168.7	129.7	36.7	56.3	203.1
<i>Leaf Area Index</i>	320.8	88.2	144.4	497.2	334.1	85.4	163.3	504.9
<i>Diameter</i>	15.2	2.4	10.4	20	16.3	2.2	11.9	20.7
<i>Height</i>	122.5	19.2	84.1	160.9	133.8	17.1	99.6	168
<i>Crown Cover</i>	57.2	11	35.2	79.2	61	11.2	38.6	83.4
<i>Forest Cover *</i>	49.5	11.6	26.3	72.7	60.1	12.3	35.5	84.7
<i>Groundcover Species Richness</i>	37.3	11.7	13.9	60.7	34.7	9.1	16.5	52.9
<i>N. Deciduous Trees (in 3 m plot)</i>	20	12	0	43.4	13	7	0	27
<i>N. Coniferous trees (in 3 m plot)</i>	5	5.1	0	15.2	7	5	0	17
<i>Forest Gain</i>	0.024	0.04	0	0.104	0.01	0.02	0	0.05
<i>Forest Loss</i>	1.12	1.29	0	3.7	1.54	1.74	0	5.02
<i>Human Footprint Index</i>	18.3	7.9	2.5	34.1	19.3	3.8	11.7	26.9

Table S2 Models in the step-wise model selection process, where herbivore and carnivore stand for the relative abundances of all species belonging to the relative functional groups. Model parameters are beaver activity (B), the number of deciduous trees (DT), the percentage cover of graminoids (G) and of mosses (M), and the percentage of forest cover loss (L). The full model includes all parameters, whereas the intercept has none. For each model, the model fitness output is shown: n. parameters K, the Akaike Information Criterion AIC, and the difference in the AIC score from the best model (ΔAIC). Highlighted in bold are the best fitting candidate models for each response variable, where $\Delta AIC=0$.

Full Model: B, DT, G, M, HFI, L		K	AIC	ΔAIC
Carnivores	B	3	-157.13	0.00
	B+DT	4	-156.75	0.37
	B+DT+G	5	-154.36	2.77
	B+DT+G+M	6	-153.16	3.97
	B+DT+L+G+M	7	-150.01	7.12
	Intercept Only	2	-147.07	10.06
	Full Model	8	-146.57	10.55
Herbivores	DT+G	4	-53.40	0.00
	B+DT+G	5	-50.96	2.43
	B+DT+G+M	6	-48.26	5.14
	B+DT+G+HFI	7	-45.26	8.14
	Intercept Only	2	-45.17	8.22
	Full Model	8	-41.94	11.46
Species Richness	B	2	116.52	0.00
	Intercept Only	1	117.51	0.99
	B+G	3	118.35	1.83
	B+DT+G	4	120.47	3.94
	B+DT+G+M	5	122.47	5.94
	B+DT+L+G+M	6	124.92	8.40
	Full Model	7	128.08	11.56
Shannon Diversity	B	3	40.03	0.00
	B+M	4	41.10	1.08
	B+G+M	5	42.03	2.00
	Intercept Only	2	42.33	2.30
	B+L+G+M	6	43.09	3.06
	B+HFI+L+G+M	7	46.06	6.03
	Full Model	8	49.39	9.36
	B	3	-0.83	0.00

Simpson Diversity	Intercept Only	2	-0.22	0.61
	B+M	4	0.04	0.87
	B+G+M	5	1.24	2.07
	B+L+G+M	6	2.44	3.27
	B+HFI+L+G+M	7	4.89	5.72
	Full Model	8	8.34	9.17

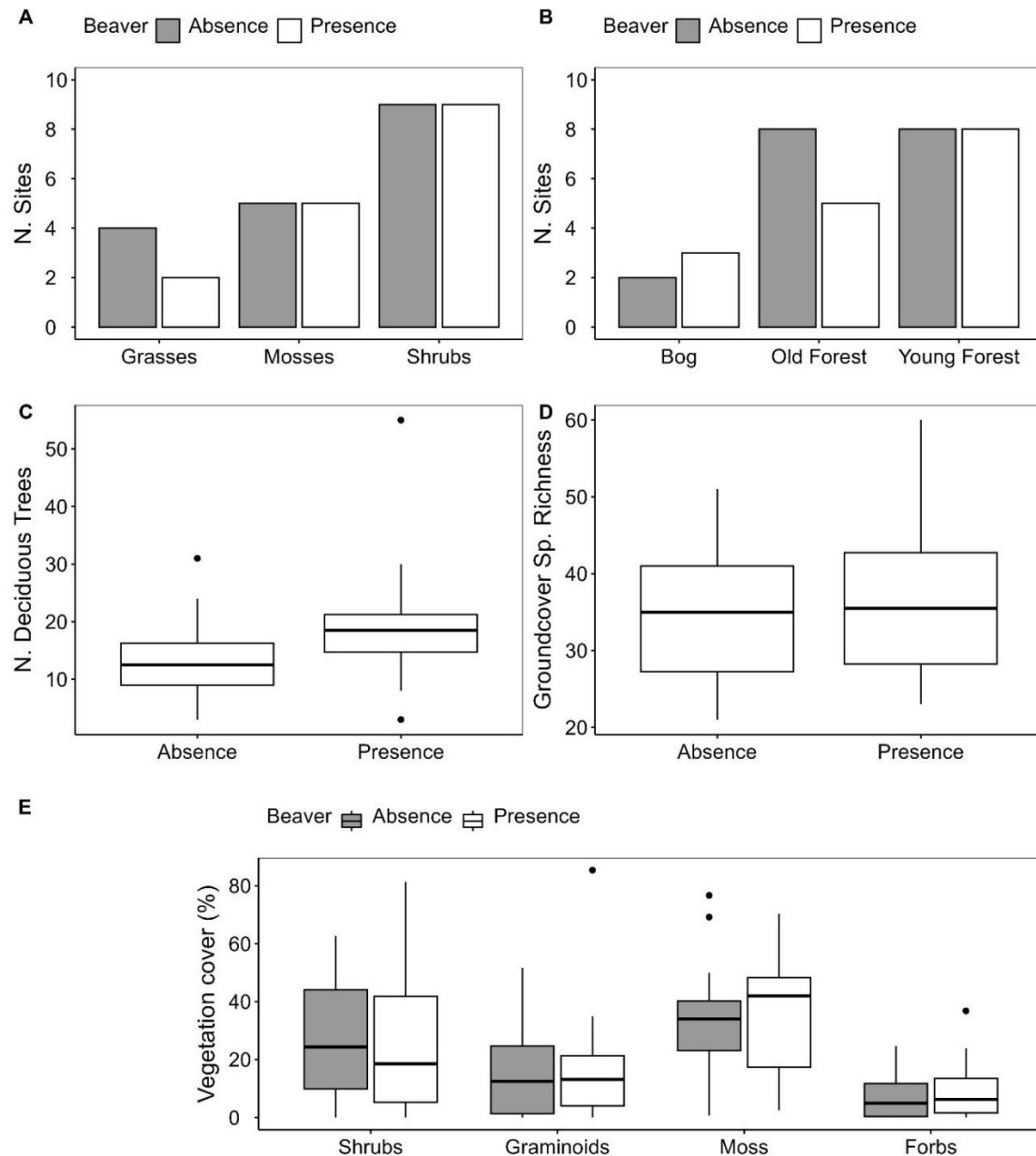


Figure S1 Columns indicate the number of sites (y-axes) where (A) groundcover vegetation and (B) habitat types were observed (x-axes). Boxplots illustrate on the y-axes the number of deciduous trees (C) and the mean groundcover vegetation species richness (D) between beaver absence and presence sites (x-axis) and the mean groundcover (%) (E) of

the respective vegetation types (x-axis) between beaver absence (white boxes) and presence (white boxes) sites. Bars represent the 95% confidence intervals.

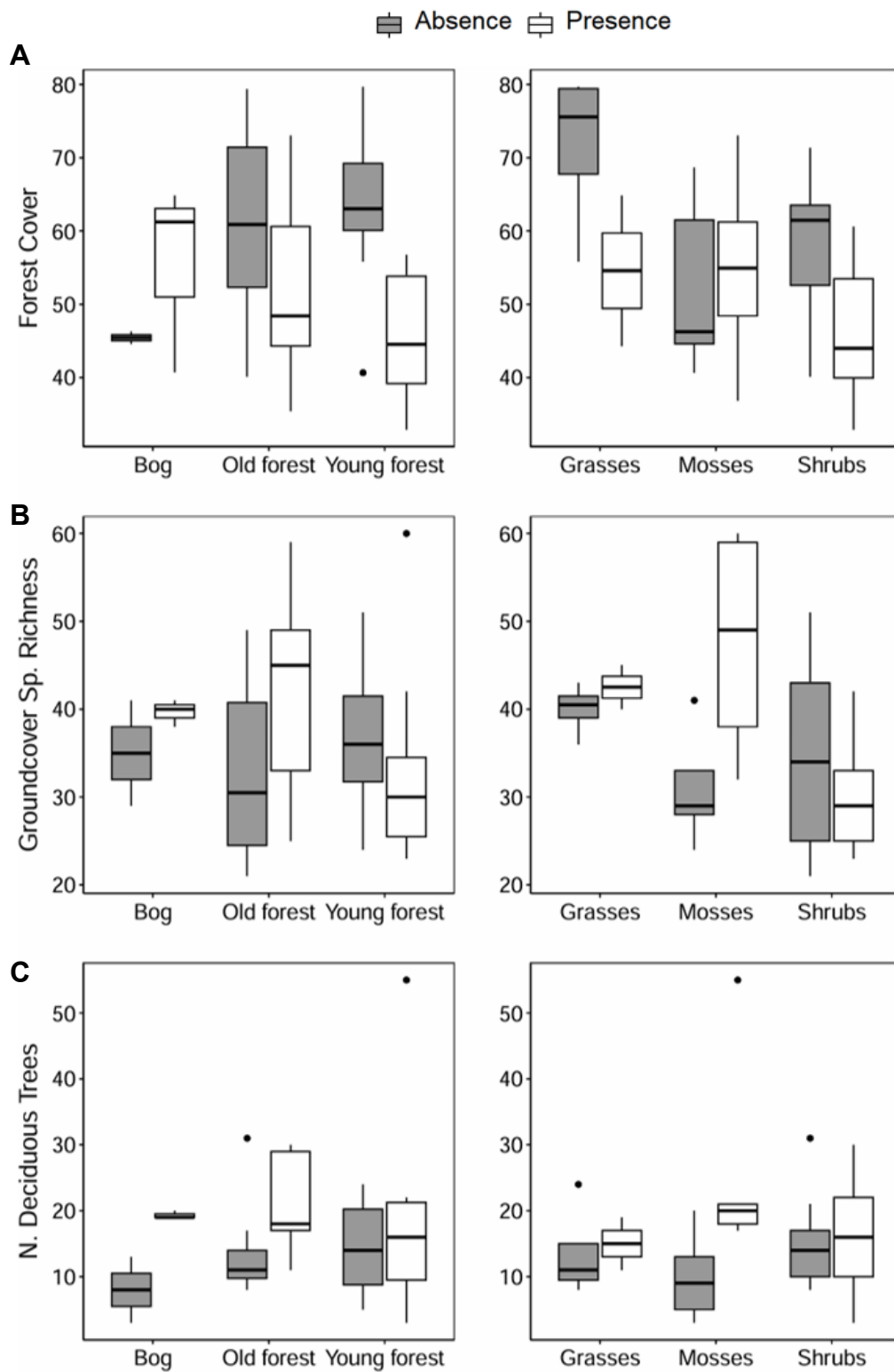


Figure S2 Forest variables at camera trap sites between beaver presence (grey boxes) and absence (white boxes) across different habitat types (left) and groundcover types (right).

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