

Beaver foraging patterns in a human-dominated landscape: Effects on woody vegetation and mammals

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ABSTRACT

Beavers can change habitat composition by cutting down trees, digging, and damming activities, thereby affecting species richness and abundance. Although there is large body of literature regarding the effects of beaver activity on a wide range of taxonomic groups, relatively little is known about how space use by ungulates is affected by beavers in the human-dominated landscapes of Europe. Here, we present a case study from Denmark that investigated potential effects of beaver activity on mammals, with a special focus on roe deer and red deer. Beavers could either facilitate the presence of deer by providing food resources (increased abundance of deciduous trees and shrubs) or compete with them for resources. Using transect counts recording both cut and uncut stems of woody plants, we describe beaver browsing patterns, providing evidence that they either select for areas with higher woody vegetation richness and diversity, or alter woody plant species composition. We then assessed deer presence and relative abundance in relation to the distance from water and in areas with varying beaver activity. Our findings provide limited evidence for exploitative competition between beavers and roe and red deer, as roe and red deer avoided proximity to water in areas with high beaver activity, and deer numbers were higher in areas with low beaver activity. We speculate that the weak effect of beaver activity on deer (and/or vice versa) might be related to the large human impacts in the area, e.g., forest management, potentially superseding effects of interspecific competition. An improved understanding of the complex effects beavers can have on ungulates in human-dominated landscapes will be relevant for wildlife and forestry management, potentially being an important tool to reduce human-wildlife conflicts.

1. Introduction

Interspecific interactions are of focal importance in ecology because they can shape patterns of distribution, abundance and diversity in ecological communities (Begon et al., 2005; Svenning et al., 2014; Freeman et al., 2022). Consequently, a better understanding of their effects will aid to develop improved management strategies for the species involved, such as increasing biodiversity or reducing human-wildlife conflicts. Species interactions can vary depending on the environmental conditions in the ecosystem (Lang and Benbow, 2013). They can be negative, such as predation, parasitism, exploitative competition (e.g., competition via depletion of food resources), or interference competition (e.g., direct exclusion of a competitor). Positive species interactions include mutualism and facilitation (Begon and Harper, 1990). Ecosystem engineers often facilitate other species due to their

ability to modify habitats (Jones et al., 1994). For example, burrows dug by monitor lizards facilitate small animal communities by providing shelter, feeding and nesting opportunities (Doody et al., 2021).

Two species whose ability of habitat modification is well-known, are the North American beaver (*Castor canadensis*) and the Eurasian beaver (*Castor fiber*). Both species are very similar in ecology and behavior (Danilov and Fyodorov, 2015; Johnston, 2017). They are central-place foragers, i.e., they bring food and other resources for dam building or food caching back to their lodge or to the shoreline for consumption (meaning both the lodge and the shoreline can be defined as central place) (Fryxell and Doucet, 1991; Hood and Bayley, 2008; Busher et al., 2020). Beaver activity is typically restricted to proximity (<50 m) to the shoreline (Graf et al., 2016). Selection for different-sized woody stems changes depending on the distance to the shoreline and distance to the lodge, balancing energy expenditure of handling and processing food

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items, in line with optimal foraging theory (Donkor and Fryxell, 1999; Haarberg and Rosell, 2006; Hood and Bayley, 2008). Beavers forage on both aquatic and terrestrial vegetation, usually selecting deciduous trees such as willow, aspen, and birch over aquatic species, grasses, and crops, although selection and diet varies seasonally and depending on availability (Haarberg and Rosell, 2006; Krojerová-Prokešová et al., 2010; Milligan and Humphries, 2010; Vorel et al., 2015).

Beaver activities, such as cutting down trees, damming, and digging channels, can increase habitat heterogeneity and resource availability that can have facilitative effects on other species (Nummi and Kuuluvainen, 2013; Nummi et al., 2019; Nummi et al., 2021; Orazi et al., 2022). For example, damming leads to flooded areas that create clearings in the forest cover (via dying trees not adapted to flooding), consequently becoming available for bushes and shrubs to emerge (Hood and Bayley, 2009; Nummi et al., 2019). Such habitat modifications can increase water quality by slowing water flow and retaining sediments and provide dead wood and habitat for a wide range of organisms, including plants, fungi, invertebrates and vertebrates (Naiman et al., 1988; Bason et al., 2017; Nummi et al., 2019). For example, habitat modifications by beavers might indirectly increase the availability of prey species for mesopredators, such as red fox (*Vulpes vulpes*) (Nummi et al., 2019). Therefore, beavers can play an important role in conservation biology, and be a valuable tool for habitat restoration and rewilding of nature (Law et al., 2017; Willby et al., 2018; Nummi et al., 2021). However, these habitat modifications can also lead to human-wildlife conflicts, e.g., when beavers flood agricultural crops or cut down economically valuable forest stands.

Deer, like beavers, fulfil important ecological functions by increasing vegetation diversity (Faison et al., 2016) and seed dispersal (Irvani et al., 2011). However, they can also have negative impacts, especially when they become overabundant due to the absence of large predators (Ritchie et al., 2012), e.g., causing damage to agricultural crops and forests stands (Putman, 1986; Fuller and Gill, 2001). These positive and negative impacts, combined with their importance for hunting, make deer a central group concerning wildlife management in many European and North American regions (Putman et al., 2011; Lesser et al., 2019). Consequently, an increased understanding of how beaver activity affects deer habitat use and population density (and vice versa) will enable us to evaluate if and how beavers could mitigate human-wildlife conflicts. For example, by providing more riparian woody vegetation for deer, beaver activity might help to decrease deer browsing damage in crop fields and economically more valuable forest stands. Conversely, if deer outcompete beavers, this might have effects on the habitat composition (Baker et al., 2012).

Although several studies investigated beaver-deer interactions in North America (Nietvelt, 2001; Baker et al., 2005; Hood and Bayley, 2008), little is known regarding this topic in the more human-dominated landscapes of Europe (Nummi et al., 2019; Fedyn et al., 2022). Here, we investigated how beaver activity affected roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and red fox in a human-dominated landscape in Denmark. Roe deer are browsers, foraging mostly on herbs, leaves, seedlings, and bushes, while red and fallow deer are mixed feeders that can act as grazers, but can shift between woody and grassy vegetation according to availability (Latham, 1999; Asferg and Olesen, 2004; Agger, 2018; Spitzer et al., 2020). Nevertheless, food niches overlap among the three deer species (Obidziński et al., 2013). Unlike beavers, deer are not central-place foragers, moving from one feeding area to another depending on resource availability, and mostly browse on leaves and buds, leaving larger stems intact (Hood and Bayley, 2008).

We describe foraging pattern by beavers and tested the hypothesis whether beaver activity (measured as proportion of cut stems and frequency of lodges/dams) affects plant species richness and diversity, thereby affecting roe deer, red deer, fallow deer, red fox, as well as mammal species richness in general, either via facilitation or competition. Specifically, we expected that higher beaver activity increases

woody vegetation species richness and diversity close to the shore (but not further from the water, because beavers have little impact there), and that these habitat modifications increase mammal species richness. Moreover, we predicted that beaver activity facilitates the presence and relative abundance of red fox and roe deer via provisioning of foraging resources (small rodents in the case of red fox and herbaceous and deciduous vegetation in the case of roe deer), but less so red and fallow deer, due to differing feeding ecology. Alternatively, if beavers reduce the availability of woody vegetation, we predicted competition between beavers and roe deer, with the latter avoiding proximity to the shoreline in areas with high beaver activity. To test these predictions, we investigated relative changes in mammal species richness and deer numbers/presence in relation to the distance from the shore and in areas of varying beaver activity.

2. Material and methods

2.1. Study area

We collected data in three different areas: (1) Klosterheden Plantage, where 18 beavers were reintroduced in 1998 after centuries of absence (Miljø- og fødevarerministeriet, 2020). In 2019, the population size in Jutland was around 240–270 individuals (Miljø- og fødevarerministeriet, 2020). The plantation has an area of 6.400 ha and is located in Western Jutland, Denmark (Fig. 1). Woody vegetation is dominated by conifers, interspersed with deciduous trees and various shrub species. There are several lakes that are interconnected by small streams (Fig. 1). (2) Hoverdal plantation is located ca. 35 km south of Klosterheden (Fig. 1) and was used as control area for our camera trap study (see below), because beavers were not present in the area at the time of the study. The habitat composition was comparable to Klosterheden. (3) Silkeborg forest, located in mid-Jutland (Fig. 1) was used as control area (beavers not present at the time of the study) for the pellet count transects (see below). It consists of deciduous, mixed and coniferous forests interspersed by farmland, and contains several larger lakes that are partly connected by the river Gudenå. Red deer, roe deer and fallow deer occurred in all study areas (Baagøe and Jensen, 2007). All work was non-manipulative and did not require animal ethics approval.

2.2. Data collection and preparation

2.2.1. Vegetation transects

From 11 October to 29 November 2018, we walked 80 transects to study beaver foraging (hereafter vegetation transects) in Klosterheden plantation, located within 8 different beaver territories (6–10 transects per territory). Transects were pre-selected in Arcmap 10.4.1 aiming to equally cover the area of each territory and were laid perpendicular to the water body (starting from the shoreline; Fig. 1). We omitted 8 transects that did not contain woody vegetation, leaving 72 transects for our analysis. Transects were 100 m long, 5 m wide, and were divided into 100 one-meter distance classes. For each distance class, we recorded the number of cut (by beaver foraging) and uncut stems of all woody vegetation and separately for 3 size classes, measured as stem diameter at 15 cm above the ground: (1) small, 1–5 cm, (2) medium, 6–15 cm, and (3) large, >15 cm. We identified plants on genus or (rarely) species level during fieldwork (Table S1). For each transect, we estimated the genus richness, Shannon-Wiener Index (hereafter Shannon index) and Simpson's Index of Diversity (hereafter Simpson index), using the R package 'vegan' (Oksanen et al., 2013), as measures of woody vegetation diversity.

2.2.2. Camera trap setup

Camera traps were deployed at 88 locations (22 transects; Fig. 1) in Klosterheden and at 12 locations (3 transects) in Hoverdal between fall 2018 and spring 2019, and at 12 locations (3 transects) in Silkeborg in fall 2021. Camera traps were placed along 100 m long transects

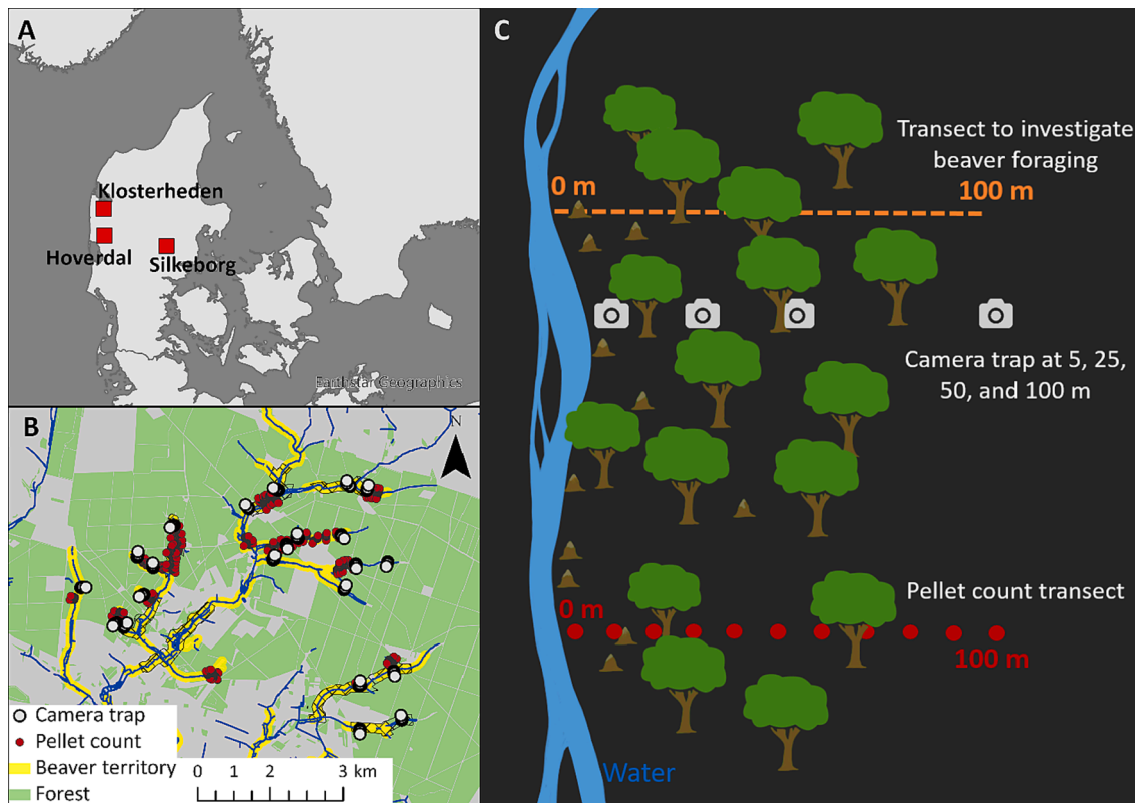


Fig. 1. Showing (A) the location of our study areas in Hoverdal (camera trap transects; beavers absent), Silkeborg forest (camera trap and pellet count transects; beavers absent), and Klosterheden (all three types of transect; beavers present). Map (B) shows Klosterheden (the main study area), indicating the location of beaver territories (yellow shading) and the location of pellet count transects and camera traps. Cross-hatched areas indicate the beaver territories where we walked vegetation transects. Plot (C) gives a schematic overview of how the different transects were set up. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

perpendicular to water bodies at 5, 25, 50 and 100 m from the shore (Fig. 1). Cameras were 24-h motion-triggered, and set to a 2 s interval between pictures, capturing one picture when triggered. They recorded between 7 and 34 days of data (mean number of days \pm SD = 31.30 \pm 3.76). All pictures were manually examined, recording each animal observation, the start and end time of the observation, the species, and number of individuals. If there were multiple photos of an animal of the same species within 15 min, it was registered as a single observation to avoid pseudo replication. If a photo contained several individuals, they were registered under 1 observation, but with multiple individuals.

2.2.3. Pellet counts

We conducted deer pellet counts along 151 transects in Klosterheden and Silkeborg between August and December 2021. The selection of pellet count locations in Klosterheden was based on existing beaver territories (5–10 transects per territory). In Silkeborg, we selected areas that provided good potential beaver habitat. Each transect was 100 m long, laid perpendicular to the water body, and consisted of 11 point count plots with a 2 m radius, located from 0 m (at the shore) every 10 m to 100 m from the shore (Fig. 1). We recorded the GPS location of each plot, and the number of deer pellet groups, defined as ≥ 1 pellet that was/did not distinguishable from other pellet groups by size, shape or freshness (though we only used presence absence of pellets for the analyses; see below). We could not reliably distinguish red and fallow deer pellets, and consequently merged these two species. Moreover, we recorded the proportion of bush and ground vegetation cover within each plot, the number of coniferous and deciduous trees, and the number of beaver-cut trees. However, this latter information provided too little data as indicator of beaver activity.

2.2.4. Beaver activity measures

We measured beaver activity (here defined as their potential impact on woody vegetation by cutting trees and building lodges and dams) on two spatial scales, (1) on transect level and (2) on territory level. We expected to find effects of beaver activity on plant diversity at the local transect level (due to plants being immobile responding directly to habitat alterations by beavers) and to find effects of beaver activity on mammals on territory rather than transect level, as mammals are mobile, using larger areas.

For the vegetation transects, we directly used the proportion of cut stems within 20 m from the shore (most of the foraging was restricted to this distance; Fig. 2A) as measure of beaver activity on transect level. We categorized beaver activity as ‘high’ if the proportion of cut stems was ≥ 0.2 , and as ‘low’ when it was < 0.2 . We did not have information regarding the proportion of cut stems for all pellet count and camera trap transects, due to logistic constraints. Consequently, to define beaver activity for pellet count and camera trap transects, we used information of active beaver lodges and dams, collected between the years 2015–2021. We categorized beaver activity as ‘high’ if an active lodge or dam was located within 100 m from the transect and ‘low’ if no lodge or dam was located within 100 m from the transect. Beavers were not present at the time of the survey in control areas (Silkeborg and Hoverdal); thus, beaver activity was defined as ‘absent’. To define beaver activity on territory level (for all types of transects), we counted the number of lodges and dams per km shoreline within each territory, and defined beaver activity as ‘high’ in territories with ≥ 2 lodges and/or dams per km shoreline, and as ‘low’ in territories with < 2 lodges and/or dams per km shoreline. For control areas, we defined hypothetical beaver territories that consisted of control transects (beaver activity ‘absent’) within an area of typical size for a beaver territory ca. 1.5–3 km

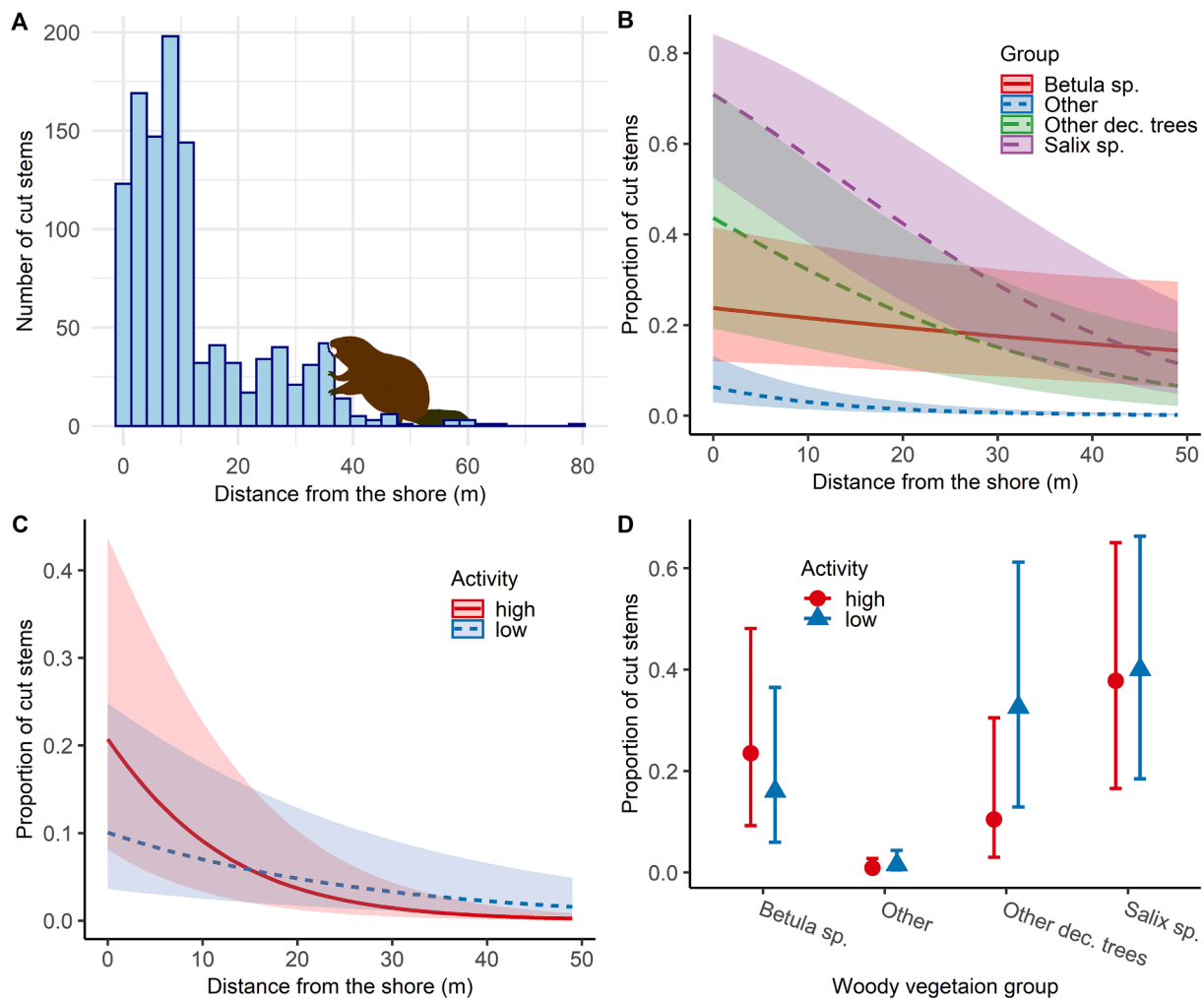


Fig. 2. Plot (A) shows the number of cut stems in relation to the distance from the shore. Moreover, the predicted proportion of cut stems in relation to the interaction of (B) woody vegetation group \times distance from the shore, (C) beaver activity (on territory level) \times distance from the shore, and (D) woody vegetation group \times beaver activity. The woody vegetation group ‘other’ consists of conifers, *Myrica* sp., and other bushes/shrubs. The 95% confidence intervals are shown as shading (B, C) or bars (D).

shoreline (Graf et al., 2016). We did this because beaver territory was used as random intercept in our analyses (see below).

2.3. Statistical analysis

2.3.1. Beaver foraging patterns

To analyze foraging patterns, we created 6 categories of woody vegetation based on genus or family level: *Betula* sp., Conifers, *Myrica* sp., *Salix* sp., other deciduous trees, and other deciduous bushes/shrubs (Table S1). Plants which could not be identified were excluded from the analysis. We conducted this analysis based on the first 50 m from the shoreline, because we only observed 9 cut stems $>$ 50 m from the shore (0.6% of all cut stems; Fig. 2). We analyzed the proportion of cut stems (estimated as number of total versus cut stems; response variable) using generalized linear mixed effects models (GLMM) with a binomial data distribution and a logit link, using the R package ‘lme4’ (Bates et al., 2015). We included the species group, distance from the shore, beaver activity on territory level, and the two-way interactions of species group \times distance from the shore, species group \times beaver activity, and beaver activity \times distance from the shore as fixed effects and territory ID as random intercept. After detecting convergence issues, we further categorized conifers, *Myrica* sp. and other bushes/shrubs as ‘other woody vegetation’, because these groups had very low proportions of cut stems (see results). In a separate analysis (to avoid overfitting our statistical

models), we included stem size instead of species group (model structure and other variables remained the same; Table S2). Finally, to avoid higher order interactions (e.g., distance from the shore \times species group \times beaver impact), we ran separate analyses (same model structure as above) for the species groups relevant for beaver foraging (willow, birch, and other deciduous trees; see results), including distance from the shore, stem size, beaver impact, and the interactions of distance from the shore \times stem size and distance from the shore \times beaver impact (Table S3).

2.3.2. Does beaver activity affect woody vegetation?

We conducted separate GLMMs with binomial distribution and logit link for birches, willows, and other deciduous trees to investigate if the proportion of small intact stems (out of all intact stems; response variable) changed in territories with high versus low beaver activity and relative to the distance from the shore, i.e., including the interaction of beaver activity \times distance from the shore. We could not run these analyses for *Myrica* sp. and other bushes/shrubs, because there was too little stem size variation (Table S4). Moreover, we initially analyzed species richness and diversity of intact woody vegetation (response variable) in relation to beaver activity (both on transect and territory level) using GLMMs of the R package ‘lmerTest’ (Kuznetsova et al., 2013). However, we could not meet assumptions of residual normality, and thus used non-parametric Wilcoxon–Mann–Whitney tests to assess

differences in species richness and diversity between areas of high versus low beaver activity (both on transect and territory level). If beavers alter species richness and diversity of woody vegetation, we expected to see differences between areas with high versus low beaver activity close to the shore, because this is where most foraging happens, but not further from the shoreline. Moreover, we calculated species richness and diversity based on all stems and based on intact stems only.

2.3.3. The effect of beaver activity on mammal species richness, number of deer and red fox observations, and deer pellet presence

We analyzed mammal species richness and the number of individuals observed (response variables in separate analyses), estimated for each camera trap location over the entire period the camera trap was deployed. We used GLMMs with a Poisson (mammal richness) or negative binomial (number of individuals) response distribution. We included the interaction of distance from the shore \times beaver activity (both on territory and transect level in separate analyses) as fixed effects, predicting that territories/transects with higher beaver activity result in higher mammal species richness close to the shore (affected by beaver activity), but not further from the shore (not affected by beaver activity). We additionally included the distance to the nearest road and the number of human observations as measure of human disturbance, the number of days the camera was deployed as measure of effort, and the territory ID as random intercept.

We then investigated if the number of roe deer, red deer, and red fox observed per camera trap (response variable in separate analyses) differed between areas of varying beaver activity in relation to the distance from the shore, using GLMMs with a Poisson distribution and a log link. We included the distance to the nearest road, the number of human observations, the number of days the camera was deployed, and the interaction of distance from the shore \times beaver activity (both on territory and transect level in separate analyses) as fixed effects, and the territory ID as random intercept. For the roe deer analysis, we additionally included red deer presence, as measure of competition (Bartos et al., 2002). We initially also analyzed roe and red deer presence on a given camera trap day using the same predictor variables, but excluded this analysis, because it yielded similar results. We could not analyze fallow deer observations (or any other species) due to too few observations (Table 2).

We defined deer pellet presence (response variable) when we observed ≥ 1 pellet group in each sampling plot. We then used GLMMs with a binomial distribution and a logit link to analyze the probability of deer pellet presence (separately for roe and red/fallow deer). We included the distance to the nearest road, proportion of bush cover, proportion of grass cover, the proportion of deciduous trees (on territory level; as proxy of forest type), and the interaction of distance from the shore \times beaver activity (both on territory and transect level in separate analyses) as fixed effects, and the territory ID as random intercept. For the roe deer analysis, we additionally included red/fallow deer pellet presence as measure of competition.

2.3.4. Model selection

We checked for correlations among numeric explanatory variables in all analyses and found no strong correlations (all Pearson $r < 0.6$). For model selection of all analyses, we performed a stepwise backward selection using the R package 'MuMIn' (Barton, 2016), and selected the most parsimonious model, defined as the model with the lowest AICc value (Wagenmakers and Farrell, 2004). Validation of the best model was made by visual inspection of residuals (Zuur and Ieno, 2016). Parameters that included zero within their 95% confidence interval were considered uninformative (Arnold, 2010).

3. Results

3.1. Beaver foraging patterns

We observed 9,505 woody plant stems, of which 8,117 (85%) were intact and 1,388 (15%) cut by beaver foraging. Beaver foraging was concentrated near the shore, with most cut stems recorded within 20 m from the water (Fig. 2A), and the average distance (\pm SD) being 12 ± 12 m (median: 8 m). Beavers mostly cut *Salix* sp. (692 stems), followed by *Betula* sp. (185 stems), *Myrica* sp. (121 stems), conifers (58 stems), other deciduous trees (48 stems), and other deciduous bushes/shrubs (4 stems; Fig. S1; 279 stems could not be identified). Compared to available stems and using other deciduous trees as reference category, beavers selected for willows, showed no selection or avoidance for birches, and avoided other woody vegetation (conifers, *Myrica* sp., and other bushes/shrubs; Table S2, Fig. S1). The proportion of cut stems generally decreased with increasing distance from the shore, but this effect was less pronounced for *Betula* sp. compared to the other groups (Fig. 2B). Moreover, the proportion of cut stems was higher in territories with high beaver activity (>2 lodges and/or dams per km shoreline), especially close to the shore (Fig. 2C). The proportion of cut *Betula* sp. stems was comparatively higher in territories with high beaver activity, whereas the reverse was the case for other deciduous trees and *Salix* sp., though this pattern was generally weak (Table S2, Fig. 2D).

The analysis including woody vegetation type performed better compared to the analysis including stem size (both analyses based on the same observations; AIC: 2,358 versus 3,836, marginal R^2 : 0.60 versus 0.40, Table S2). We detected 815 small stems, 247 medium-sized stems, and 37 large stems that were cut by beavers within 50 m from the shore (Fig. S2). Compared to available stems (5,115 small, 364 medium, and 322 large stems), beavers selected for medium-sized stems, and comparatively more so in territories with low beaver activity (Table S2, Fig. 3A, Fig. S2). The interaction of distance from the shore \times stem size was included in the best model but was uninformative. When analyzing selection for stem sizes in the different groups of woody vegetation, we excluded large stems (except for birches where 27 large stems were cut), because there were too few cut stems to achieve model convergence. Beaver selection for willow decreased with increasing distance from the shore, and more so in territories with high beaver activity (Fig. 3B, Table S3). The interactions of stem size \times distance from the shore and stem size \times beaver activity were not included in the best model. Selection for birches also decreased with increasing distance from the shore, but less so for small stems (Fig. 3C, Table S3). The interactions of beaver activity \times distance from the shore was not included in the best model. Selection for other deciduous trees was best explained by distance from the shore, with the proportion of cut stems decreasing further from the shore (Table S3). No other variables were included in the best model.

3.2. Beaver effects on woody vegetation

The proportion of the different groups of woody vegetation did not markedly change in territories with high versus low beaver activity (Fig. S1). The proportion of small intact birch stems was generally higher in territories with low beaver activity, and more so close to the shore though this effect was generally small (Fig. S3, Table S4). There was no statistical difference in the proportion of small stems for willow and other deciduous trees in territories with high versus low beaver activity and depending on the distance from the shore.

Genus richness of woody vegetation ranged from 1 to 12 genera (mean \pm SD: 3.6 ± 2.3), Shannon diversity from 0 to 1.78 (0.73 ± 0.53), and Simpson diversity from 0 to 0.82 (0.39 ± 0.27), and was generally higher 21–80 m from the shoreline compared to 0–20 m from the shore (Fig. 4). When analyzed on transect level and when species richness and diversity were estimated from all stems, woody plant diversity was higher in transects with higher beaver activity within the first 20 m from the shore, but not > 20 –80 m from the shore (Fig. 4; Table 1). When

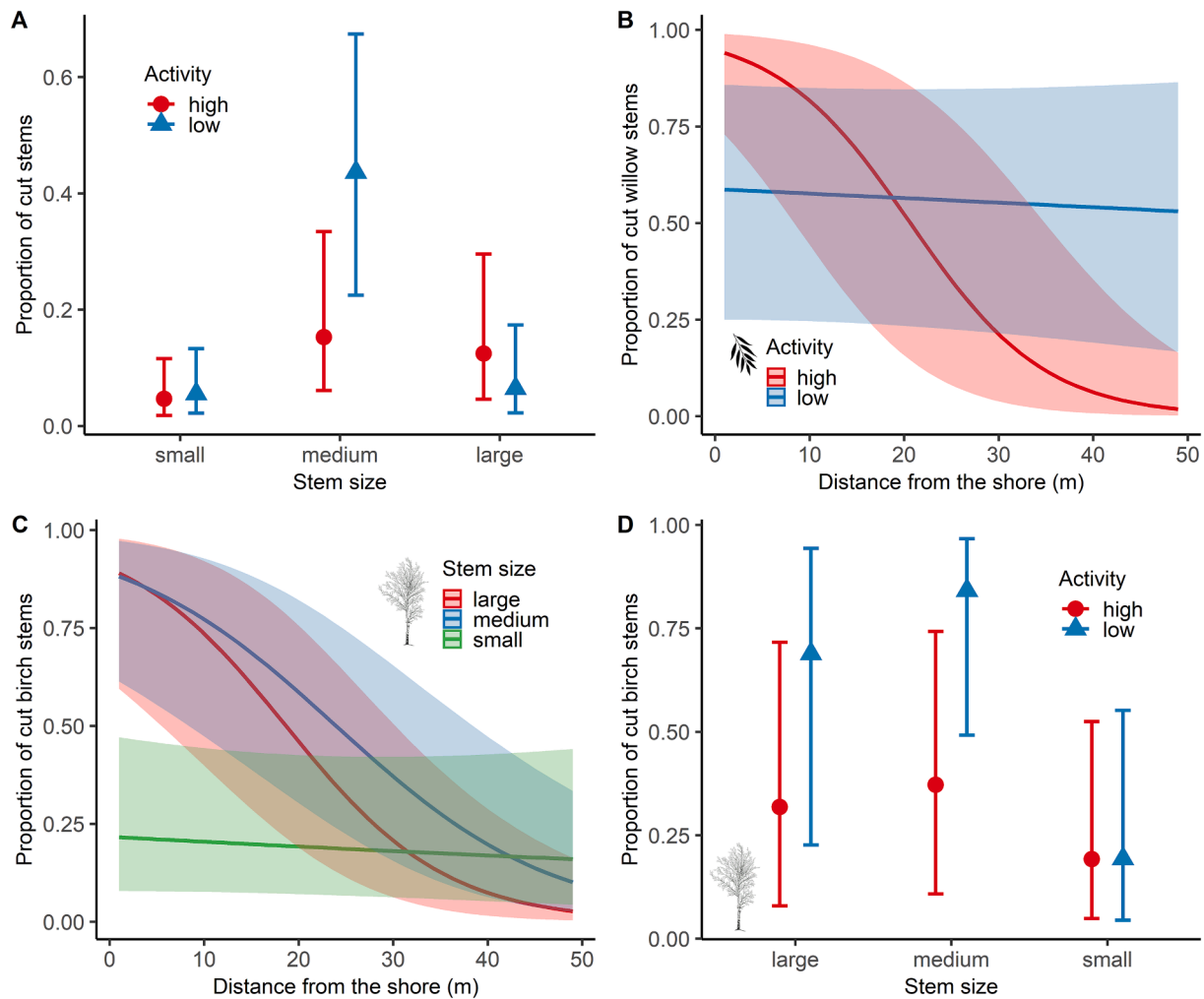


Fig. 3. The predicted effect of (A) stem size \times beaver activity on the proportion of cut stems (all woody vegetation), (B) distance from the shore \times beaver activity on the proportion of cut willow stems, and (C) distance from the shore \times stem size and (D) stem size \times beaver activity on the proportion of cut birch stems. The 95% confidence intervals are shown as bars (A, C) or shading (B, D).

species richness and diversity were estimated from intact stems only, there was no significant difference between transects with high versus low beaver activity, both close and further from the shore (Fig. 4, Table 1). Based on territory level, species richness and diversity did not significantly differ between territories with high or low beaver activity, both when diversity was estimated based on all or intact stems, and both close and further from the shoreline (Fig. 4, Table 1).

3.3. Effects of beaver activity on mammals

We recorded 2,286 mammal observations (4,658 individuals) during 3,772 camera trap days, consisting of 11 species excluding humans (Table 2). We recorded between 0 and 7 mammal species per camera trap location (mean \pm SD: 2.7 ± 1.3). Mammal species richness was not explained by any of the factors included in the analysis (distance from the shore, beaver activity based on territory and transect level, number of humans observed, distance from roads), though there was a trend that mammal species richness increased with increasing camera trap days (Estimate \pm SD: 0.03 ± 0.01 , 95% confidence interval: -0.001 ; 0.06). The number of mammal observations increased with camera trap days (Estimate \pm SD: 0.05 ± 0.02 , 95% confidence interval: 0.02 ; 0.09), but no other variable was included in the best model. When comparing the number of observations per camera (no statistical comparison was possible due to low sample sizes), red fox and raccoon dogs were recorded more often in Klosterheden (beavers present) than in Hoverdal

and Silkeborg (beavers absent), whereas there were little differences in the other species (Table 2).

When analyzing the number of roe and red deer from camera traps, the interaction of distance from the shore \times beaver activity was retained in the best model, both when beaver activity was estimated on territory or transect level (Table S5). However, this interaction was often uninformative, with confidence intervals overlapping zero (Table S5). In areas where beavers were absent, the number of roe deer was highest at 50 m from the shore compared to the other distance classes (Fig. 5A). When beaver activity was estimated on transect level, in areas with high beaver activity, roe deer numbers tended to be comparatively lower closer to the shoreline, but this interaction was uninformative (Fig. 5A, Table S5). In areas with beaver activity estimated on territory level, no clear pattern emerged (Fig. S4). In areas with no and high beaver activity, red deer numbers were generally higher further from the shore. This effect was stronger in areas with high beaver activity compared to areas where beavers were absent (Fig. 5B). There was no clear pattern in areas with low beaver activity, though red deer observations tended to be higher close to the shore (Fig. 5B). Moreover, the number of red deer was positively correlated with increasing distance from roads and negatively with the number of humans observed (Table S5). The number of camera trap days positively correlated with the number of roe and red deer in all analyses (Table S5). The number of red fox observations per camera trap correlated positively with increasing distance from roads and number of humans recorded (Table S6). The interaction of beaver activity

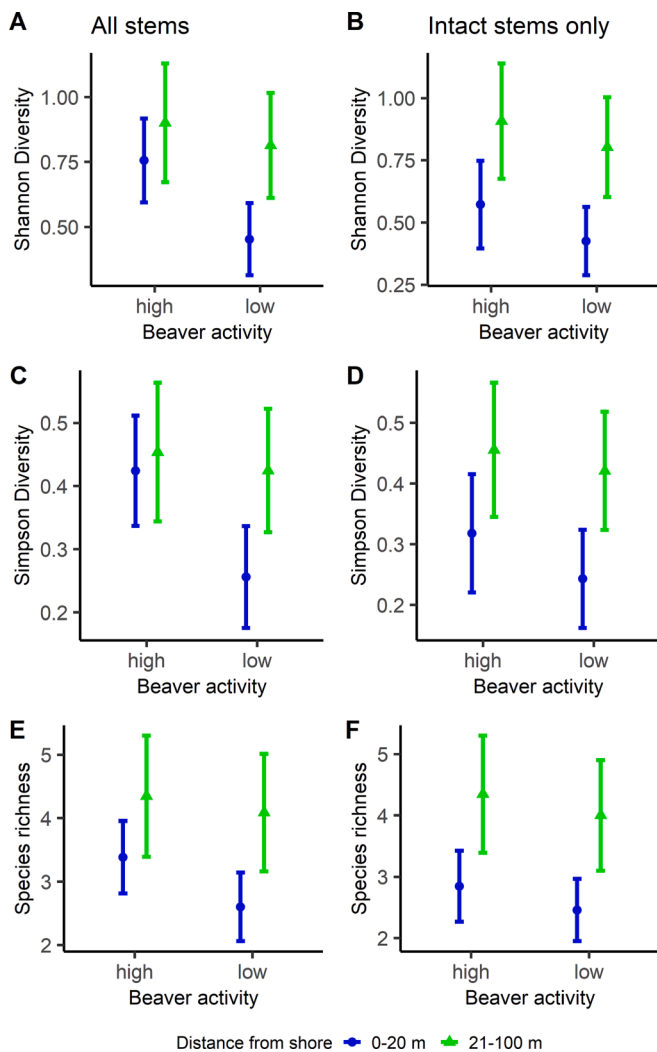


Fig. 4. Shannon diversity (A, B), Simpson diversity (C, D), and species richness (E, F) of woody vegetation shown separately for areas with high versus low beaver activity estimated on transect level and for the first 20 m from the shore versus larger distances (21–100 m). The left panel shows diversity and species richness calculated from all stems (significant differences between high versus low beaver activity transects within 20 m from the shore), and the right panel from intact stems only (no significant differences).

(estimated on transect level) and distance from the shore was included in the best model but was uninformative (Table S6).

We recorded 348 roe deer pellet groups and 107 pellet groups of red or fallow deer on 154 transects (1,611 sampling plots). The interaction of distance from the shore \times beaver activity was never included in the best model (Table S7). The probability of roe deer pellets being present was higher in areas with low beaver activity estimated on territory level compared to areas with high or no beaver activity (Table S7). Moreover, roe deer pellet presence correlated positively with increasing distances from roads (Fig. 5C), with decreasing proportion of grass cover, and decreasing proportion of deciduous trees (the latter being only informative in the analysis with beaver activity estimated on territory level; Table S7). Red/fallow deer pellet presence correlated positively with increasing distance from the shoreline (Fig. 5D). The proportion of deciduous trees was included in the best model, but uninformative (Table S7).

4. Discussion

Our study confirms that beavers select for proximity to water and for

Table 1

Showing the *W*- and *P*-value for comparisons of Shannon diversity, Simpson diversity, and species richness between territories of high versus low beaver activity, shown separately for distance from the shore (0–20 m and 21–100 m), all stems and intact stems only, and for activity estimated on territory and transect level.

| Parameter | Diversity based on Distance from shore | all stems | | intact stems | |
|------------------------|--|------------|-----------------|--------------|-----------------|
| | | <i>W</i> | <i>P</i> -value | <i>W</i> | <i>P</i> -value |
| <i>Territory level</i> | | | | | |
| Shannon Diversity | 0–20 m | 553 | 0.191 | 548 | 0.213 |
| Simpson Diversity | 0–20 m | 552 | 0.196 | 534 | 0.298 |
| Species richness | 0–20 m | 532 | 0.307 | 542 | 0.235 |
| Shannon Diversity | 21–100 m | 436 | 0.691 | 427 | 0.598 |
| Simpson Diversity | 21–100 m | 432 | 0.649 | 425 | 0.578 |
| Species richness | 21–100 m | 405 | 0.394 | 410 | 0.431 |
| <i>Transect level</i> | | | | | |
| Shannon Diversity | 0–20 m | 635 | 0.009 | 532 | 0.265 |
| Simpson Diversity | 0–20 m | 624 | 0.014 | 537 | 0.235 |
| Species richness | 0–20 m | 610 | 0.021 | 539 | 0.208 |
| Shannon Diversity | 21–100 m | 495 | 0.564 | 507 | 0.452 |
| Simpson Diversity | 21–100 m | 483 | 0.688 | 491 | 0.604 |
| Species richness | 21–100 m | 499 | 0.522 | 506 | 0.457 |

willows and birches (Fryxell and Doucet, 1991; Haarberg and Rosell, 2006; Vorel et al., 2015), and indicates that beavers alter their foraging patterns within areas of increased activity. Moreover, our findings indicate that beavers either increase woody vegetation diversity and species richness or select for these areas. However, we found no effects of beaver activity on mammal species richness and red fox observations, and only weak evidence for exploitative competition between beavers and roe and red deer, indicated by avoidance of proximity to water by deer in areas with high beaver activity and potentially by lower beaver activity in areas of high deer abundance. The absence of strong inter-specific interactions might be related to the area being highly human modified.

4.1. Beaver foraging patterns and impacts on woody vegetation

In line with the central-place foraging hypothesis, beavers selected woody vegetation close to the shore, likely as response to availability of preferred vegetation, energetic costs associated with terrestrial movements, and potentially (perceived) predation risk (Basey and Jenkins, 1995; Haarberg and Rosell, 2006; Swinnen et al., 2015). Beavers selected for willows, other deciduous trees (mostly *Prunus* sp. and *Quercus* sp.) and birches, and avoided conifers and *Myrica* sp., also shown in previous studies (Erome and Broyer, 1984; Nolet et al., 1994; Vorel et al., 2015). They selected for willows and other deciduous trees over birches close to the shore, but this difference disappeared at greater distances from the shore (>30 m). This pattern was mostly driven by the selection for small and medium-sized birch stems further from the shore. Thus, beavers likely avoided cutting down larger trees further from the shore due to constraints regarding handling time (cutting and transportation time), with handling costs exceeding energy gain (Wetterer, 1989). As predicted, beaver foraging also differed in territories with high versus low activity. Unsurprisingly, the probability of stems being cut was higher in territories with high beaver activity (measured on territory level), i.e. beavers probably affect vegetation more in areas where they built more dams and lodges, with dam building usually depending on landscape composition and resource availability (St-Pierre et al., 2017). Similarly, selection for woody vegetation (and stem size) also differed between territories of high and low beaver activity, respectively, though these differences were generally small. More generally, we found evidence that beavers deplete woody vegetation close to the shore, as the proportion of cut stems increased in areas with high beaver activity, while the number of intact small birch stems declined. It was previously suggested that the impact of beavers as a keystone species might not be as pronounced in boreal forests, at least

Table 2

The number of camera trap observations (number of individuals in parenthesis) separately for the different mammal species and for Hoverdal and Silkeborg (beavers absent) and Klosterheden (beavers present).

| Species | Area | Observations (individuals) | Observations per camera | Area | Observations (individuals) | Observations per camera |
|---|------------------------|----------------------------|-------------------------|--------------|----------------------------|-------------------------|
| Domestic cat (<i>Felis catus</i>) | Hoverdal and Silkeborg | 0 (0) | 0.00 | Klosterheden | 4 (4) | 0.05 |
| Eurasian beaver (<i>Castor fiber</i>) | Hoverdal and Silkeborg | 0 (0) | 0.00 | Klosterheden | 2 (2) | 0.02 |
| European badger (<i>Meles meles</i>) | Hoverdal and Silkeborg | 5 (5) | 0.28 | Klosterheden | 8 (10) | 0.10 |
| European hare (<i>Lepus europaeus</i>) | Hoverdal and Silkeborg | 1 (1) | 0.06 | Klosterheden | 5 (5) | 0.06 |
| Fallow deer (<i>Dama dama</i>) | Hoverdal and Silkeborg | 8 (20) | 0.44 | Klosterheden | 68 (127) | 0.84 |
| Human (<i>Homo sapiens</i>) | Hoverdal and Silkeborg | 54 (79) | 3.00 | Klosterheden | 974 (1,837) | 12.02 |
| Marten (<i>Martes sp.</i>) | Hoverdal and Silkeborg | 2 (2) | 0.11 | Klosterheden | 17 (17) | 0.21 |
| Raccoon dog (<i>Nyctereutes procyonoides</i>) | Hoverdal and Silkeborg | 0 (0) | 0.00 | Klosterheden | 18 (22) | 0.22 |
| Red deer (<i>Cervus elaphus</i>) | Hoverdal and Silkeborg | 176 (474) | 9.78 | Klosterheden | 433 (1,458) | 5.35 |
| Red fox (<i>Vulpes vulpes</i>) | Hoverdal and Silkeborg | 15 (15) | 0.83 | Klosterheden | 185 (189) | 2.28 |
| Red squirrel (<i>Sciurus vulgaris</i>) | Hoverdal and Silkeborg | 2 (2) | 0.11 | Klosterheden | 11 (11) | 0.14 |
| Roe deer (<i>Capreolus capreolus</i>) | Hoverdal and Silkeborg | 63 (77) | 3.50 | Klosterheden | 235 (301) | 2.90 |

regarding woody plant composition, because selective foraging by beavers on deciduous trees leads to more coniferous-dominated forest (Hyvönen and Nummi, 2008; Nummi and Kuuluvainen, 2013).

The diversity and species richness of woody vegetation close to the shore was higher in areas with high beaver activity compared to areas with low beaver activity. However, this effect was only significant when estimated from all stems, but not when estimated from intact stems only (though the direction of the effect remained the same). Thus, rather than facilitating more diverse and species-rich woody vegetation, beavers might have selected for areas with higher diversity and species richness of woody vegetation although the two hypotheses are not mutually exclusive. Similarly, Voeker and Dooley Jr (2008) found little evidence that beaver foraging activity might be directly altering forest plant composition. Nevertheless, woody vegetation diversity and richness only differed close to the shore, where beavers forage, and not further away. This partly supports the hypothesis that beavers influenced woody vegetation composition. If beavers only select for areas of higher woody vegetation diversity and richness, we would have expected to find a difference also further from the shore. However, this would not necessarily have to be the case considering differences in riparian shore vegetation and forest vegetation away from the shore. In any case, it was previously shown that beavers can affect vegetation composition via tree cutting and flooding (Wright et al., 2002; Law et al., 2014; Stringer and Gaywood, 2016), sometimes in combination with deer (Hood and Bayley, 2009).

One main shortcoming of our study was that we did not compare woody vegetation diversity between areas with and without beavers. However, even if we would have collected this data, a true comparison would be complicated due to inherent differences in vegetation between regions. For example, Silkeborg area (beavers absent) consists of markedly different forest compared to Klosterheden (beaver present), and these differences are predominantly driven by forestry management and potentially other factors, such as climate and soil composition. Ideally, future studies should measure the vegetation diversity before and after the establishment of beavers or using exclosures in order to find causal links between beaver activity and their effects on vegetation.

4.2. Impacts on mammal species richness

Beaver activity did not affect mammal species richness at the local (proximity to water) and regional scale (beaver activity based on territory level). Similarly, Sundell et al. (2021), did not detect differences in the number of small mammal species in their study of beaver-modified sites versus control sites, but they did find a compositional difference in species assemblage between the two types of sites. Importantly, our setup did not allow us to examine the effects of beaver activity on smaller mammals, such as rodents, shrews and weasels, because camera traps were set approximately 1 m above ground to record deer. Nummi et al. (2019) found that mammal species richness and abundance was higher in beaver ponds than in control sites, with red fox, weasels and pine martens being more abundant, potentially due to an increased amphibian prey availability. Similarly, Fedyn et al. (2022) reported that small and large carnivores occurred more frequently and were more active at beaver sites. In this study, we only detected raccoon dogs in areas where beavers occurred, as well as more martens and red foxes in areas with beaver activity. However, these differences might have been related to landscape-scale differences unrelated to the occurrence of beavers, such as habitat type, forest management, and hunting. Generally, these latter factors might have been more important in affecting mammal species richness and abundance in this system.

4.3. Beaver-deer interactions

Our camera trap analysis indicated that on a local (transect) scale, both roe and red deer tended to avoid proximity to the shore when beaver activity was high compared to transects with low or no beaver activity. This provides limited evidence for exploitative competition between beavers and deer, i.e. competition for the same resources, such as small branches, twigs and leaves of edible plants (Tixier and Duncan, 1996; Krojerová-Prokešová et al., 2010). Beavers might monopolize food items preferred by deer by cutting down whole stems. However, deer avoidance of areas with beaver activity was very small and partly uninformative, and did not hold up when analyzed on territory level and when based on pellet counts, similar to a study from Finland (Nummi et al., 2019). Moreover, when only comparing transects and territories with low versus high beaver activity (located in the same region; i.e.,

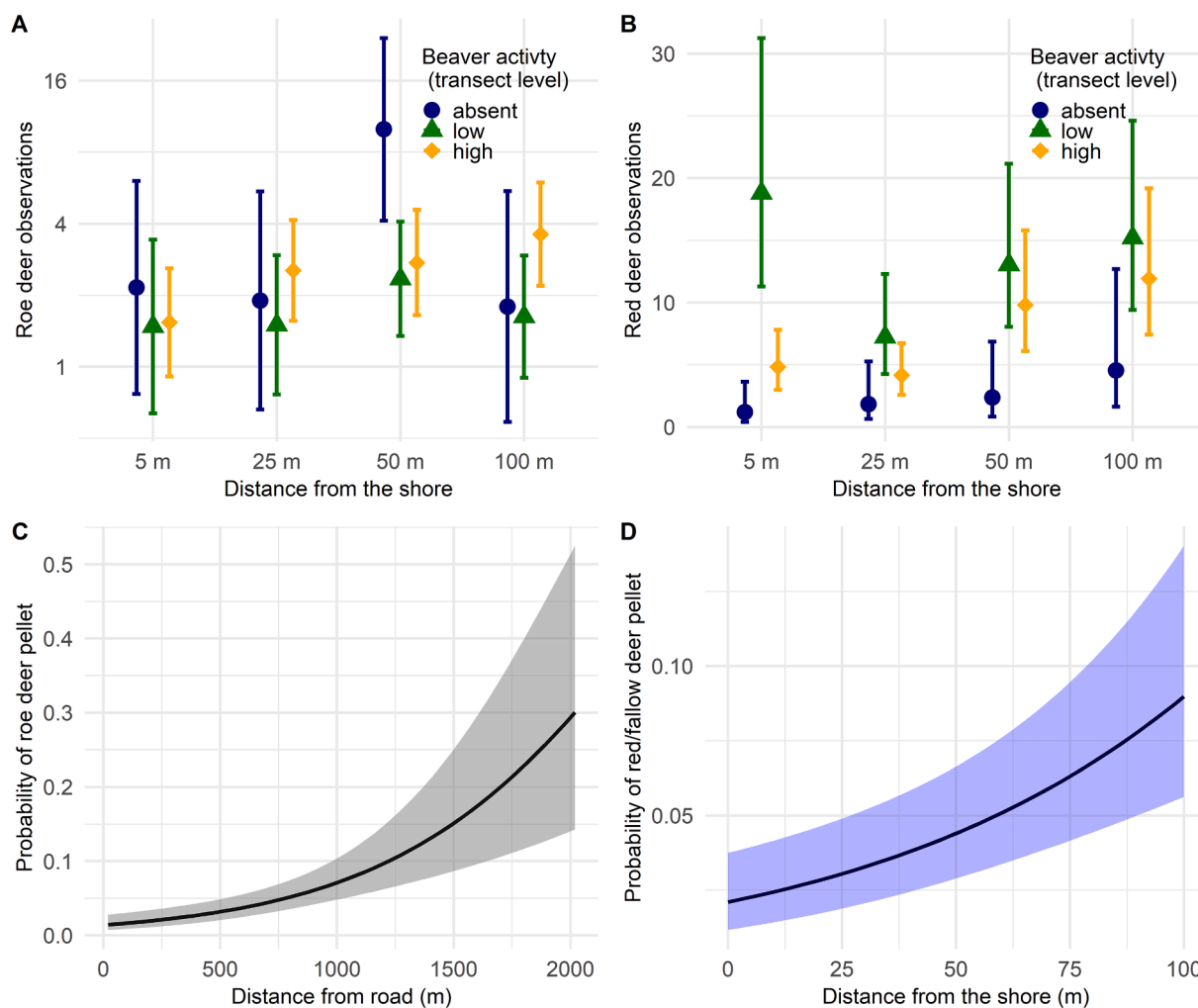


Fig. 5. The predicted effect of distance from the shore \times beaver activity estimated on transect level on the number of (A) roe and (B) red deer observations (from camera traps). Moreover, the predicted effect of (C) distance from roads on the probability of roe deer pellet presence and (D) distance from the shore on the probability of red/fallow deer pellet presence. Note that the y-axis of plot A is on log-scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

excluding control areas that were located elsewhere), we generally observed more roe and red deer in areas of low beaver activity, especially in proximity to the shore in the case of red deer. This might indicate that rather than beaver influencing deer, the opposite might be the case. That is, high red and roe deer abundance (being the most observed animals in Klosterheden) might reduce beaver activity. Similarly, increasing in elk densities were shown to cause beaver declines, potentially by exploitative exclusion via willow browsing (Nietvelt, 2001; Baker et al., 2012). Compared to beavers, deer move over larger areas on land when foraging (Hood and Bayley, 2008), which might give them a competitive advantage regarding resource exploitation, because it is easier for them to move to alternative foraging patches. Overall, habitat characteristics unrelated to beaver activity likely were the main driver of deer abundance, movement, and habitat use (Fedyń et al., 2022). This might be especially the case in human-dominated landscapes where forest structure is shaped by humans, as compared to pristine forest, where beavers can in some cases be the main actor creating early successional phases preferred by deer.

The different findings between camera trap pictures and pellet counts indicate that there might be a difference in how we measured deer presence/activity. Camera traps mostly captured active animals. Deer pellets likely represented data during high activity times (traveling and foraging) and directly subsequent to resting (Collins and Urness, 1981). These slight differences might explain why our findings

were not consistent. We deem the camera trap data less biased compared to the pellet group observations, because pellet detectability might have varied across and within transects. Although our pellet counts were conducted mostly within the same season, we cannot exclude the possibility that local conditions, such as variation in the amount of fallen leaves, affected pellet detectability (Lioy et al., 2014). This might explain why the probability of roe deer pellets declined in areas with higher proportions of deciduous trees, contradicting our predictions that roe deer select for deciduous forest (Borkowski et al., 2020). Additionally, pellet detectability likely varied within transects, being lower within the first 20 m from the shore, due to higher ground vegetation (grass, bushes, etc.), which could explain the negative correlation between roe deer pellet presence and grass cover.

4.4. Conclusions and future perspectives

Except from weak evidence of exploitative competition between beavers and deer, we found clear road avoidance by roe and red deer and red fox, indicating that our sample size was sufficient to detect animal space use patterns. Moreover, this finding implies that animals are strongly affected by human impacts, such as roads and forest management, also shown previously (Shepard et al., 2008; Jerina, 2012; Bischof et al., 2017). This raises the question how human impacts affect species interactions and ecosystem services. For example, it was shown that

deer-mediated ecosystem services depend on forest management intensity (Stokely and Betts, 2020), and that human actions can weaken the ecological effects of large carnivores in anthropogenic landscapes (Kuijper et al., 2016). In line with these studies, it is conceivable that human impacts disturb or supersede beaver-deer interactions and their respective roles in the ecosystem, including important ecosystem services. We did not detect strong effects of beaver activities on woody plant diversity and mammal species richness, calling into question if they can be considered a keystone species in this context (though importantly, beavers might have facilitated other organisms not investigated here). More generally, considering the large monetary, social, and cultural value mammals can provide for us (Sinclair, 2003; Okello et al., 2008; Di Minin et al., 2021), it is crucial to understand the impacts of human activities on ecosystem services by mammals.

Author contributions.

M.M. conceived the original ideas and supervised M.S.P. and J.R.A., and all authors contributed to the data collection, statistical analyses, and writing of the manuscript.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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