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The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals

Petri Nummi [a, *], Wenfei Liao [b], Ophélie Huet [c, e], Erminia Scarpulla [d, e], Janne Sundell [e]

[a] *Department of Forestry, University of Helsinki, P.O.Box 27, FI-00014, University of Helsinki, Finland*
[b] *Faculty of Biological and Environmental Sciences, University of Helsinki, P.O.Box 65, FI-00014, University of Helsinki, Finland*
[c] *Department of Animal Biology and Genetics, Master Behavioural Ecology, Evolution and Biodiversity, University of Tours, Faculty of Sciences and Technologies, Grandmont Park, 37200, Tours, France*
[d] *Department of Biological, Geological and Environmental Sciences, University of Bologna, via Francesco Selmi 3, 40126, Bologna, Italy*
[e] *Lammi Biological Station, University of Helsinki, Pääjärventie 320, FI-16900, Lammi, Finland*

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ABSTRACT

Beavers are ecosystem engineers which are capable to facilitate many groups of organisms. However, their facilitation of mammals has been little studied. We applied two methods, camera trapping and snow track survey to investigate the facilitation of a mammalian community by the ecosystem engineering of the American beaver (*Castor canadensis*) in a boreal setting. We found that both mammalian species richness (83% increase) and occurrence (12% increase) were significantly higher in beaver patches than in the controls. Of individual species, the moose (*Alces alces*) used beaver patches more during both the ice-free season and winter. The Eurasian otter (*Lutra lutra*), the pine marten (*Martes martes*) and the least weasel (*Mustela nivalis*) made more use of beaver sites during the winter. Our study highlights the role of ecosystem engineers in promoting species richness and abundance, especially in areas of relatively low productivity. Wetlands and their species have been in drastic decline during the past century, and promoting facilitative ecosystem engineering by beaver is feasible in habitat conservation or restoration. Beaver engineering may be especially valuable in landscapes artificially deficient in wetlands.

1. Introduction

Ecological facilitation is a form of species interaction in which a species may render a habitat more suitable for other organisms (Bertness and Callaway, 1994; Stachowicz, 2001; Soliveres et al., 2015). Facilitation is assumed to be especially important in harsh and moderately stressful environments (Holmgren and Scheffer, 2010; He and Bertness, 2014). Habitat modification by facilitation can include processes that lead to structural amelioration and/or resource enhancement in the environment (Bruno et al., 2003). Traditionally, facilitation has been documented especially in plant communities and among sessile animals; it has been found both in aquatic and terrestrial habitats, such as salt marshes, rocky shores and forests (Bertness and Leonard, 1997; Brooker et al., 2008). Although relatively few studies have focused on facilitation between more

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* Corresponding author.
E-mail address: petri.nummi@helsinki.fi (P. Nummi).

mobile animal species, accumulated research shows that facilitation also strongly affects animal species abundances and occurrences along with community structures (Van der Wal et al., 2000; Pringle, 2008; Nummi and Holopainen, 2014; Li et al., 2018).

Ecosystem engineers are a group of organisms that can bring about facilitation by affecting the habitat and resource availability to other species (Jones et al., 1994; Wright and Jones, 2006). A recent meta-analysis revealed that the overall effect of ecosystem engineers on diversity corresponds to a 25% increase in species richness globally (Romero et al., 2015). This is an important finding considering the decline in biodiversity worldwide (Grooten and Almond, 2018). Parallel to facilitation, ecosystem engineering is predicted to positively affect species richness, especially when it increases productivity in a low-productivity system (Wright and Jones, 2004).

Ecosystem engineers can be either autogenic or allogenic. Autogenic engineers are themselves a part of the new physical state, while allogenic engineers can create a structure but are not a part of the new physical state (Jones et al., 1997). Ecosystem engineers can also be classified into obligate and facultative engineers. Obligate ecosystem engineers make changes in habitat and community structure even when occurring in low numbers, whereas the impact of facultative engineers can only be detected in certain conditions such as at higher population densities (Coggan et al., 2018).

Beavers, i.e. Eurasian beavers (*Castor fiber*) and American beavers (*C. canadensis*), are allogenic and obligate ecosystem engineers, who are capable of changing multiple structural and abiotic variables in their riparian environment (Johnston, 2017). Via dam building, beavers create patch disturbances, which promote heterogeneity at both patch and landscape levels (Wright et al., 2002; Nummi et al., 2019; Willby et al., 2018). Damming changes both abiotic and biotic conditions in riparian areas. A water-level rise often considerably widens the wetland area and modifies the physical, chemical and biological conditions in the riparian zone. Beaver flooding leads to an increase in productivity, as e.g. carbon is released from the flooded soil and dying vegetation of the flooded area (Vehkaoja et al., 2015; Nummi et al., 2019). Additional engineering by beavers includes tree cutting, aquatic herbivory and channel digging. Tree cutting creates forest openings (Johnston and Naiman, 1990a), aquatic herbivory affects the habitat structure in the water column (Parker et al., 2007; Law et al., 2014), while channel digging provides more riparian connectivity into the landscape (Hood and Larson, 2015). Both beaver species are assumed to have equivalent effects on the environment (Danilov and Fyodorov, 2015).

At the beginning of the 20th century, beavers were on the verge of extinction both in America and Eurasia due to over-harvest. Both species have thereafter partially recovered. In North America, beavers had returned to most of their original range by the 1950s (Jenkins and Busher, 1979), and their present population is estimated at 30 million (Whitfield et al., 2015). The increase in the Eurasian beaver population is more recent; the species is recolonizing or has recolonized many parts of its original range. The population amounts to at least one million individuals and is increasing (Halley et al., 2012). With the demise of beavers, most of their ecosystem services in riparian ecosystems, including biodiversity maintenance, were also lost (see Law et al., 2017). During recent centuries, wetlands have been dramatically affected also because of other anthropogenic activities, such as overexploitation, flow modification, destruction or degradation of habitat, and changing climate (Dudgeon et al., 2006, Reid et al., 2019).

The occupation time of a beaver colony at a certain site varies from three years to many decades (Johnston and Naiman, 1990b; Hyvönen and Nummi, 2008). A beaver patch undergoes various successional phases over time (Naiman et al., 1988; Wright et al., 2004). First, an impoundment is formed by the water raised due to damming. This phase lasts from a few years to a few decades depending on the duration of the flood (Johnston and Naiman, 1990b; Hyvönen and Nummi, 2008). After beaver abandonment and dam breaching, terrestrial succession gradually begins at the patch and forms a beaver meadow (Johnston, 2017); in low-gradient landscapes, paludification may begin from beaver patches (Nummi et al., 2018). From a landscape perspective, beavers create a shifting mosaic of patches at various phases of succession in a wet-dry continuum.

Various species are facilitated at different phases of beaver patch succession. During the flooding phase, the abundance and diversity of animals, such as fish, frogs, waterbirds, and bats, increases (Snodgrass and Meffe, 1998; Dalbeck et al., 2007; Nummi et al., 2011; Nummi and Holopainen, 2014). In the beaver meadow phase, high nitrogen levels add plant diversity to the landscape level, which provides habitat harbouring e.g. threatened butterflies (Wright et al., 2002; Bartel et al., 2010). In the early phase of terrestrial succession, abundant saplings of deciduous trees provide food for herbivores (Wolfe, 1974; Hyvönen and Nummi, 2008). In landscapes long inhabited by beavers, beaver patches at a given time are in various successional phases in the landscape, thus many different species can concurrently be present.

Apart for otters and bats (e.g. LeBlanc et al., 2007; Ciechanowski et al., 2011), the knowledge of beaver facilitating other mammals is mainly based on separate observations rather than quantified information (Rosell et al., 2005). The known increase of abundance of organisms of various trophic levels (e.g. plants, invertebrates, vertebrates) should also affect mammalian species using them as food. In this study, we aimed to reveal the facilitative effect of beaver on other mammals by using two methods: camera trapping and snow tracking. We hypothesize that on a patch scale, beavers have a positive effect on mammal species richness and their occurrence of, at least, some of the species.

2. Methods

2.1. Study area

We collected data in a watershed (area 39 km^2) at Evo (61°12′ N, 25°07′ E) in southern Finland (Nummi and Pöysä, 1993; Arvola et al., 2010). The study lakes are oligotrophic and relatively small (0.3−13.7 ha, mean = 3.0 ± 3.4 ha). Boreal forest

covers most of the area, interspersed with lakes and mires. Agriculture and human settlement are limited and local. Apart from beaver-created variability, the landscape-level habitat structure of the Evo lakes has been fairly stable for the past 25 years (Suhonen et al., 2011; Thompson et al., 2016). At Evo, beavers move from one lake to another every three years on average, thus new beaver habitat patches are continuously created while old ones are abandoned (Hyvönen and Nummi, 2008). The beavers at Evo are introduced American beavers (Parker et al., 2012). The lakeshores of the study area are generally steep, with sparse emergent vegetation consisting mainly of sedges (*Carex* spp.) and common reed (*Phragmites australis*). Emergent vegetation is usually lined with narrow belts of floating vegetation, consisting of yellow water lilies (*Nuphar lutea*) and water lilies (*Nymphaea candida*); submerged vegetation is very sparse. The lake margins are lined with *Sphagnum* mosses or dwarf shrubs, and sedges dominate in drawdown areas abandoned by beavers. Coniferous spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate the surrounding forests, but the lakes are often lined with a narrow belt of deciduous birches (*Betula* spp.), alders (*Alnus* spp.) and willows (*Salix* spp.). Some lakes are typically situated on the glacio-fluvial sandy deposits in the lower part of the area and others are located on the till deposits in the upper areas (Arvola et al., 2010). The shore profile of beaver ponds are significantly shallower than non-beaver ponds and contain inundated herbaceous vegetation and bushes (Nummi and Hahtola, 2008). Located in a cool continental climate, all wetlands freeze over from November to April, which is also the timing of the snow cover.

In this study, we compared the composition of mammal fauna of 10 beaver-modified sites with 10 control sites. A beaver-modified site is a wetland formed following the construction of a beaver dam, in the outlet of a river or lake. The water table of two beaver-modified sites was lowering due to recent beaver abandonment (1−2 years), and the age of the eight beaver flowages varied from 2 to 33 years. The control sites are lakes within the same drainage basin as the beaver sites but not altered by beavers. Out of the 10 control patches, 6 were never engineered by beavers and 4 were engineered but then abandoned patches (5−11 years earlier); no significant difference of these never-beavered sites and long-abandoned sites were found with two-sided Wilcoxon's test (Table 1).

2.2. Camera trapping

Camera traps were used to evaluate how the ecosystem engineering by beavers affects other mammal species (Mishin and Trenkov, 2016). Cameras (Uovision UV595-Full HD, Ltl 8219A and Burrel S10/S12 HD) were active in the study sites for approximately eight months in total during two periods (12.9.−21.11.2017 and 15.1.−17.7.2018). At each study site, the cameras were installed parallel to the shore at a 2−5-m distance from the shore in small open areas with good visibility. Each camera was installed at a height of 120 cm from the ground level. The cameras were set to take three pictures per trigger with a 1-min delay after each picture. Each study site had one stationary camera, and ten additional cameras were rotated between study sites at approximately two-week intervals. The cameras used were capable of taking night photos. We did not use lures to attract animals, and cameras were active 24 h daily.

The pictures were checked at the end of the camera trapping period. Detections of the same species at the same site within 30 min were calculated as one detection. We pooled the camera trappings as one observation per pond per season. We classified 15th April to 31st May as spring, 1st June to 31st July as summer, 1st September to 30th November as autumn, and 1st January to 14th April as winter. In total, we had 80 observations from 20 sites.

2.3. Snow tracking

Snow tracking was conducted during the wintertime, from 15th February to 12th April 2018, with each site visited five times during the survey. In total, we had 100 observations from the 20 sites. Because the snow must be deep and fresh enough so that identifiable prints are left by the animals, mammal tracks were counted 1−4 days after the last snowfall (Sulkava, 2007; Riistakolmiot, 2016). Transects were made around all the water bodies with a distance of 5−20 m from the shore line, and mammal tracks crossing the counting route were listed as one observation for a species. Cases where an animal was following the trail were counted as one observation. Tracks were identified to species or species group levels; the latter mainly included different hares, including brown hare (*Lepus capensis*) and mountain hare (*L. timidus*), and small mammals, including voles (Arvicolinae), mice (Murinae) and shrews (Soricinae).

Table 1
Data exploration of the differences of mammal species number and visits between never-beaver ponds and beaver-abandoned ponds with two-sided Wilcoxon's test. No significance was found between the two types of non-beaver ponds.

	Data Types	Never-Beaver	Beaver-Abandoned	p-value
Camera Data	**Species Number**	0.75 ± 0.99	0.63 ± 0.89	0.771
	Mammal Visits	1.13 ± 1.54	1.19 ± 1.79	0.964
Snow Track Data	**Species Number**	1.37 ± 0.89	1.50 ± 0.89	0.503
	Number of Snow Tracks	10.87 ± 11.02	14.70 ± 14.31	0.250

2.4. Statistical analysis

We conducted all data analyses using statistics software R (R Core Team, 2018). The response variables, species numbers and mammal visits from the wildlife camera and species numbers from the snow track surveys followed a Poisson distribution. In data exploration, we detected zero inflation in the camera data due to many photos without animals pictured; thus, we applied zero-inflated Poisson (ZIP) models with the package "glmmTMB" (Brooks et al., 2017). Additionally, we included the study sites and the seasons as potential random effects in the mammal visit model to avoid pseudo-replication and to account for the differences among sites and seasons (Zuur et al., 2010). In the snow track data, we detected no random effects affecting species numbers and thus applied generalised linear models (GLM).

In the models, we used sampling effort and patch categories, i.e. beaver-modified and control patches, as explanatory variables (Appdendix 1). We standardized sampling effort, i.e. trapping nights in the camera data and survey route length in the snow track data, and used them as covariates. We chose the optimal model based on the lowest Akaike information criterion (AIC) values. To validate the models, we simulated 10 000 datasets to check whether the models could generate similar data to the observed data (Zuur and Ieno, 2016).

Due to serious overdispersion caused by large variations, we did not use GLM to analyse the snow track number data in this paper. Instead, we compared the snow track numbers in the beaver and control patches with the one-sided Wilcoxon's test using the function "wilcox.test" (R Core Team, 2018). Additionally, we tested three individual mammal species with more than 20 presence observations in the camera data: the moose (*Alces alces*), the raccoon dog (*Nyctereutes procyonoides*) and the red fox (*Vulpes vulpes*). In the snow track data, we tested the number of snow tracks per kilometre per survey for eight species/guilds (Appendix 2).

3. Results

Altogether, we found 11 species in the beaver patches and 9 species in the controls during the camera trapping, and 10 species/species groups in the beaver patches and 8 in the controls during the snow track surveys. On average, we found 1.28 species per season in beaver patches and 0.70 species per season in control patches for the camera trapping (Fig. 1A); 2.71 species per kilometer per survey in beaver patches and 2.41 species per kilometer per survey in control patches for the snow track survey (Fig. 1B).
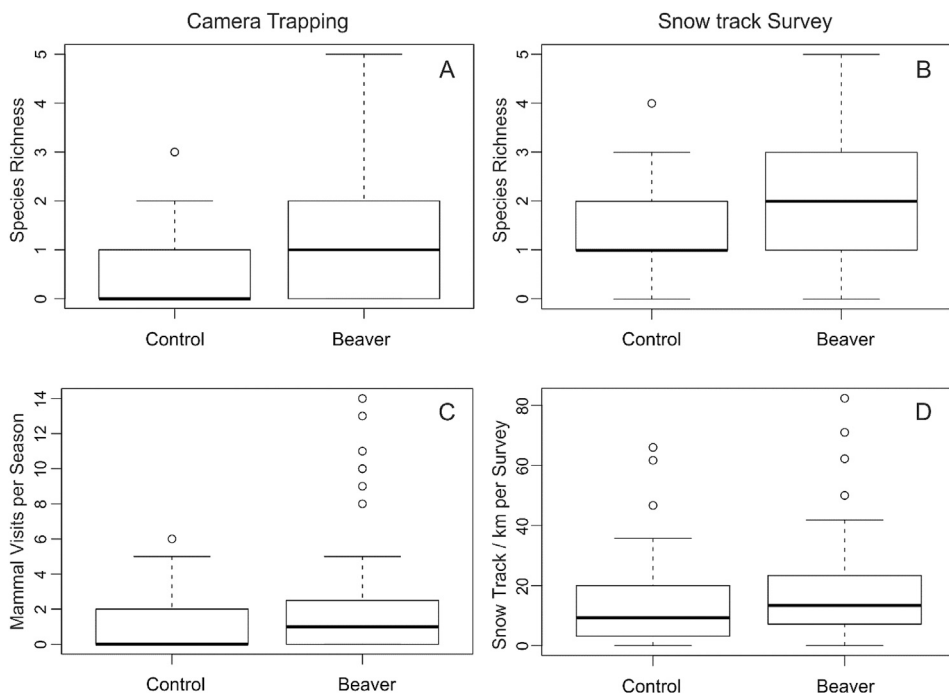

Fig. 1. Boxplots of the camera trapping and the snow track survey. Species richness in camera trapping (A) and snow survey (B), mammal visits per season in camera trapping (C), and snow track counts/km per survey (D).
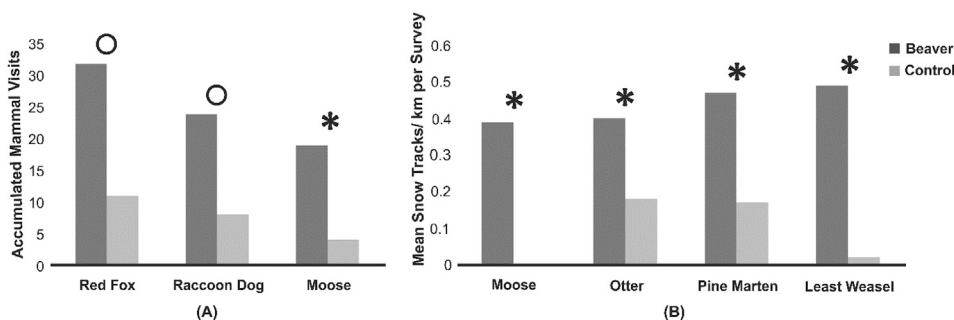
Fig. 2. (A) Accumulated mammal visits in beaver and control patches according to camera trappings; **(B)** mean snow track numbers per kilometre per survey route of four species in beaver and control patches. Only species showing P < 0.05 (*) or P < 0.10(○) shown in figures (for all species, see text and Appendix 2).

3.1. Camera results in beaver and control ponds

The result of the optimal ZIP model reveals that mammal species number was significantly higher in beaver patches than in the control patches (p = 0.024, Appendix 1.1). The optimal ZIP model shows that no covariates can explain mammal presence and absence, but mammals visited beaver patches more than the controls (p = 0.046, Appendix 1.2). Wilcoxon's test results showed that moose visited beaver ponds significantly more than the control ponds (p = 0.042). A similar trend was also evident for the red fox and the raccoon dog (Fig. 2). Red squirrels (*Sciurus vulgaris*), mountain hares, brown hares, white-tailed deers (*Odocoileus virginianus*), roe deers (*Capreolus capreolus*), and badgers (*Meles meles*; see Appendix 2) were additional species identified in the cameras.

3.2. Snow tracks

The snow tracks also showed species number to be higher in beaver patches than in control patches (p = 0.013, Appendix 1.3) along with their activity. The mean track number in beaver patches was 18.37 tracks per kilometer per survey route, while we observed 13.77 tracks per kilometer per survey route in the control patches (Wilcoxon's test, p = 0.035). For single species, observations of moose (p = 0.041), otter (*Lutra lutra*, p = 0.048), least weasel (*Mustela nivalis*, p = 0.007) and pine marten (*Martes martes*, p = 0.021) were significantly more numerous in beaver patches than in controls (Fig. 2B). Other detected mammal tracks belonged to small mammals, red squirrels, hares, the red fox, the raccoon dog, the wolf (*Canis lupus*) and the lynx (*Lynx lynx*; see Appendix 2).

4. Discussion

In our study, for the first time, a significantly greater number of terrestrial and semi-aquatic mammal species were observed in beaver patches than in the control patches. Our study area represents a boreal coniferous forest ecosystem of relatively low productivity, thus, circumstances are favourable for facilitation (Bertness and Callaway, 1994; Holmgren and Scheffer, 2010). Facilitation by the beaver has previously been found in the very same landscape in bats (Nummi et al., 2011), frogs (Vehkaoja and Nummi, 2015), and in the entire waterbird guild (Nummi and Holopainen, 2014). The number of species in beaver patches was significantly higher than in the controls, as well as their activity. This is true for both the camera traps and the snow tracks. When comparing small mammal communities, Samas and Ulevicius (2015) also found more species in beaver lodges (11) than in the nearby forest (5).

Nummi and Hahtola (2008) concluded that beaver facilitated the ducklings of the common teal (*Anas crecca*) by both structural amelioration of the riparian habitat and resource enhancement. The creation of a wider shallow littoral zone is an important structural change of beaver-modified patches in the boreal. This shallow zone harbours a more abundant invertebrate fauna than non-beaver ponds do (Nummi, 1989; McDowell and Naiman, 1986). Similarly, bats have been observed to benefit from both structural changes in the form of forest openings (Ciechanowski et al., 2011) and resource increase in the form of a growing number of emerging insects (Nummi et al., 2011).

In this study, we do not have detailed knowledge of the resources or habitat structure. We assume, however, that the general increase in mammal species at the beaver ponds is partly caused by the general productivity increase in the aquatic-terrestrial interface (Vehkaoja et al., 2015). In the aquatic phase, the abundance of organisms at different trophic levels of the aquatic food chain increases. When a beaver meadow exists, greater production of herbs and grasses takes place, because nutrients become available in the previously anoxic soil after beaver abandonment (Johnston, 2017).

Moose were more active in beaver patches according to both camera traps and snow tracks. Moose and other herbivores may benefit from the small openings created by beavers that contain young saplings of deciduous trees (Johnston and Naiman, 1990a). After beaver flooding, the shore tree stands also become more dominated by deciduous trees (Hyvönen and Nummi, 2008). In theory, abandoned beaver patches could also have had more moose activity, but it didn't seem to

be the case. Wolfe (1974) noted that the bulk of trees felled by beavers often remains where they fall. The bark and branches of these trees increase the food supply for species, such as moose, roe deer and white-tailed deer, during autumn and winter because some tree parts remain above the snow surface (Rosell et al., 2005, Nummi, pers. obs.). Additionally, the regrowth of aspen, birch and willows after beaver abandonment are highly preferred food for these species. Moose often feed on aquatic plants, such as water lilies in older beaver ponds, and find relief from biting insects (Stoffyn-Egli and Willison, 2011). With limited data, Mishin and Trenkov (2016) also found more moose visits in camera traps at beaver ponds than in a marsh situated in the same landscape.

According to snow tracks, small mammals were more active in beaver patches but without statistical significance. Apart from grasses as food, small mammals may benefit from sheltering structures of abundant beaver-created dead wood, some of which is lying on the ground (Samas and Ulevicius, 2015; Thompson et al., 2016). They also find food and shelter in beaver lodges (Samas and Ulevicius, 2015). Furthermore, shrews may also have contributed to the activity of small mammals. Shrews are insectivorous and may find more invertebrate prey around beaver ponds. Although least weasels and pine martens are not considered as riparian species, their activities were higher in beaver patches, very likely because small mammals are their main food in boreal ecosystems (Korpimäki et al., 1991; Pulliainen and Ollinmäki, 1996).

The red fox tended to be more active in beaver patches according to the camera trapping. Mishin and Trenkov (2016) noted more red fox activity by beaver ponds than in the control area in summer and autumn. According to the snow track survey, however, the red fox seemed not to be significantly more active in beaver patches than the control in winter. During the ice-free period, large number of frogs in beaver ponds found in our study area (Vehkaoja and Nummi, 2015) is beneficial for predatory species, such as the red fox and the raccoon dog (Knudsen, 1962; Sutor et al., 2010).

Semi-aquatic predators, e.g. minks and otters, benefit from abundant invertebrates, fish, and frogs in flowages (Nummi, 1989; Snodgrass and Meffe, 1998; Dalbeck et al., 2007). They may also use abandoned or active beaver lodges, and bank dens for shelter and breeding. In winter, beavers make ice holes around their lodges and food caches. These ice-free lake parts provide otters with access to water, which is essential to their foraging activities and survival in winter (Reid et al., 1994; Bromley and Hood, 2013). In accordance with our study, Reid et al. (1994) found river otters (*Lontra canadensis*) preferred beaver ponds especially during winter, often using inactive beaver lodges for denning. In a summertime study of river otters, their activity was linked with active beaver ponds and with the abundance of fish prey, very likely because otters benefit from a beaver landscape with both inactive ponds for shelter and active ones for foraging (LeBlanc et al., 2007). A commensal relationship of the predators with beavers has been suggested underlining the importance of beavers to otters (Tumlison et al., 1982; Reid et al., 1994; LeBlanc et al., 2007). Our study adds to the literature, highlighting the role of ecosystem engineers in creating habitat heterogeneity and promoting species abundance and richness in a variety of ecosystems (Romero et al., 2015; Coggan et al., 2018), especially when an ecosystem engineer increases the productivity of a low-productivity patch (Wright and Jones, 2004; Nummi and Holopainen, 2014).

From a landscape perspective, there appears to be a difference in the occurrence patterns of plants and of mobile animals. According to Wright et al. (2002), the number of plant species was not higher in beaver patches than along non-disturbed shoreline, but the plant species occurring only in the beaver patches added to the landscape-level diversity. In the case of mobile animals, Nummi et al. (2019) found a more prominent increase in common teal pair numbers in a landscape with beavers compared with a landscape without beavers. In our study, we found that mammal species richness was higher in beaver patches than in the controls at the patch level, but the same mammal species visited both beaver and control patches at different frequencies. In our study, however, a single observation of wolf tracks was found in a control patch and two observations of lynx tracks were found only in beaver patches, but these observations are too few to conclude that beaver patches add mammalian diversity at the landscape level. Similarly, the increasing activity of mammals may indicate their increasing abundance due to beaver facilitation. For larger mammals, however, we cannot rule out the possibility that at the landscape scale, the same number of animals are present but occurred more near beaver patches due to their behavioral preference for these sites. Further studies should investigate how beavers facilitate mammal species richness and abundance at a landscape level by comparing landscapes with and without beavers.

From the aspect of habitat conservation or restoration, it is feasible to identify beavers as facilitators and to promote their populations (Byers et al., 2006), since restoration is especially needed in wetlands due to the loss of 60−90% of these habitats in Europe (Junk et al., 2013). Beavers can be especially valuable in landscapes artificially deficient of wetlands and lacking processes naturally driving heterogeneity (Willby et al., 2018). Many organisms have benefited from beaver-created productivity coupled with an increase of suitable habitat structures (Rosell et al., 2005; Stringer and Gaywood, 2016), both of which affected mammalian diversity and activity at the patch level in our study. We should note that an overabundance of ecosystem engineers may lead to decreased heterogeneity and thereby detrimental diversity development (Pringle, 2008; Nummi and Kuuluvainen, 2013). With present-day low numbers of large predators, beavers may become overabundant if not managed sensibly (Ritchie et al., 2012).

Author contributions

PN and JS designed the study, OH and ES conducted the field work, WL performed the statistical analyses, PN lead the writing and all authors contributed to the final manuscript.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00701.

Appendix 1. Descriptions of the full models and results of the optimal models.

The full ZIP model for mammal species number (Equation (1)) is given by the following:

$$E(Y_{ij}) = \mu_{ij} \times (1 - \pi_{ij})$$

$$\log(\mu_{ij}) = \alpha_1 + \beta_1 \times Patch\_Category_{ij} + \beta_2 \times Sampling\_Effort_{ij},$$

$$\pi_{ij} = \frac{e^{\nu_1 + \gamma_1 \times Patch\_Category_{ij} + \gamma_2 \times Sampling\_Effort_{ij}}}{1 + e^{\nu_1 + \gamma_1 \times Patch\_Category_{ij} + \gamma_2 \times Sampling\_Effort_{ij}}} \tag{1}$$

where Y_{ij} is the species number observations in season j at site i. Term π_{ij} is the probability of false zeros for the binomial distribution, which was modelled in terms of the patch category and the standardized sampling effort. When parameters γ_1 and γ_2 of the patch category and sampling effort are equal to 0, π_{ij} is a constant, which was the case in our optimal ZIP model. The ZIP model has the mean, $\mu_{ij} \times (1 - \pi_{ij})$, where term μ_{ij} is the mean of the positive counts and term $1 - \pi_{ij}$ is the probability of the counts and true zeros. The mean μ_{ij} was modelled in terms of the patch category and sampling effort.

The mammal visit observations were modelled in a similar way but with random effects (Equation (2)). Term Y_{kl} is the mammal visit times in season l at site k. The sites (a_{kl}) and seasons (b_{kl}) are random effects in the count part, both of which follow a normal distribution with mean 0 and variance σ_k and σ_l, respectively.

$$E(Y_{kl}) = \mu_{kl} \times (1 - \pi_{kl})$$

$$\log(\mu_{kl}) = \alpha_2 + \beta_3 \times Patch\_Category_{kl} + \beta_4 \times Sampling\_Effort_{kl} + a_{kl} + b_{kl},$$

$$\pi_{kl} = \frac{e^{\nu_2 + \gamma_3 \times Patch\_Category_{kl} + \gamma_4 \times Sampling\_Effort_{kl}}}{1 + e^{\nu_2 + \gamma_3 \times Patch\_Category_{kl} + \gamma_4 \times Sampling\_Effort_{kl}}} \tag{2}$$

The full GLM for the species number of the snow track data (Equation (3)) is described below:

$$Y_{mn} \sim Poisson(\mu_{mn})$$

$$\log(\mu_{mn}) = \eta_{mn}$$

$$\eta_{mn} = \alpha_3 + \beta_5 \times Patch\_Category_{mn} + \beta_6 \times Sampling\_Effort_{mn} \tag{3}$$

where the species number observation during survey n at site m, Y_{mn}, is Poisson distributed with mean μ_{mn}, and modelled in terms of the patch category and sampling effort.

Appendix 1.1. The results of the optimal ZIP model for mammal species numbers in the camera traps comparing beaver and control patches. "SSE" means standardized sampling effort; SE means standard error and SD means standard deviation; the symbol "" indicates significance and symbol "-" means not included; the same below.*

Parameters	Occurrence Model				Abundance Model			
	Estimate	SE	Z-value	P-value	Estimate	SE	Z-value	P-value
Intercept	−1.28	0.59	−2.19	0.028*	−0.12	0.24	−0.50	0.614
Beaver	−	−	−	−	0.59	0.26	2.26	0.024*
SSE	−	−	−	−	0.17	0.13	1.27	0.205

Appendix 1.2. The result of the optimal ZIP model for mammal visits in the camera traps comparing beaver and control patches.

Fixed Parts	Occurrence Model				Abundance Model			
Parameters	Estimate	SE	Z-value	P-value	Estimate	SE	Z-value	P-value
Intercept	−0.76	0.37	−2.07	0.039*	−0.37	0.35	−1.07	0.284
Beaver	−	−	−	−	0.69	0.35	2.00	0.046*
SSE	−	−	−	−	0.26	0.18	1.47	0.143
Random Parts								
Groups			Variance					Variance
Sites			−					0.54^2
Seasons			−					0.30^2

Appendix 1.3. Poisson GLM results of mammal species numbers of snow tracks comparing beaver and control patches.

	Estimate	SE	Z-value	P-value
Intercept	0.35	0.12	2.96	0.003*
Beaver	0.38	0.15	2.48	0.013 *

Appendix 2. Wilcoxon's test results of mean visits per season per patch and snow tracks per kilometer per survey by the beaver and the control patches. BP is abbreviation for beaver patches, and CP for control patches. The symbol "*" indicates significance, and the symbol "-" means no observation, or the observations were too few to test the significance.

Species	Camera trappings			Snow tracks		
	BP	CP	P-value	BP	CP	P-value
Small Mammals	−	−	−	6.07	4.85	0.119
Hares	0.38	0.18	−	5.98	4.84	0.292
Brown Hare	0.05	0.08	−	−	−	−
Mountain Hare	0.33	0.10	−	−	−	−
Moose	0.48	0.10	0.042*	0.39	0.00	0.041*
Roe Deer	0.08	0.08	−	−	−	−
White-tailed Deer	0.23	0.05	−	−	−	−
Pine Marten	0.03	0.00	−	0.47	0.17	0.021*
Squirrel	0.05	0.03	−	1.67	0.61	0.317
Least Weasel	−	−	−	0.49	0.02	0.007*
Badger	0.05	0.05	−	−	−	−
Lynx	−	−	−	0.05	0.00	−
Otter	0.05	0.00	−	0.40	0.18	0.048*
Raccoon Dog	0.60	0.20	0.070	0.02	0.00	−
Red Fox	0.80	0.28	0.051	2.79	3.79	0.400
Wolf	−	−	−	0.00	0.03	−

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