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Research article

Can reintroduction of beavers improve insect biodiversity?

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ABSTRACT

Ecosystem engineering species, such as beavers, may help the restoration of biodiversity. Through the building of dams and lodges and altering the natural hydrology, beavers change the habitat structure and create multiple habitats that facilitate a wide variety of other organisms including terrestrial invertebrate communities. Here we study the effect of beaver reintroduction in Klosterheden in Denmark on biomass of flying invertebrates and diversity of moths. Further, aerial photos were used to assess riparian structure and productivity using the normalized difference vegetation index (NDVI). Our findings show that the presence of beavers affected flying invertebrate biomass, but that this was dependent on time of the year. Further, a strong effect of presence of beavers was found on diversity of moths. The results also show an increase in vegetation productivity and structural heterogeneity at sites with presence of beavers. Overall, our results demonstrate the importance of beavers as important ecosystem engineers that affect invertebrate species composition and abundance, as well as riparian structure and productivity.

1. Introduction

On a global scale, the species diversity is strongly declining (36–81%) (Ceballos et al., 2015; McCallum, 2015; Régnier et al., 2015). However, the rate of decline is ecosystems dependent (WWF 2016) with freshwater ecosystems losing biodiversity faster than terrestrial habitats (Dudgeon et al., 2006). If this trend continues, it will not only lead to a world with fewer species but may also result in the loss of ecosystem functioning. In recent years, rewilding has emerged aiming to restore natural processes and functions in ecosystems, and often focus on the re-introduction of missing large wildlife species (Corlett, 2016). One aspect of this includes reintroduction of key ecosystem engineering species that can help restoration of biodiversity (Bakker and Svenning, 2018), with the re-introduction of wolves and beavers and their effect on the entire ecosystem being some of the most famous examples (Laundré et al., 2001; Rosell et al., 2005; Stringer and Gaywood, 2016; Boyce, 2018; Rozhkova-Timina et al., 2018; Willby et al., 2018; Brazier et al., 2021).

Reintroductions of beavers were partly to maintain the beaver population, but also to exploit the ecosystem engineering activities of beavers and thus to rewild landscapes and to bring back natural ecological processes (Law et al., 2017; Marr et al., 2018; Halley et al., 2021). The beaver has proven particularly successful in repopulating new territories following reintroductions (Halley et al., 2021, Bouros et al., 2022). In Europe, reintroduction programs have restored the beaver population from only 1200 individuals in the early 20th century to more than 1.2 million individuals in 2020 (Wróbel, 2020; Halley et al., 2021). There are several good examples of the natural expansion of beaver populations after releases (Bouros et al., 2022; but see also Ceña et al., 2004). Both legal and illegal releases of beavers have taken place in Europe (Pucci et al., 2021; Calderón et al., 2022), but regardless of how the beaver arrived, it is protected by the EU Habitats Directive.

Beavers have a profound ability to modify ecosystems and their role as ecosystem engineers have been established in multiple studies (Rosell et al., 2005; Stringer and Gaywood, 2016; Rozhkova-Timina et al., 2018; Willby et al., 2018; Brazier et al., 2021). Beavers create dams and lodges by using wood, stone, and mud to manipulate the hydrology (Rosell et al., 2005; Puttock et al., 2017), thereby increasing the water level and surface area and providing greater safety and transportation possibilities for the beaver. In doing so, beaver activities create heterogenic habitats that provide habitats for a wide variety of other organisms (Rosell et al., 2005; Stringer and Gaywood, 2016; Brazier et al., 2021). For example,

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beaver activity can result in an increase of decomposing wood and a change in vegetational diversity and structure (Wright et al., 2002; Stringer and Gaywood, 2016; Willby et al., 2018) as well as increase the water bird diversity (Nummi and Holopainen, 2014). Though several of these studies have been performed on the American beaver (*C. Canadensis*), studies in the Eurasian beaver suggest is also has a positive impact on its environment (Brazier et al., 2021; Orazi et al., 2022).

Studies have investigated the effects of beavers on the surrounding fauna (Rosell et al., 2005; Stringer and Gaywood, 2016), primarily with focus on the effects on water-associated organisms (Rosell et al., 2005; Simanonok et al., 2011; Stringer and Gaywood, 2016; Nummi et al., 2021) (but see (Dalbeck, 2011)). However, wetland ecosystems contain a diverse invertebrate assemblage of both aquatic and terrestrial species (You and Li, 2006; Anderson et al., 2013) and the riparian zone has been documented to be biologically rich and dynamic in terms of terrestrial invertebrate communities (Ramey and Richardson, 2017). Consequently, a loss or change of wetland ecosystems can be fatal not just to aquatic invertebrates but also terrestrial arthropod species (Kay, 1994; Wohl, 2021).

In the present study, we examine if beaver activity (where beavers were reintroduced 20 years prior to this study) affect the terrestrial arthropod community (biomass of flying insects and diversity of moths) in comparison to areas with no beaver activity. As we expect beaver activity to increase habitat heterogeneity (Hood and Larson, 2014; Willby et al., 2018), and since an increased habitat heterogeneity has been found to increase the invertebrate diversity in other riparian studies (Popescu et al., 2021), we expected sites with beaver activity to have a higher diversity. We choose to look at insect biomass as several studies have shown that this is affected by changes in ecosystems (Thomas et al., 2004; Shortall et al., 2009; Habel et al., 2016; Hallmann et al., 2017; Høye et al., 2021). Further, we focused on moth diversity as moths are good bioindicators due to the high number of taxa (Habel et al., 2019) and high sensitivity to changes in the landscape (Rákosy and Schmitt, 2011; Chaundy-Smart et al., 2012; Mangels et al., 2017). Most lepidopteran studies focus on butterflies, but moths contain more species and have been suggested as better bioindicators intended for dense and open forest, consisting of shrubs and trees, ruderal vegetation, and grassland patches (Rákosy and Schmitt, 2011; Habel et al., 2019), making them well-suited to study the effect of presence of beavers. Further, we test the hypothesis that beaver activity will lead to an increased vegetation productivity and structural heterogeneity, here measured as NDVI.

2. Materials and methods

2.1. Study area

The study took place in Klosterheden, Denmark (Fig. 1). Klosterheden is a plantation forest with a vegetation dominated by coniferous trees, containing multiple valleys dominated by small streams and a more deciduous plant composition in the riparian zone (Berthelsen, 2000). During autumn 1999, 18 Eurasian beavers (*Castor fiber*) were released on Klosterheden (Elmeros et al., 2003). Twenty years later, the population was estimated to consist of 243–269 beavers (Sunde and Elmeros, 2020).

2.2. Sampling design

The study took place during the summer and autumn of 2020 (July

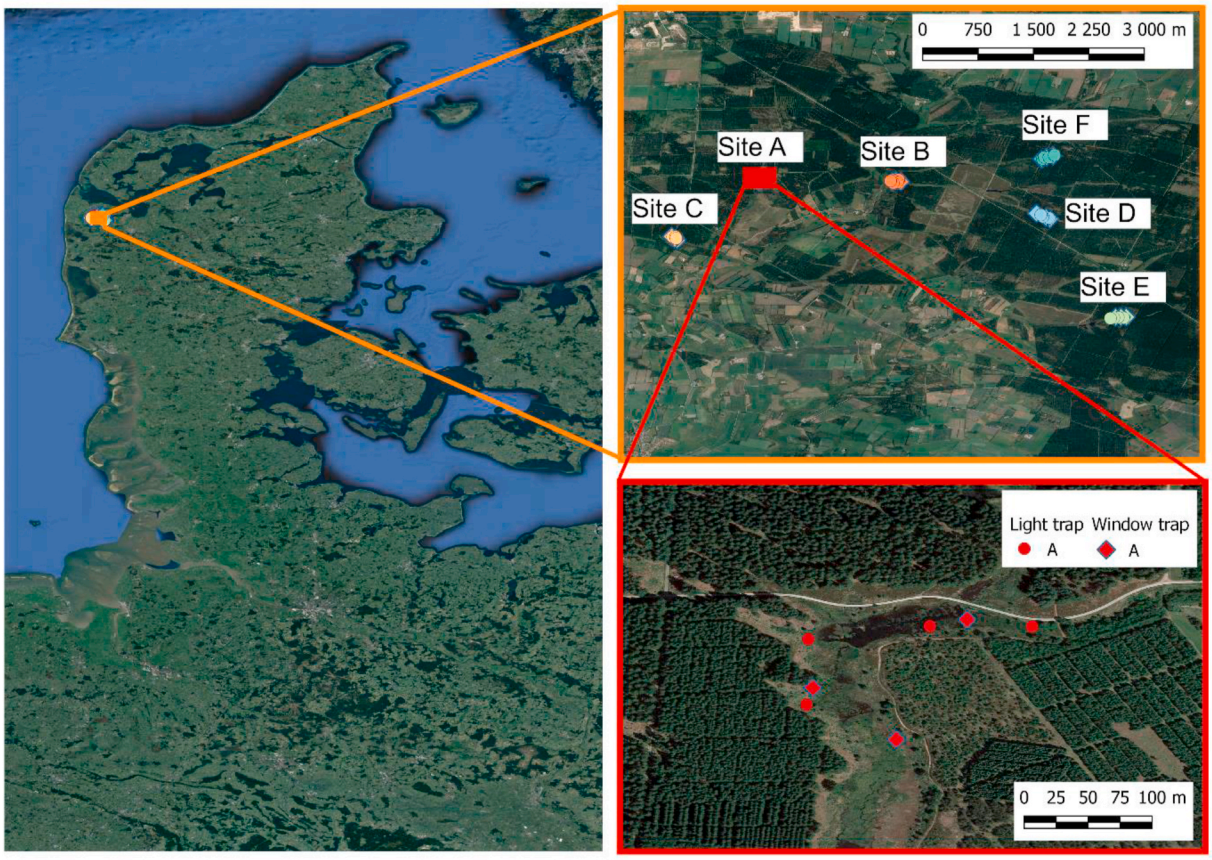

Fig. 1. Map of the sampling area in Klosterheden. Beaver activity was found at sites A, B and C, while sites D, E and F had no beaver activity. Within each site, light traps and window traps were placed. The window traps were stationary and emptied continuously. One light trap was moved between four locations within a site.

7th to October 25th). Three sites with high beaver activity (Sites: A, B & C, hereafter beaver sites) and three control sites with no visible beaver activity (Sites: D, E & F, hereafter non-beaver sites) were identified by the local Danish Nature Agency (Fig. 1). Beaver dams were found at all beaver sites, whereas beaver lodges were present on sites A and C. The non-beaver sites are subject to anthropogenic disturbance caused by clear-cutting, which keep the habitats from following a natural succession, and thereby remain open.

Flight interception traps (cross vane window traps, which throughout this study is referred to as "window traps") were used to sample flying invertebrates for biomass estimations (Bouget et al., 2008; Anderson et al., 2013). Three window traps were randomly located at each site using QGIS (QGIS Development Team, 2020) (Fig. 1). Flight interception traps were built following Nageleisen and Bouget (2009), but with the following modifications making them suitable for placement at the sampling sites: each flight interception trap consisted of two transparent, perpendicular panels measuring 50 × 80 cm, where the panels were placed on top of a black barrel Ø50 cm, and the black barrel was placed on top of a wooden frame with the top of the black barrel being 150 cm above ground. The window traps were set up the July 7, 2020 and emptied once a week throughout the sampling period until the September 22, 2020. Insects were stored in a 70% ethanol solution until biomass estimation.

Ultraviolet-light traps were used to target adult moths. They effectively lure moths, even for low-wattage traps with a range <10 m (Merckx and Slade, 2014). Traps were set up approximately once a week in the period July 7, 2020 till October 25, 2020. Light traps were setup before dusk on the warmest night of each week with the lowest wind speed (based on local weather forecast, www.DMI.dk) and specimens collected the following morning. In total six light traps were used during each sampling event, with one trap placed in each of the six sites. Traps were relocated between four locations within a site between each sampling event, where the four locations were randomly identified using QGIS (QGIS Development Team, 2020) (Fig. 1). Light traps used in the study were 12 V Portable Heath Moth Traps that housed a 6 W Actinic Bulb and were powered by a Lucas Rechargeable 12 V 18Ah Battery (NHBS Ltd 2020), and inside the trap Trinol 308 was sprayed. Moths were stored in plastic containers at −5 °C and subsequently, the macro lepidopteran moths were identified to species level using identification keys Pettorelli et al., (2005), Hayden and Karl (2006), Aarvik and Elven (2014), Waring and Townsend 2018, and for genitalia examination keys by Wheeler et al. (2020).

2.3. Riparian vegetation productivity and structure

Riparian vegetation productivity and structure was measured using the normalized difference vegetation index (NDVI). NDVI is a remote-sensed measure of vegetation productivity widely used to quantify vegetation structure and dynamics in response to environmental changes (Pettorelli et al., 2005; Huntington et al., 2016; Fesenmyer et al., 2018). NDVI was calculated in QGIS (QGIS Development Team, 2020) by the formula; NDVI = (NIR- RED)/(NIR + RED), where NIR and RED are the amount of near-infrared light and red light reflected by the surface and captured by the sensor on the aerial camera, respectively (Pettorelli et al., 2005). NDVI ranges from −1 to 1, where negative values correspond to the absence of vegetation. NDVI was generated using spring orthoimages from Kortforsyningen (2019) from 2016, 2017, 2018, and 2019. Orthoimages from end of March to the beginning of May are taken annually with a pixel resolution of 12.5 cm (Kortforsyningen, 2019). From every pixel, NDVI was computed. Data were gathered by randomizing 600 points for each site for all years using QGIS (QGIS Development Team, 2020). From each point, point-sampling tool was used to extract data from the 600 datapoints within each site.

2.4. Biomass estimates

Window trap catches were stored in 70% ethanol prior to biomass estimation. The biomass was measured in an alcohol-wet state following a modified method of (Hallmann et al., 2017). To ensure constant ethanol concentration and density prior to biomass estimation, the ethanol solution of each sample was replaced with new 70% ethanol 48 h and 24 h. To estimate the biomass (g), the sample was first poured through a sieve (0.25 mm mesh width) secured at a 30° angle above a plastic container, to allow the ethanol to sieve through. The ethanol drop sequence was monitored with a stopwatch, so by the time the drop sequence reached 10 s between two drops, the biomass was weighed with a labor atory scale (Mettler PJ3600 DeltaRange®, 0.01 g). To estimate potential procedure error, two samples were picked out and weighed ten times where an average deviation from the mean value fluctuated less than 2% (1.77%) between measures (Appendix 1).

2.5. Statistical analysis

In order to test whether the invertebrate biomass differed between sites with and without beavers as well as across time, a linear mixed model was run using R package lme4. In the model, beaver activity and time (expressed as sampling weeks) were coded as fixed factors, whereas site and location were coded as random factors to account for repeated measurements. The biomass data were log-transformed prior to analysis in order to normalize and homogenise the variances of the data's distributions.

The moth species data were merged into two groups consisting of the summer sampling (July–August) and autumn (September–October) sampling. We calculated the biodiversity using the Hill number diversity (Hill numbers 0–2), in which the Hill number diversity 0 corresponds to the rarefied species richness, 1 corresponds to the Shannon diversity and 2 to the Simpson diversity. Prior to the calculations, data was submitted to a rarefication process ensuring an even sampling size across seasons and sites. We extrapolated/interpolated data to two times the minimum abundance (in this case, 34). Both the rarefied richness, Shannon and Simpson diversity indexes were fitted in linear mixed models to determine whether they differed between sites with and without beaver activity. Beaver activity and season (summer, autumn) were coded as fixed factors, site as a random factor taking repeated measures into account. Further, we wanted to determine whether the moth species composition differed between sites with and without beavers and between seasons. To do this, we used non-metric multidimensional scaling (NMDS) to visualize the difference, and PERMANOVAs to test for significant differences.

A principal component analysis (PCA) was used to visualize differences in NDVI between sites with and without beaver activity as well as between individual sampling sites and years. Further, *t*-tests were used to test for significant differences between the mean productivity based on NDVI within beaver and non-beaver sites. As a measure of heterogeneity, *F*-tests were used to examine if the variances of the NDVI distributions were significantly different between beaver and non-beaver sites across years.

All data analyses were conducted in R 4.0.5 (R Core Team, Vienna, 2021). Graphs were created using ggplot2 (Wickham, 2016). All codes used in the analyses can be found in Appendix 2.

3. Results

3.1. Biomass

Invertebrate biomass changed with sampling time, where biomass was generally higher during week 29–32 and at sites without beaver activity (Fig. 2, Table 1). However, log transformed flying terrestrial invertebrate biomass was not significantly different between sites with and without beavers ($p > 0.05$), but there was a significant effect of time

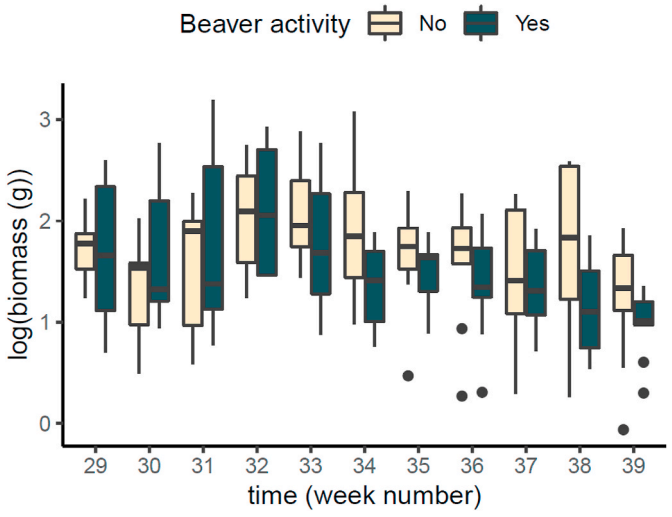

Fig. 2. The biomass (log transformed) collected across all beaver and non-beaver sites over summer and autumn. The plot depicts the median, the upper and lower hinges correspond to the 75th and 25th percentiles and the whiskers show the larges values within 1.5 times the interquartile range.

Table 1
Model results from the linear mixed model on biomass (log-transformed).

	Chi-square	df	*p*
Beaver activity	0.17	1	*>0.05*
Time	79.21	10	*<0.001*
Interaction	25.33	10	*<0.01*

($p < 0.001$), and interaction between beaver activity and time ($p < 0.01$) on biomass. For example, we found that the biomass was significantly larger in the sites without beaver activity compared to sites with beaver activity in week 38 ($p < 0.05$).

3.2. Diversity and species composition

During the 14 weeks of light trapping 1239 individuals of 111 species were collected (species list can be found in appendix 3). A total of 42 species were only found on beaver sites, 10 unique species were only found at non-beaver sites. An overall overlap of 59 species was discovered in across both beaver and non-beaver sites.

The rarefied species richness was higher in summer and for sites with beaver activity (Fig. 3a, Table 2). In accordance with this, there was a significant effect of beaver activity ($p < 0.05$) and time ($p < 0.001$) on richness. The interaction term (beaver activity X time) was not significant ($p > 0.05$). A similar pattern was seen for Shannon diversity (Fig. 3b) for which a significant effect of site ($p < 0.05$) and time ($p < 0.001$) on Shannon diversity was found. The interaction term (site X time) was not significant ($p > 0.05$). The Simpson diversity was higher in summer and for sites with beaver activity in Autumn (Fig. 3c, Table 2). However, the effect of beaver activity on Simpson diversity was only significant for time ($p < 0.001$), but not site ($p > 0.05$) nor the interaction (site X time) ($p > 0.05$).

Visually, the NMDS showed good separation between the beaver sites and non-beaver sites as well as between seasons (Fig. 4) (NMSD stress value of 0.13). Beaver activity explained 8.9% of the variation in the data but had no significant effect on species composition (PERMANOVA, $p > 0.05$). Time, on the other hand, did have a significant effect on species composition, and explained 40.5% of the variation in species composition (PERMANOVA, $p < 0.01$). Site explained 31.0% of the variation in species composition ($p > 0.05$).

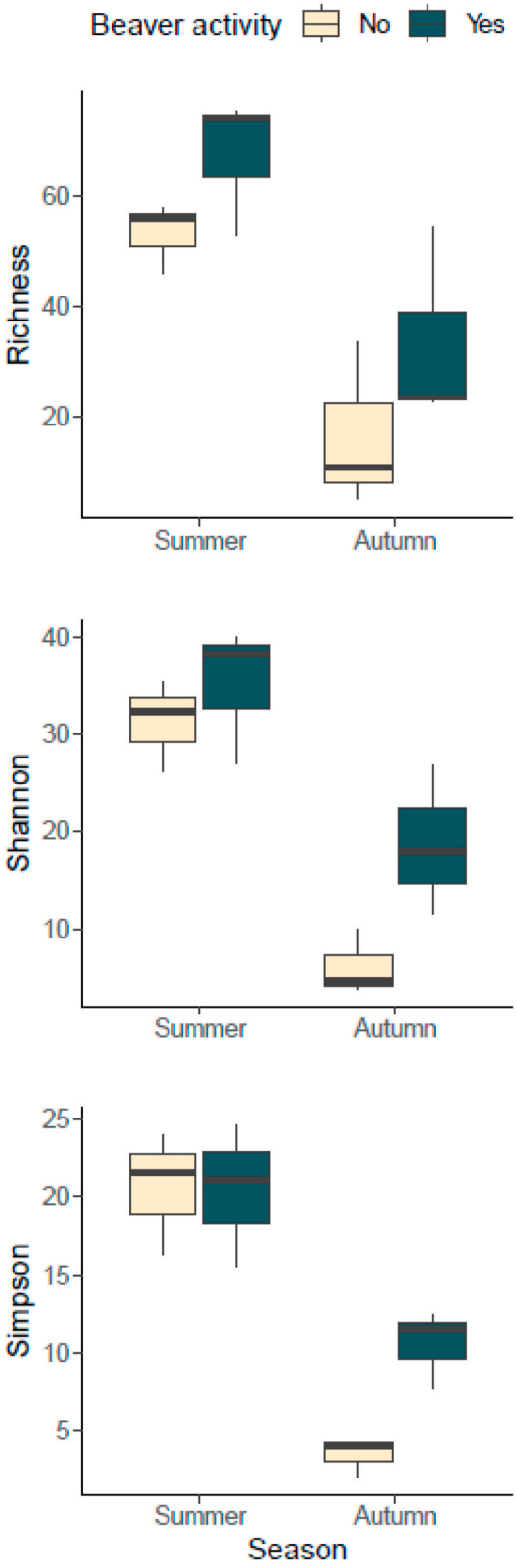

Fig. 3. Boxplot of the moth diversity: The rarefied species richness (q = 0), Shannon diversity (q = 1) and Simpson diversity (q = 2) for moths in the light traps. The plot depicts the median, the upper and lower hinges correspond to the 75th and 25th percentiles and the whiskers show the larges values within 1.5 times the interquartile range.

Table 2
Model results for each of the diversity measures.

	Chi-squared	df	*p*
Rarefied species richness			
Beaver activity	3.67	1	<0.05
Time	21.24	1	<0.001
Interaction	0.03	1	>0.05
Shannon			
Beaver activity	5.72	1	<0.05
Time	36.29	1	<0.001
Interaction	1.63	1	>0.05
Simpson			
Beaver activity	3.26	1	>0.05
Time	49.92	1	<0.001
Interaction	3.63	1	>0.05

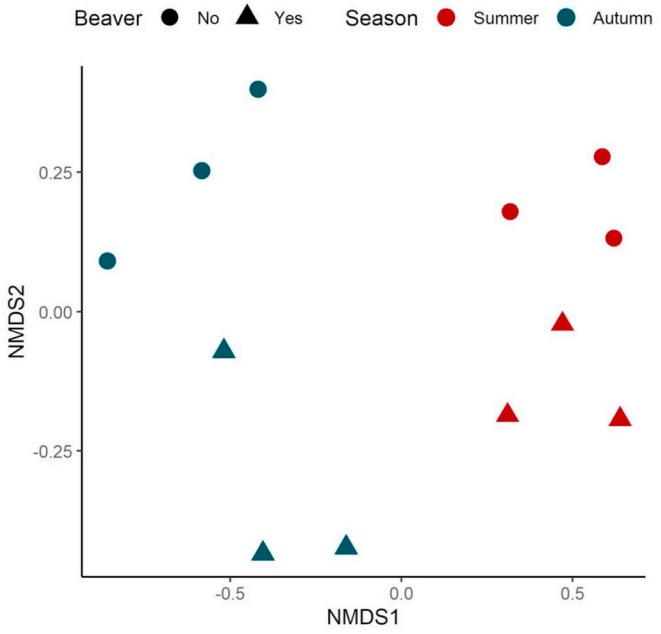

Fig. 4. Non-metric multidimensional scaling (NMDS) of moth species composition in relation to beaver activity, site, and week.

3.3. NDVI

To visualize whether the NDVI differed between sites with and without beaver activity, we ran a PCA (Fig. 5). We found that 38.45% of the variation in the data was explained by principal component (PC) 1, while an additional 22.76% of the variation was explained by PC2, summing to 61.21% of the variation explained on the first two axes. The years 2016, 2018 and 2019 were best explained by PC1, while 2017 were best explained by PC2. Mean NDVI was significantly greater for beaver activity sites compared to non-beaver sites for all years ($p < 0.001$). Significantly greater variance was observed at beaver sites for 2016 ($F = 1.94$, $p < 0.001$), 2017 ($F = 1.39$, $p < 0.001$), 2018 ($F = 1.96$, $p < 0.001$), and 2019 ($F = 1.47$, $p < 0.001$).

4. Discussion

4.1. Biomass of terrestrial invertebrates

Rewilding has emerged as a way to restore natural processes in ecosystem and ecosystem functioning and may thus also play an important role for the abundance and diversity of terrestrial arthropods species, and we therefore expected beaver activity to influence the terrestrial arthropod biomass. We found that beaver activity did not

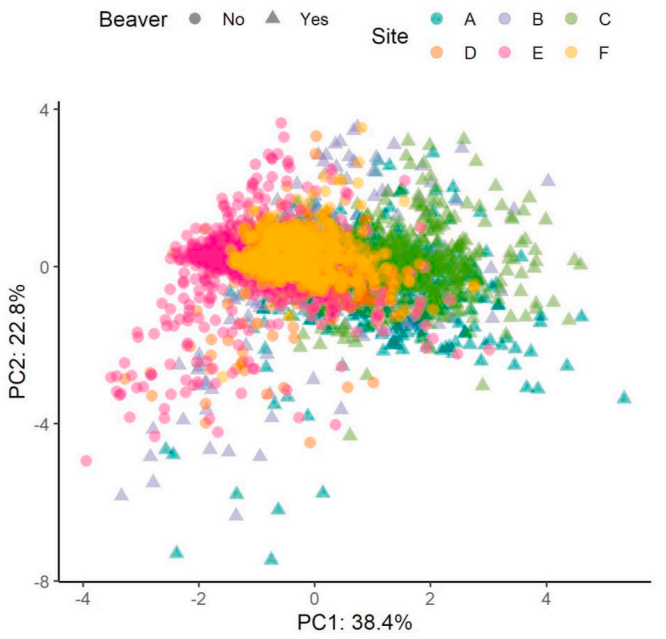

Fig. 5. PCA of NDVI values showing the variation between areas with and without beaver activity and the various sites.

have an overall significant effect on arthropod biomass, but instead depended on time of the season as the insect biomass was lower at beaver sites late in the season. Only a limited number of studies have directly or indirectly investigated the importance of beavers on terrestrial invertebrate biomass. Nummi et al. (2011) found an increase in bat detection in beaver ponds compared to ponds without beaver presence. As bats depend on the insect activity at their foraging sites in order to feed, the invertebrate biomass is considered an important factor for bats (Voigt et al., 2017), especially the activity of moths (Arlettaz et al., 1997). Therefore, the increased bat detection indicates a relation between insect biomass and beaver activity (Nummi et al., 2011), suggesting that beavers increase the aerial invertebrate biomass. Another study examined terrestrial invertebrates at now abandoned beaver sites compared to non-beaver sites, and discovered a 2–2.5 times increase in the abundance of soil invertebrates and invertebrates of the herb layer (Fyodorov and Yakimova, 2012). The temporal variation in biomass, with a significant decrease over time from the beginning of July to end September, was expected and has also been reported in other studies (Moeed and Meads, 1987; Andersen et al., 2021).

4.2. Biodiversity and the moth community

As expected, we found species richness and Shannon diversity significantly higher in beaver compared to non-beaver sites. The mean hill diversity for all orders at beaver sites was more than 24% larger compared to non-beaver sites. Moths are highly sensitive to changes in the terrestrial ecosystem (Rákosy and Schmitt, 2011; Chaundy-Smart et al., 2012; Mangels et al., 2017) and the increase in moth species richness diversity could be a result of the habitat disturbance caused by beavers. This is in agreement with van Klink et al. (2018) who found that beaver wetlands harbor a higher invertebrate diversity in streams due to an increased habitat heterogeneity.

Despite not finding a significantly different species composition between beaver and non-beaver sites, we found more species to be associated to beaver sites compared to non-beaver sites with 42 species uniquely found at beaver sites compared to 10 species only found at non-beaver sites. The large numerical difference in the number of unique species between beaver and non-beaver sites is likely found in the landscape change caused by the beaver. Habel et al. (2019) showed that

a high moth diversity was linked to a mosaic landscape consisting of various vegetation structures, such as shrubs and forests, ruderal vegetation, and grassland patches. This landscape bears similarity to landscapes influenced by high beaver activity (Stringer and Gaywood, 2016). Sites exposed to beavers contain a higher vegetation diversity in the riparian zone (Wright et al., 2002; Bartel et al., 2010; Willby et al., 2018), which could impact the diversity of herbivory moths. Further, the landscape created by the beaver can impact rare Lepidoptera species, as was shown by Bartel et al. (2010). Here, the beaver-created disturbance increased the vegetation diversity and changed the vegetation composition, thereby creating a unique riparian zone supporting rare butterfly *Neonympha mitchellii francisci* (Bartel et al., 2010). In a study by Dalbeck (2011) grasshopper species richness was found to be positively correlated with clearings made by the beaver. In comparison to our findings, the increase in grasshopper species, are inter estingly, similar and might well be the overlapping interactions facilitated by the beaver.

The diversity differed between beaver and non-beaver sites for the Shannon, but not the Simpson diversity. This could be explained by Shannon's increased sensitivity to species richness and rareness, where Simpson's index is more sensitive to common species and the evenness distribution within (Yeom and Kim, 2011).

4.3. NDVI

As we expected prior to commencing this study, we found a higher NDVI at beaver sites compared to non-beaver sites. This is in agreement with previous studies (Fesenmyer et al., 2018; Fairfax and Whittle, 2020), Further, the significantly greater variance at beaver sites comparison to non-beaver sites indicated that beavers facilitate a greater structural heterogeneity in. The increased vegetation productivity in the riparian zone could result from newly emerged plants and a subsequent increased vegetational biomass following the disturbance created by beavers (Baker et al., 2005; Fesenmyer et al., 2018). Beaver herbivory might lower the amount of dead grass, which could promote early light sensitive plants to emerge, which will increase spring NDVI. Fairfax and Whittle (2020) found an increase in greenness at beaver sites compared to control sites because of more well hydrated vegetation. We suggest that similar processes might explain the increased vegetation productivity demonstrated in our study. In the current study, three sites either with or without beavers were included. It is unknown whether beavers also seek areas with a high NDVI and thereby chose these sites due to higher food quality. If so, this may also explain some of the variation in NDVI across sites with or without the presence of beaves.

The increase in variance and mean NDVI at beaver sites could explain their higher moth richness. For butterflies, Bailey et al. (2004) found a positive correlation between species richness and maximum NDVI, but did however not find a correlation between butterfly richnees and NDVI variance. Contrary to butterflies, some moth species depend on downed woody debris, which is negatively correlated with NDVI (Zielewska--Büttner et al., 2020), and which could help explain why we found a higher moth diversity as well as a higher species richness at beaver sites. It is however worth noting that we examined the biomass and diversity from summer to autumn and calculated NDVI from early spring photos.

4.4. Conclusions

In this study, we demonstrated that the reintroduction of beavers have a profound effect on the riparian zone as indicated by the increased moth richness and diversity as well as increased greenness and habitat heterogeneity found at beaver sites. Thus, when reintroducing the beaver, its effect is not limited to the aquatic environment, but spans into the riparian zone. Our findings show that the presence of beavers affected flying invertebrate biomass, but that this was dependent on time of the year.

Credit author statement

Line Holm Andersen: Writing - original draft, Formal analysis, Visualization, Supervision, Methodology, Christian Ransborg: Funding acquisition, Writing - original draft, Investigation, Conceptualization, Formal analysis, Methodology, Cino Pertoldi: Writing - review & editing, Conceptualization, Supervision, Methodology, Sussie Pagh: Writing - review & editing, Conceptualization, Supervision, Methodology, Simon Bahrndorff: Writing - original draft, Conceptualization, Supervision, Methodology.

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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.117719.

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