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Impact of European Beaver (*Castor fiber* L.) on Vegetation Diversity in Protected Area River Valleys

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Abstract: The aim of the study was to evaluate the impact of European beaver (*Castor fiber* L.) on vegetation diversity and the expansion of non-native plant species in areas surrounding watercourses in Polesie National Park, Poland. The investigation was carried out within six watercourses inhabited by beavers and four comparison watercourses where beaver were absent. European beaver living in the park had a small excursion range, reaching a maximum distance of 25 m from the watercourse so that effects on vegetation diversity were limited to the immediate vicinity of the watercourse. Beaver significantly influenced diversity of the tall tree and forest floor vegetation, while it did not significantly modify the diversity of the low tree and shrub layer. Five alien plant species were documented. The alien species most strongly associated with beaver activity was devil's beggartick (*Bidens frondosa* L.), which occurred in the immediate vicinity of beaver dams. Other alien species most benefiting from the presence of beaver were giant goldenrod (*Solidago gigantea* Aiton) and black cherry (*Prunus serotina* Ehrh.). Our study confirmed hypotheses found in literature according to which beaver activities that reduce the proportion of native species can promote the expansion of plant alien species.

Keywords: Polesie National Park; species diversity; *Castor fiber*; European beaver; alien and invasive species

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Citation: Piętka, S.; Misiukiewicz, W. Impact of European Beaver (*Castor fiber* L.) on Vegetation Diversity in Protected Area River Valleys. *Conservation* **2022**, *2*, 613–626. https://doi.org/10.3390/conservation2040040

Academic Editors: Luca Luiselli, Giovanni Amori and Daniele Dendi

Received: 14 September 2022
Accepted: 9 October 2022
Published: 13 October 2022

1. Introduction

River valleys perform an important environmental function as dispersal routes for many plant species [1–4]. A number of factors favor plant species expansion in river valleys. Among the most important are: the movement of water in the river; reduced competition resulting from erosion that creates areas with highly reduced vegetation cover; the formation of new areas along rivers by sediment and material carried downstream; and the presence of animals that contribute to the transport of seeds and plant parts [5–7]. Even plant species without adaptations to hydrochory can spread efficiently and over long distances along rivers, which move not only seeds, but also vegetative propagules (e.g., rhizomes) and even intact pieces of turf [8]. However, river hydrochory has the limitation of one-way migration, that is, with the downstream. Additionally, migration is disrupted by human regulation of river water level and variability of river flow and artificial dams [9,10]. Disruption of plant dispersal is a limiting factor for diversity, although the effects can be reversed [11]. Alien and invasive species are increasingly threatening the biodiversity of river valleys [4,12–17]. Invasive species are much more common in anthropogenically transformed habitats, but also affect natural habitats [18,19].

In a study by Wróbel (2017) [20] on regulated rivers, the largest number of invasive species sites was recorded on various types of hydraulic structures, including bank reinforcements. While protected areas are highly resistant to invasive species encroachment, river valleys may be more susceptible to them [15,18]. Two factors strongly promoting the encroachment of invasive species into river valleys are exposed soil substrate and the periodic occurrence of pioneer site conditions [3,19,21].

The European beaver (*Castor fiber* L.) is an important factor generating pioneer conditions in river valleys. The dams it constructs slow the movement of water and create new meanders and backwater areas. Temporary flooding can limit the occurrence of typical terrestrial plants and create niches for hydrophyte phytocoenosis. Trees knocked down as a result of flooding or felling, as well as material carried with water and deposited on the dam, form islands on which seeds carried by the river can germinate [22–24]. Seed movement by beavers is not yet well understood and described, but long-term submergence of seeds of invasive species such as Himalayan balsam (*Impatiens glandulifera* Royle) can reduce viability and germinative capacity of these plants [25]. A meta-analysis by Stringer and Gaywood (2016) [26] found that of the 63 articles reviewed, 73% indicated an increase in European beaver on species diversity, 17% indicated no effect, while 10% indicated reduced diversity. Stringer and Gaywood (2016) [26] did not find negative impacts of beaver on vegetation diversity. Some studies indicate that beaver activity indirectly promotes the expansion of invasive plant species. Juhász et al. (2020) [27] in a study in Hungary showed that beavers preferred native tree species such as *Salix* and *Populus* over invasive species such as *Acer negundo*, *Fraxinus pennsylvanica* and *Amorpha fruticosa*. Lesica and Miles (2004) [28] showed that European beaver feed mainly on native species, creating conditions conducive to the expansion of non-natives, such as Russian olive (*Elaeagnus angustifolia* L.) and tamarisk (*Tamarix* spp.). Studying this issue, Juhász et al. (2022) [29] referred to the enemy release hypothesis (ERH) according to which species will spread faster in the new environment when their natural enemies are not present. Kimball and Perry (2008) [30] indicated that beaver food preference can be altered to reduce tamarisk populations. It thus appears that European beaver can have both favorable and limiting effects on the distribution of invasive species, but that additional research is needed to better understand such relationships.

Alien and invasive plant species from 68 taxa are found in 19 of Poland's 23 national parks [17]. The most common species are Small balsam, Giant goldenrod and Black locust. Among species preferring river valleys habitats are Himalayan balsam and Japanese knotweed, found in 15 of the 23 parks, and Wild cucumber, found in 13 parks.

In Polesie National Park where this study was conducted, there have been increases in the area of water features—lakes, ponds, rivers and channels [31]. Studies indicate that this increase is due to both human activity and activity of European beaver, which was reintroduced to the park in the 1990s [32]. The first 13 beaver were released in the area in 1992, which is a relatively short period of time for impacts to be expressed in the forest near the watercourses. Since 2012, the population has been stable at about 400 individuals [33]. The European beaver has spread to surrounding areas, where it creates wetlands and significantly affects water retention [32]. Beaver in Polesie National Park can affect a significant proportion of park area due to the flat terrain and numerous drainage channels and ditches. The dense network of drainage channels extending outside the park also increases vulnerability to the intrusion of alien and invasive species. Seventeen species of non-native plants are currently identified in the Polesie National Park area. Significant areas of the park are covered by peat bogs, which are resistant to encroachment by alien species as long as proper water conditions are maintained [3].

In this study, we assess the impact of European beaver in Polesie National Park on vegetation diversity in river valleys and examine the influence of beaver on the spread of invasive and alien plant species.

2. Materials and Methods

The study was conducted in Polesie National Park in eastern Poland (Figure 1). The park covers an area of 9760 ha, of which 4865 ha are covered with forests. The non-forest areas consist mainly of swamps and arable lands. The largest forest area is occupied by the communities of *Querco roboris-Pinetum* (30.1%), *Betuletum pubescentis* (23.2%) and *Ribo nigri-Alnetum* (14.6%). The largest area is covered by forests with a dominant share of downy birch (*Betula pubescens Ehrh.*) (39.5%), Scots pine (*Pinus sylvestris* L.) (32.3%) and black alder (*Alnus glutinosa* (L.) Gaertn) (20.3%).

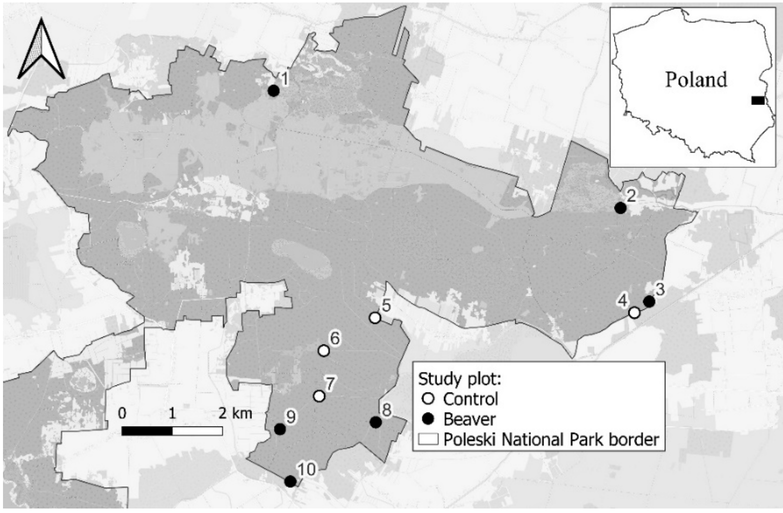

Figure 1. Location of survey plots in Polesie National Park.

Ten survey plots were established. One plot was on a river (plot 2 on the Włodawska River) and nine plots were on drainage channels. The measurement plots were assumed to run along a straight section without meanders on the section of the Włodawka river. The width of the river and the channels is 4–7 m. Six survey plots were established at beaver dam sites, while four plots were established at sites where beaver have not been observed. Survey plot 10 was established in the vicinity of a human-made water gate. The beavers used the water gate as their own dam as trees felled by beaver were discovered near the water gate. In plots 4 and 7, the channel was the boundary between forest and non-forested land, while in plot 3 forest occurred more than 50 m from the banks of the channel. Only in plot 3, measurements were carried out in the non-forested land.

Forests surrounding watercourses were dominated by black alder (*Alnus glutinosa* (L.) Gaertn), silver birch (*Betula pendula* Roth), common aspen (*Populus tremula* L.) and Scots pine (*Pinus silvestris* L.) (Appendix A, Table A1). The shrub and low tree layer ($h < 10$ m) was dominated by black cherry (*Prunus serotina* Ehrh), common hazel (*Corylus avellana* L.), alder buckthorn (*Frangula alnus* Mill.), willows (*Salix*) and common hornbeam (*Carpinus betulus* L.). The only non-native tree species found was black cherry, which occurred in plots 1 and 3.

Three transects of 50 × 6 m running perpendicular to the axis of the river or channel were established at selected points (Figure 2). Each transect included three 6 × 6 m subplots located at 0–6 m (zone a), 22–28 m (zone b) and 44–50 m (zone c). In plots located where beaver were present, the first transect was established at the beaver dam (0). Subsequent transects were established 50 m upstream (+) and 50 m downstream (−). In control plots, where beaver dam were not present, the first transect was established at a randomly selected location. The location of the measurement point was selected on the map. The measuring point was found using a GPS receiver.

The number of beaver bite marks, the distance of bite marks from the river axis, the type of wood with bite marks (i.e., felled tree, standing tree or stump) and the species with bite marks were determined along the length of each 50 × 6 m transect. On each 6 × 6 m subplot, floristic surveys were carried out in three layers of the forest: forest floor (III), low trees ($h < 10$ m) and shrubs (II), and tall trees ($h > 10$ m) (I). On each sub-plot, the area of land occupied by species of trees, shrubs and undergrowth vegetation was measured. In the case of trees, the measurements were based on the crown projection area (CPA).

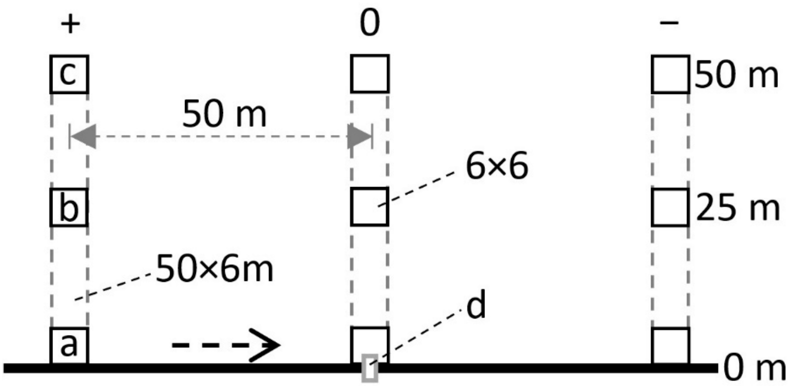

Figure 2. Sampling scheme for assessing beaver foraging and floristic characteristics of sample plots. Location relative to the dam (d): "+"—Upstream; 0—Dam zone; "−"—Downstream. Distance from the river: a (0–6 m), b (22–28 m), c (44–50 m). Black line—river. Arrow—water flow direction.

Two biodiversity indices, Margalef (1958) and Shannon (1949), and Simpson's (1949) species dominance index were used to describe vegetation diversity. Due to the difficulty in determining the number of individuals of ground cover species occurring in patches, e.g., goldenrod, these indicators were modified to use the area occupied by species (Table 1). In its modified version, the Margalef index (R) retained information on the number of species (S), while the Shannon-Wiener (H) and Simpson (C) indexes relied entirely on information on the area occupied by plant species. In the case of trees, the information on the crown projection area (CPA) was used. This feature is quite well correlated with the features of the tree such as DBH, basal area and tree volume [34–37]. We assumed that CPA would reflect tree biomass quite well. The applied modifications of the indicators were inspired by the research carried out by Nagendra (2002) [38], Sienkiewicz (2010) [39] and Lasota et al. (2017) [40].

Table 1. Ecological indexes.

Index	Equation	Legend
Margalef (R)	$R = \frac{S}{log\ N}$	S—number of species
Shannon-Wiener (H)	$H = -\sum(pi)\ (logpi)$ $pi = \frac{n_i}{N}$	n_i—area occupied by plants of particular species
Simpson (C)	$C = \sum(\frac{n_i}{N})^2$	N—area occupied by plants of all species

Non-parametric tests were used to compare the values of the indicators used in the research—the Mann-Whitney U test was used for two independent samples and the Kruskal-Wallis ANOVA with Dunn Bonferroni post-hoc test for comparisons of more than two factors. The tests were carried out on data subjected to log transformation. Data were compiled using an Excel spreadsheet and tests run using the PQ Stat statistical package.

3. Results

Traces of foraging in the form of gnawed and damaged trees indicated the relatively short distance from the river used by beavers. On average, the maximum occurrence of damage was 6.2 m from the river or channel bank. The farthest feeding traces were encountered upriver from the dam and in the vicinity of the dam (Upstream), a distance of 25 m. In the area below the dam (Downstream), evidence of feeding was found at most 15 m from the edge of the watercourse. Interestingly, where a man-made water gate dammed the river, the farthest sign of beaver foraging was only 5 m from the watercourse bank.

Most of the stems left by beavers in the survey plots were stumps (92%). Beavers left few felled trees (7%) or standing damaged trees (1%), indicating that most trees felled were removed. Beavers mainly felled common hazel (34.8%) and bearded birch (26.1%). There were no bite marks by beaver on conifers or oak. Interestingly, bite marks on hornbeam were encountered, but only on young trees from the second layer of the forest. Beavers travelled furthest from rivers to obtain common hazel, black alder and hornbeam (10 m on average). The shortest treks were to obtain willow (1.5 m on average), which was found mainly near the banks of watercourses (Appendix A).

Plots where beaver were present contained on average 17 species of trees and shrubs, while plots without beaver averaged only 12 species (Table 2). Whether beaver were present or not, the same species dominated the forest overstory (layer 1): black alder (48–50%), silver birch (16–24%) and Scots pine (10–19%). In layer II, in plots where beaver were present, black alder (19.9%) together with alder buckthorn (29.1%) occupied half of the survey area. Plots without beaver were dominated by black cherry (23.7%), hazel (13.7%) and alder buckthorn (14.5%). Where a species was found in both layers 1 and 2, the abundance in layer 2 was usually less than in layer I. Common aspen was an exception, occupying 6.8% of the area in layer I and 8.0% in layer II. In layer II, there was a significant decrease in the abundance of alder when beaver were present (3.1%). Without beaver, the abundance of alder was much higher (19.9%).

Table 2. Species composition of I and II forest layers and species of trees with bite marks.

Species	Share of Species in the Number of Bite Marks (Average Distance of Bite Marks from the River Edge) % (m)	With Beaver		Without Beaver	
		Layer [1]			
		I %	II %	I %	II %
Black alder	11.6 (10.0)	48.3	3.1	49.8	19.9
Silver birch	26.1 (4.1)	16.1	3.9	23.1	5.4
Scots pine	-	10.7	1.7	18.1	0.0
Pedunculate oak	-	7.9	5.8	7.6	0.6
Common aspen	14.5 (4.3)	6.8	8.0	1.4	0.2
Norway spruce	-	8.7	0.0	0.0	0.0
Norway maple	-	1.5	0.7	0.0	0.0
Common ash	-		0.8		0.0
Hornbeam	10.1 (10.0)		4.0		10.4
Willows	2.9 (1.5)		5.0		5.6
Mountain ash	-		2.2		2.0
Bird cherry	-		23.7		12.6
Black cherry	-		5.8		0.0
Common hazel	34.8 (8.8)		13.7		12.8
Alder buckthorn	-		14.5		29.1
Common dogwood	-		1.2		1.1
Euonymus	-		1.1		0.0
Common hawthorn	-		5.0		0.0
Guelder rose	-		0.0		0.4
Total	100 (6.2)	100.0	100.0	100.0	100.0

[1] Layer I (trees taller than 10 m), layer II (trees shorter than 10 m and shrubs).

Indicators of species diversity show that the European beaver in the study area had a significant but weak impact on vegetation (Table 3). Plots where beaver were present had a higher Shannon-Wiener diversity index in Layer I (trees > 10 m). Within the zones, only the "a" zone was characterized by a significantly higher value of the Shannon-Wiener diversity index. Although zones further from the water's edge still showed higher diversity and lower dominance of species at beaver sites, differences were not statistically significant. The absence of differences in the Margalef index due to beaver indicates that the impact was manifested through changes in the proportion of species (Shannon-Wiener index) and not through decreased species number. This is confirmed by Simpson's dominance index, which was higher in plots without beaver. Richness of Layer II (trees < 10 m and shrubs) was unaffected by the presence of beaver or distance from their dam, with one exception.

Simpson's dominance index in plots without beaver was significantly higher in zone b compared to other zones. In layer III (forest floor) there was significantly higher variation based on the Margalef index when beaver were present. As was the case for layer I, beaver caused significant differences in forest floor vegetation only directly bordering the banks of watercourses. In forest floor vegetation plots nearest the water where beaver were present there was significantly higher species diversity according to the Margalef index. The lack of differences in the Shannon and Simpson indices suggests that the beaver generated a higher richness expressed by the number of species than the richness expressed by the area they occupied. This is also evidenced by the number of species between variants found in this layer.

Table 3. Number of species and indicators of diversity of forest layers with or without beaver present and with distance from the watercourse. The average variation was determined for three plots with a combined area of 108 m^2. B—plots with beaver, N—plots without beaver.

Index	Variant	a (0–6 m)		b (22–28 m)		c (44–50 m)		All	
		(i) Average ± Standard Deviation [1,2] (n) Average Number of Species							
		Layer I (trees taller than 10 m)							
		i	n	i	n	i	n	i	n
H	B	0.64 ± 0.31 Aa	2.2	0.63 ± 0.38 Aa	2.2	1.08 ± 0.38 Aa	3.0	0,76 ± 0.41 A	2.5
	N	0.37 ± 0.10 Ba	2.0	0.43 ± 0.24 Aa	2.2	0.60 ± 0.71 Aa	2.5	0.47 ± 0.41 B	2.3
R	B	0.47 ± 0.19 Aa	2.2	0.44 ± 0.17 Aa	2.2	0.73 ± 0.31 Aa	3.0	0.53 ± 0.25 A	2.5
	N	0.41 ± 0.04 Aa	2.0	0.43 ± 0.09 Aa	2.2	0.47 ± 0.32 Aa	2.5	0.44 ± 0.18 A	2.3
C	B	0.59 ± 0.15 Aa	2.2	0.58 ± 0.24 Aa	2.2	0.39 ± 0.13 Aa	3.0	0.53 ± 0.22 B	2.5
	N	0.79 ± 0.07 Ba	2.0	0.75 ± 0.16 Aa	2.2	0.67 ± 0.24 Aa	2.5	0.74 ± 0.23 A	2.3
		Layer II (trees shorter than 10 m and shrubs)							
H	B	1.10 ± 0.28 Aa	4.4	0.74 ± 0.50 Aa	3.6	0.72 ± 0.41 Aa	3.8	0.85 ± 0.42 A	3.9
	N	1.00 ± 0.20 Aa	3.5	0.54 ± 0.45 Aa	3.5	1.11 ± 0.17 Aa	4.2	0.87 ± 0.39 A	3.8
R	B	1.09 ± 0.49 Aa	4.4	0.78 ± 0.26 Aa	3.6	0.81 ± 0.49 Aa	3.8	0.89 ± 0.42 A	3.9
	N	0.97 ± 0.38 Aa	3.5	0.74 ± 0.51 Aa	3.5	0.87 ± 0.10 Aa	4.2	0.85 ± 0.34 A	3.8
C	B	0.42 ± 0.14 Aa	4.4	0.58 ± 0.29 Aa	3.6	0.61 ± 0.19 Aa	3.8	0.54 ± 0.22 A	3.9
	N	0.41 ± 0.06 Ab	3.5	0.71 ± 0.25 Aa	3.5	0.38 ± 0.07 Ab	4.2	0.51 ± 0.22 A	3.8
		Layer III (forest floor vegetation)							
H	B	2.16 ± 0.42 Aa	24.4	1.67 ± 0.34 Aa	14.0	2.02 ± 0.31 Aa	12.4	1.95 ± 0.40 A	16.9
	N	1.95 ± 0.97 Aa	18.5	1.84 ± 0.69 Aa	16.0	2.02 ± 0.64 Aa	13.0	1.85 ± 0.71 A	16.2
R	B	4.02 ± 0.50 Aa	24.4	2.61 ± 0.49 Ab	14.0	2.78 ± 0.71 Ab	12.4	3.14 ± 0.69 A	16.9
	N	3.28 ± 0.67 Ba	18.5	2.84 ± 1.02 Aa	16.0	2.43 ± 0.64 Aa	13.0	2.85 ± 0.80 A	16.4
C	B	0.21 ± 0.15 Aa	24.4	0.30 ± 0.13 Aa	14.0	0.19 ± 0.06 Aa	12.4	0.23 ± 0.12 A	16.9
	N	0.29 ± 0.31 Aa	18.5	0.29 ± 0.23 Aa	16.0	0.30 ± 0.23 Aa	13.0	0.29 ± 0.23 A	16.2

[1] The same capital letters of the alphabet indicate no statistically significant differences between plots with and without beaver, while different letters indicate significant differences (based Mann-Whitney U test, α = 0.05).
[2] The same lower letters of the alphabet indicate no statistically significant differences between zones (0–6 m, 22–28 m, 44–50 m) based on a Kruskal-Wallis ANOVA with Dunn Bonferroni post-hoc test (α = 0.05).

The presence of beaver dams was related to significant differences in species diversity within the tall-tree layer (Table 4). Significant differences were shown between transects upstream and downstream from dams. Both the Margalef index and the Shannon-Wiener index indicated higher species diversity among tall trees upstream from the dam (Table 4). No significant differences in Simpson's dominance index were found in the tall-tree layer for any location. Species diversity of the shorter tree and shrub layer was not significantly different among locations for any of the diversity indexes.

Significant differences in forest floor species diversity occurred between the area upstream from the dam and the area immediately adjacent to the dam (Table 4). The area where beaver were damming the river or channel had higher forest floor plant species diversity and lower dominance rates than the area adjacent to the dam. Results for the Shannon-Wiener index suggest that proximity to the dam did not increase forest floor richness, but did alter where this richness was observed. This is shown in Table 3, where differences in values of the Shannon-Wiener index with and without beaver were not significant.

Table 4. Indicators of species diversity of forest layers related to distance from beaver dams. Average variation was determined for an area of 108 m^2 (3 measurement plots).

Index	**Transect Location**					
	Upstream		**Dam**		**Downstream**	
	(i) Average ± Standard Deviation [1] (*n*) Average Number of Species					
	Layer I (trees taller than 10 m)					
	i	*n*	i	*n*	i	*n*
H	0.67 ± 0.34 [a]	2.5	0.57 ± 0.55 [ab]	2.1	0.39 ± 0.26 [b]	1.7
R	0.57 ± 0.35 [a]	2.5	0.48 ± 0.26 [ab]	2.1	0.36 ± 0.11 [b]	1.7
C	0.65 ± 0.33 [a]	2.5	0.66 ± 0.31 [a]	2.1	0.75 ± 0.17 [a]	1.7
	Layer II (trees shorter than 10 m and shrubs)					
H	0.71 ± 0.59 [a]	3.5	0.85 ± 0.58 [a]	4.0	0.90 ± 0.34 [a]	3.8
R	0.73 ± 0.49 [a]	3.5	0.87 ± 0.44 [a]	4.0	0.84 ± 0.37 [a]	3.8
C	0.61 ± 0.31 [a]	3.5	0.54 ± 0.29 [a]	4.0	0.50 ± 0.19 [a]	3.8
	Layer III (forest floor vegetation)					
H	2.27 ± 0.27 [a]	22.0	1.69 ± 0.41 [b]	16.8	1.98 ± 0.28 [ab]	18.4
R	3.82 ± 0.51 [a]	22.0	2.95 ± 0.40 [b]	16.8	3.34 ± 0.60 [ab]	18.4
C	0.16 ± 0.03 [b]	22.0	0.35 ± 0.14 [a]	16.8	0.23 ± 0.16 [ab]	18.4

[1] Different lowercase letters indicate statistically significant differences between transect locations based on the Kruskal-Wallis ANOVA with Dunn Bonferroni post-hoc test (α = 0.05).

Five species of alien plants were found during the study, most of which were forest floor species—giant goldenrod (*Solidago gigantea* Aiton), devil's beggartick (*Bidens frondosa* L.), small balsam (*Impatiens parviflora* DC.) and hedge bindweed (*Calystegia sepium* (L.) R.Br). Only one alien plant species, black cherry (*Padus serotina* (Ehrh.) Borkh.), was found in Layer II (low trees and shrubs). Near beaver dams, all the alien species noted above were present, except for small balsam. In areas without European beaver, black cherry and devil's beggartick were not found.

Non-native species occupied a total of 143.1 m^2, which accounted for 4.3% of the area in all experimental plots (Table 5). Where beaver were not present, the percentage area occupied by non-native species was 3.2%, while in areas adjacent to watercourses with a beaver dam present it was 5.1%. In sites without beaver, goldenrod was the alien species making up the greatest proportion of the groundcover (2.1%) and small balsam was least prominent (1.0%). On sites with beaver, the alien species with the highest coverage of the area were cherimoya (2.0%), goldenrod (1.3%), and devil's beggartick (1.8%).

Table 5. Area and percentage of area occupied by alien species in relation to proximity to beaver dams.

Variant/Location	**Sum of Occupied Area (m^2)**	**Area Share (%)**
	Presence of beaver	
With beaver	98.5	5.1
Without beaver	44.6	3.2
	Transect location	
Upstream	24.5	3.8
Dam	68.4	10.6
Downstream	5.6	0.9
	Distance from river	
a (0–6 m)	62.6	1.7
b (22–28 m)	22.9	0.6
c (44–50 m)	57.6	1.6
Total	143.1	4.3

Within plots established where beaver were present, alien species reached their highest coverage in the transect centered on the dam (10.6% of the plots). In plots upstream from the dam their coverage was lower (3.8% of the area), while the lowest coverage by alien species was downstream of the dam (0.9%). In the vicinity of the dam, greatest coverage was by devil's beggarticks (5.0%), goldenrod (3.3%) and black cherry (2.2%). Upstream from the dam, black cherry (3.5%) and devil's beggartick (0.3%) were the most common alien species, while downstream the most common aliens were goldenrod (0.6%), black cherry (0.2%) and hedge bindweed (0.1%).

Similar coverage (1.6–1.7% of the area) by non-native species was found nearest to the watercourse (within 6 m) and furthest from the watercourse (44–50 m). In the area bordering the watercourse, devil's beggarticks (1.0%), goldenrod (0.7%), hedge bindweed (0.1%) and black cherry (0.03%) were all present. The intermediate zone located 22–28 m from the watercourse contained small balsam (0.4%), goldenrod (0.2%), and cherimoya (0.03%). Only two alien species were present in zone c: black cherry (1.0%) and goldenrod (0.6%).

4. Discussion

The impact of beaver on species diversity was not clear. Contradictory results were obtained for the same forest layer; for instance, where significant differences were shown with and without beaver being present for the Margalef index, differences were not significant for the Shannon-Wiener index. Such discrepancies may be due to differences in how diversity indicators were obtained. We used a modified version of the Margalef index that took into account the number of species, while the Shannon-Wiener index was based entirely on the area occupied by species. The Shannon-Wiener index as we used it was more sensitive to changes in the proportion of species, while the Margalef index was more sensitive to changes in their abundance. The indicators used thus described diversity from different perspectives. As a result, we not only described diversity, but also showed how transformations in the environment are associated with the presence of beaver.

In the layer I, the local beaver population equaled the proportions of the area occupied by species (Shannon-Wiener index), but did not cause the appearance of new species (Margalef's index). Conversely, in the case of forest floor species, beaver were associated with the appearance of new species, but the share of area covered by species differed. The reason for the observed environmental impacts of beaver may be the young age of the local beaver population. Beavers were first released in Polesie National Park in 1992 [33]. This 30-year period may have been too short for new tree species to establish in response to beaver activity. In the initial period after beaver colonization of the area, one would expect to see changes in the proportion of species currently present on the sites, but only in the long term would other species be expected to appear in niches newly created by beaver activity. This may be what is currently happening around rivers populated with beavers, which would explain the lack of differences in Margalef index values and, at the same time, significant differences in Shannon-Wiener index values within the tree layer.

Some of the seemingly contradictory results in this study were cases in which there were significant vegetation differences between locations in relation to proximity to beaver dams, while at the same time finding no significant difference between plots near beaver dams compared to areas without beaver. These situations were observed using the Margalef index for the tall-tree layer and the Shannon-Wiener index for forest floor vegetation. In these cases, it is feasible that beaver do not increase species diversity, but only redistribute the existing species in the vicinity of the dam, increasing diversity upstream from the dam and reducing it downstream, without causing significant changes compared to areas where beaver is not present.

Our investigation of the relationship between European beaver and the spread of alien species confirmed the thesis of Lesica and Miles (2004) [28], Juhász et al. (2020) [27] and Juhász et al. (2022) [29] according to which beaver activities that reduce the proportion of native species can promote the expansion of alien species. In the present study, in the tree and shrub layer, black cherry (a species not observed to have been a food source of beaver in Polesie National Park), occurred only on watercourses where European beaver were active. Beaver fed mainly on hazel, birch and aspen. In the forest, beaver created conditions allowing the spread of aspen, while limiting the amount of black alder. The presence of pine in the shorter-tree and shrub layer near beaver dams indicates that light conditions were favorable for the establishment of black cherry.

In the forest floor layer, beaver seemed to have no effect on the presence of alien species, such as small balsam and hedge bindweed. Giant goldenrod benefited from the presence of beaver but did not need beaver to be present to encourage their expansion—goldenrod was abundant in the immediate vicinity of the dam, but also beyond the beaver's foraging range. Devil's beggartick was strongly associated with the presence of beaver, occurring only in areas with beaver. Our research confirmed the proposition that riverine invasive species are favored by exposed soil and conditions favoring the establishment of pioneer plant species [3,19,21]. Devil's beggartick took advantage of pioneer conditions created by beaver but did not spread beyond the vicinity of the dam, especially downstream. This species was more dependent on the presence of beaver than goldenrod. Beaver dams provided a foothold on which devil's beggartick developed, while at the same time acting as a barrier to further expansion of the species. Goldenrod is a greater threat to the diversity of the park's rivers and canals than devil's beggartick because it is adapted to a wider range of habitats.

The emergence of small balsam could be significant problem for the Park Service. Currently, it is the most widely spread invasive species of river valleys in Polish national parks [17]. The species prefers areas that are vulnerable to periodic flooding, such as riparian forests or river valleys [41–44]. On the basis of our research, we assume that beaver activity can both favor and inhibit the expansion of small balsam in Polesie National Park. On the one hand, pioneer conditions generated in the vicinity of the dams may favor the acquisition of new footholds by small balsam and accelerate its expansion. On the other hand, the dam can create a barrier stopping the spread of waterborne displaced seeds. The concentration of plants around the dam should also facilitate their removal. Beaver dams may also contribute to the elimination of the existing seed bank, since prolonged submergence reduces small balsams' ability to germinate [25].

It is difficult to obtain a clear understanding of the role of beaver in the spread of alien species. In the case of protected areas where beaver and alien plant species have been present for a considerable time, assessing their interactions can be challenging. Areas such as Polesie National Park, which are characterized by a relatively small number of non-native plant species and a young population of European beaver provide opportunities to trace the process of alien plant expansion from its early stages and thereby to assess the role the European beaver plays in their spread.

5. Conclusions

- The impact of beaver was limited to the immediate vicinity of watercourses. The farthest bite marks were recorded only 25 m from the axis of the watercourse.
- Beaver significantly increased species diversity in the tall-tree layer and in the forest floor layer, with no significant effects on the low tree and shrub layer.
- Five species of alien plants were found during the survey: Giant goldenrod, devil's beggartick, small balsam, hedge bindweed, and black cherry. Except for small balsam, all the listed alien species were present in plots colonized by European beaver. Giant goldenrod, small balsam and hedge bindweed were found in comparison plots where beaver were not present.
- The alien species most strongly associated with beaver activity was devil's beggartick, which occurred mainly in the vicinity of dams. Giant goldenrod benefited from the presence of beaver but did not require its presence for expansion. Black cherry occurred only in areas with dams and was not gnawed by beavers. It may benefit from the strong preference of beaver for native species.

- Our study confirmed hypotheses found in literature according to which beaver activities that reduce the proportion of native species can promote the expansion of alien species.

Author Contributions: Conceptualization, S.P. and W.M.; methodology, S.P.; software, S.P.; validation, S.P. and W.M.; formal analysis, S.P.; investigation, W.M.; resources, W.M.; writing—original draft preparation, S.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by forest fund under an agreement between the General Directorate of State Forests in Warsaw and the Polesie National Park. Contract number NB520-1/2021.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A

Table A1. Species Composition of Stand Layers on Survey Plots by Variant (with and without Beaver) and Distance Zones From the River Axis (a—0–6 m; b—22–28 m; c—44–50 m).

Species	Beaver Presence/Absence, Plot Number and Distance Zone																													
	With Beaver									Without Beaver														With Beaver						
	1			2			3 [1]			4			5			6			7			8			9			10 [2]		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Layer I (trees taller than 10 m)																														
Black alder				=	=	−				=	±		±	±	=	+	=	−	+	+	+	−		−	=	=	+		−	−
Silver birch	=	=			−	−				−			−	−	+	−	−	−	−	−						=	=	−	−	−
Scots pine	−			−	=	=						=						=						−				−		−
Pedunculate oak											−							−					=	=						−
Common aspen																	−	−				−		−				−	−	−
Norway spruce																							=	=						
Norway maple																						−								
Layer II (trees shorter than 10 m and shrubs)																														
Black alder													=		−	−			=		−				−					−
Silver birch	−	−	−											−	−														−	−
Scots pine		−																												
Pedunculate oak																−	−											−	−	=
Common aspen	=																−						−					−		−
Norway spruce																														
Norway maple																							−	−						
Common hornbeam				−	−	−						+																		
Common ash																								−				−		
Mountain ash												−				−	−	−	−				−						−	−
Bird cherry				−							±	−				−	−	−	=	−	−	−	−	=	−	−	−	−	−	
Black cherry	−	−	+						−																					
Common hazel					=	−										−	=	=		−		+	=	−						
Alder buckthorn				−								=	−	−	−	=	−	−	−	+	=			−	−	−	−	−	−	−
Willows	−												−	−	−		−								−	−		−		−
Common dogwood																		−				−		−						
European spindle																						−								

Table A1. *Cont.*

Species	Beaver Presence/Absence, Plot Number and Distance Zone																													
	With Beaver									Without Beaver												With Beaver								
	1			2			3 [1]			4			5			6			7			8			9			10 [2]		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Common hawthorn																									–					
Guelder rose																–					–									

[1] Non-forested area. In plot 3, non-forested areas are located on both sides of the canal. Forest occurred more than 50 m from the banks of the channel. [2] Beaver dam absent, beaver bite marks were found near the water gate. Legend:

Species share in occupied area:	0%	≤25%	26–50%	51–75%	76–100%
		–	=	+	±

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