

# Mowing regimes and their impact on beaver presence

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## Contents

Abstract .....	3
Introduction .....	4
Methods.....	6
Results.....	11
Discussion .....	13
Management implications and recommendations .....	17
Conclusions.....	20
References.....	21
Appendix I .....	27
Appendix II .....	28

## Abstract

The Eurasian beaver (*Castor fiber*) is a keystone species that strongly shapes freshwater ecosystems, and its activity can increase habitat complexity and biodiversity. However, this may be influenced by human management practices such as large-scale vegetation mowing in areas like the Drentsche Aa National Park where the beaver has been reintroduced in 2007-2012. This study gains insight into how annual vegetation mowing (woody vegetation availability) and water depth affect beaver occurrence in the Drentsche Aa. I hypothesized that beaver occurrence is lower in annually mowed areas and in locations with insufficient water depth. Beaver occurrence was surveyed along ~105km of streams and agricultural ditches during the winter of 2025-2026, using field observations and complemented with provincial data. Waterways were divided into 1km sections approximating beaver territory size, with occupied and unoccupied segments defined to standardize habitat comparisons and enable analysis of water depth and woody vegetation influence on beaver presence. Beaver occurrence was analyzed using a binomial generalized linear model relating beaver presence-absence to water depth and riparian woody vegetation availability. We found that water depth was a significant predictor of beaver occurrence, with substantially higher presence in deep sections ( $\geq 50\text{cm}$ ) compared to shallow sections ( $< 50\text{cm}$ ). Woody vegetation showed a positive but non-significant relationship with beaver presence, although occupied river sections tended to have a higher mean riparian woody availability than unoccupied ones. This indicates that maintaining sufficient water depth may be crucial for facilitating beaver recolonization, and that water management practices may directly influence their distribution. This could inform management decisions on how vegetation and water level regulation may facilitate or constrain beaver recolonization and associated ecosystem effects.

Keywords: Eurasian beaver (*Castor fiber*), habitat selection, water depth, riparian woody vegetation, managed lowland river system, Drentsche Aa National Park

## Introduction

As natural engineers, beavers (*Castor fiber*) play a central role in shaping freshwater ecosystems, often creating conditions that many other species depend on. Through dam building, lodge construction and channel digging, beavers modify hydrological and geomorphological processes by slowing water flow, raising local water tables, and altering sediment and nutrient dynamics (Brazier et al., 2020; Larsen et al., 2021; Kałuża et al., 2025). These physical modifications create new habitat features such as ponds, wetlands, dead wood and woody debris, fundamentally restructuring river valleys and riparian zones (Jones et al., 1994; Gurney & Lawton, 1996; Larsen et al., 2021).

Together with their foraging behavior, beavers maintain landscape heterogeneity and generally have positive effects on biodiversity by creating new aquatic and terrestrial habitat types (Wright et al., 2002; Stringer & Gaywood, 2016; Brazier et al., 2020; Mortensen et al., 2021). Beaver foraging further alters vegetation composition and structure along riverbanks, influencing forest regeneration and ecological trajectories (Jenkins, 1980; Donkor & Fryxell, 1999; Fustec et al., 2001; Gerwing et al., 2012). Research confirms that active and abandoned beaver ponds differ fundamentally from other wetlands in structural complexity and species diversity across multiple biotic groups and extends beyond the immediate watercourse (Willby et al., 2018; Washko et al., 2022; Fedyń et al., 2024). As such, beavers are widely regarded as keystone species whose activities support the persistence and diversity of numerous taxa (Naiman et al., 1986; Rosell et al., 2005).

Since their reintroduction in 2007-2012, beavers have been in an active colonization phase. During this phase, beavers typically occupy the most optimal habitats first, gradually expanding into suboptimal areas as population density increases (Pinto et al., 2009; John et al., 2010). Finding which habitat characteristics determine river section presence-absence at this stage can therefore help predict where beavers are likely to expand next.

Across much of Europe, riparian landscapes are strongly shaped by active management aimed at conserving open, species-rich grasslands (Naiman & Decamps, 1997). One of the most widespread tools is annual mowing, which prevents shrub- and tree encroachment and maintains nutrient-poor conditions favorable to many rare plant species, it also alters the availability of woody plants and may reduce habitat quality in winter (Smith et al., 2018). In river valley systems such as those of the Netherlands, including the Drentsche Aa National Park, mowing is a large-scale intervention used to promote biodiversity conservation and keep cultural landscape values (Nationaal Park Drentsche Aa, n.d.-a; n.d.-b) However, such management also alters riparian vegetation structure in ways that may interact with, or even constrain, the ecological processes created by beavers and therefore limit the aforementioned positive ecological impacts of beavers on ecosystems (Nilsson & Svedmark, 2002; Brazier et al., 2020). This study exemplifies the challenge in conservation biology where management measures designed to protect one species can accidentally constrain the recovery of another (Roemer & Wayne, 2003; Peterson et al., 2004). Resolving such inter-species conservation conflicts requires a broader perspective rather than species-centric management approaches (Karp et al., 2015; van Lanen et al., 2023).

Where mowing removes woody vegetation, beaver winter foraging opportunities are likely significantly reduced as woody vegetation is essential for food and construction material (Ritter et al., 2020). This could cause beavers to avoid colonizing intensively mowed parts of landscapes (Wang et al., 2019; Juhász et al., 2023; Pejstrup et al., 2023). If this is the case and mowing restricts beaver spatial behavior, it may also reduce all ecological impacts in the landscape. Understanding how conservation mowing affects beaver habitat use is therefore essential for resolving potential conflicts between management strategies during the beaver's colonization stage.

Management in the Drentsche Aa could interfere with the beaver's needs. They need sufficient water levels (60-70cm deep) to ensure safe lodge entrances, facilitate movement, and reduce predation risk (Collen & Gibson, 2000; Hartman & Tornlov, 2006; Raffel et al., 2009; Swinnen et al., 2019). For example, removal of dams (Bos et al., 2020), prevents beavers from raising local water levels. This could limit their occurrence and ability to maintain in streams, smaller watercourses and agricultural ditches (Butler & Malanson, 2005).

Despite growing the knowledge that low levels of woody vegetation negatively impact beaver occurrence (Ritter et al., 2020; Wang et al., 2019); studies do not address how mowing affects beaver presence. In particular, the combined effects of water depth and woody vegetation availability on beaver territory occupation in actively managed riparian landscapes remain poorly understood.

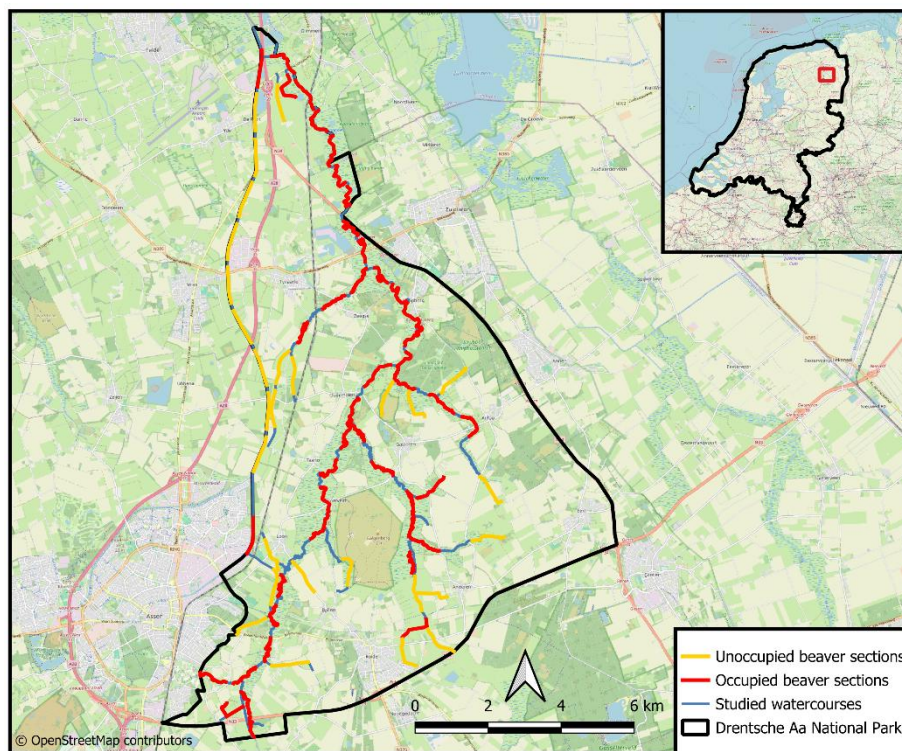
To address this gap in knowledge, the objective of this study is to gain insight into the presence or absence of mowing/woody vegetation and low and high-water depth on the occurrence of beavers at the landscape level. I hypothesized that beaver occurrence is lower in annually mowed areas and in locations with insufficient water depth.

Understanding how mowing influences beaver occurrence can inform management of the cultural and natural landscape of the park. If mowing reduces beaver settlement or changes their spatial behavior, this has direct implications like promoting or excluding beavers and their impacts from certain parts of the park. With the population still expanding and management decisions being made now that will shape where beavers can establish for decades to come, understanding the habitat factors that drive their occurrence is now both pressing and consequential. Managers could use vegetation management to reach biodiversity goals and use the ecological functions created by beavers for their goals. It underscores a broader need for a more refined and long-term monitoring strategy to fully understand how beavers shape ecosystem dynamics in actively managed lowland river systems like the Drentsche Aa.

## Methods

### Study area

The Drentsche Aa is a lowland stream valley system located in the province of Drenthe, the Netherlands. We surveyed approximately 105 km of the stream system and ditches within the national park of 10.000 ha. Surveys were conducted among both banks where accessible, but not consistently on both sides throughout the entire study area. The Drentsche Aa system is a slow flowing river system, characterized by meandering streams with a low gradient. The watershed encompasses both the main streams and a lot of connected ditches. Water authority management removes many dams, preventing beavers from raising water levels. The vegetation along the waterways includes riparian forest, alder carr, willow scrub and (mowed) wet meadows, as documented in the 2015-2016 vegetation survey carried out by EGG consult for the state forestry (Everts et al., 2017). The national park is designated as a Natura 2000 site and is managed by the state forestry service.



*Fig. 1: Drentsche Aa National Park with the occupied and unoccupied river sections (OpenStreetMap contributors, 2026).*

Between 2007 and 2012, about twenty-nine beavers were relocated to the provinces of Drenthe and Groningen after being extinct in the Netherlands for more than a century. The population has expanded and is currently estimated at around 400 individuals in the two provinces. Vegetation management is an important part of maintaining cultural landscape of Drentsche Aa National Park. Each year, around September, everything that is not woody vegetation is mowed, with a few exceptions. No fertilizers are applied and the mown biomass is removed. That way the soil remains

nutrient poor which prevents overgrowth and creates space for rare flowers and plants like orchids and marsh marigold. Additionally, grazing by cows and sheep is used as a method to keep the area open (Nationaal Park Drentsche Aa, n.d.-c). Maintaining appropriate water levels is essential for vegetation management, as well as sufficient flow conditions (without dams) for rare species such as the river lamprey (*Lampetra fluviatilis*.) (Oliveira et al., 2022). The water levels are maintained above a threshold by weirs with groundwater and periodic flooding playing a key role in maintaining necessary moisture conditions (BIJ12, n.d.; Natuurkennis, n.d.). Mowing as a management tool is important to maintain wet hay meadows such as marsh-marigold hay meadows (Nationaal Park Drentsche Aa, n.d.-d; Kołos & Banaszuk, 2013). The effect of mowing on vegetation is relatively larger in wetter zones, but mowing is practically impossible when water levels are too high (Kołos & Banaszuk, 2018).

## Data collection

Field surveys were conducted in the winter of 2025-2026 (November 2025 - February 2026), coinciding with peak beaver activity when behavioral signs such as tree cuttings, girdles and foraging trails are clearly visible. Surveys were carried out on foot along all watercourses and their banks, a mix of managed streams and agricultural drainage ditches. Evidence of beaver presence was systematically recorded throughout the study area (Campbell-Palmer et al., 2021; Graham et al., 2022). The geographic positions of all signs of beaver activity, including lodges, burrows, foraging signs (5 or more cut trees or branches), small foraging signs (less than 5 cut trees or branches and girdles), dams, foraging trails and feeding spots were recorded by Garmin GPSmap 64st (accuracy ~10 meters). We subsequently recorded our tracks with the Garmin GPS device. Our field surveys provide high-confidence detections, but non-detections do not guarantee true absence, as beavers may have been present but undetected during the survey. To minimize this, surveys were conducted systematically across watercourses and banks during peak activity in winter, when behavioral signs are most visible.

Additionally, data of the local provinces Drenthe and Groningen was used to create additional occupied and unoccupied sites, and to increase the sampling area (Provinces of Drenthe and Groningen, 2025). These data were compiled from multiple sources, including provincial field mapping applications, citizen science observations, and targeted field verification by the author (C. de Jonge, personal communication, March 16, 2026). This dataset provides detailed information on presence of beaver lodges, burrows, dams and foraging signs. Because the provincial dataset has not been independently verified in the field, it may contain false negatives (areas where beavers are present but not recorded). We partially assessed this by comparing the provincial data with our systematic field surveys covering ~60% of the park, which allowed us to estimate the likelihood of such omissions in the dataset. A comparative matrix was constructed to classify each section as (i) agreement in presence-absence (87.2%), (ii) omission (beaver presence in recorded field data but not in provincial data) which had 7.6% errors, or (iii) commission (beaver presence recorded in provincial data but not in field data) which had 5.1% errors. From this classification, these proportions of agreement and error types were calculated for the surveyed portion of the study area (~60%) and this level of agreement supports the use of the provincial dataset for the remaining non-

surveyed portion of the study area. Of the 72 sections, 39 were derived from field survey data (~105km of waterway) and 33 from the provincial dataset (~50km of waterway).

Water depth was measured in the field at 2-6 points per river section along the waterway by recording depth using a graduated measuring stick. The mean depth of each 1km section was then calculated from these measurements. River sections were classified as deep ( $\geq 50\text{cm}$ ) or shallow ( $< 50\text{cm}$ ) based on their mean water depth. This classification is based on literature which states beavers occur and feel “safe” in about 60-70cm depth (Collen & Gibson, 2000; Hartman & Tornlov, 2006; Swinnen et al., 2019). Although optimal water depths for beavers are reported to be deeper, we used a threshold of 50cm to distinguish shallow from deep sections. This represents a conservative lower limit for presence-absence rather than an optimal depth. The water depth data was supplemented with existing data (2005 - 2023) from the Hunze & Aa’s water authority based on cross sections with one to six measurement points per section. The temporal mismatch between these records and the current study period was considered acceptable because water levels in the Drentsche Aa are actively managed above a threshold by weirs, resulting in relatively stable depth conditions over time. The binary classification into deep ( $\geq 50\text{cm}$ ) and shallow ( $< 50\text{cm}$ ) categories also means that minor year-to-year fluctuations are unlikely to shift a section across the classification threshold.

In this study, non-woody areas were assumed to reflect either actively mowed or naturally open habitats. Both conditions were considered functionally equivalent as they result in the absence of woody vegetation and likely have the same effect on beaver occurrence. Consequently, woody vegetation availability was used as a proxy for both food availability in winter and the effects of conservation mowing.

The proportion of woody vegetation availability in sites was calculated using LGN 2023 (land-use) raster data at a 5-meter resolution (Hazeu et al., 2025). This dataset was reclassified in two categories: “Woody vegetation” and “no woody vegetation”. Appendix 1 illustrates the classes included in the “woody vegetation” category; non woody classes are not shown. Woody vegetation represents foraging and construction material for beavers. By reclassifying the LGN 2023 dataset into these two categories, the proportion of woody vegetation was calculated within a buffer of 60 meters on either side of the river section (Jenkins, 1980; Donkor & Fryxell, 1999; John & Kostkan, 2009; Zwolicki et al., 2019).

All sections and variables were subsequently compiled into a single dataset used for further analysis. In total 72 river sections were defined with 44 being occupied and 28 unoccupied.

### **Data processing/GIS analysis**

To assess the ecological factors shaping beaver occurrence at the landscape level, we demarcated sites occupied and unoccupied by beavers within the national park. Sites were defined as 1km watercourse sections. This length was based on previous studies suggesting that the average beaver territory size included approximately 1km of river (Rosell et al., 1998; Rosell & Hovde, 2001). Although this means the full territory was not always included, this delineation likely captured the core area of activity by beavers, defining the center and marking 500m upstream and 500m

downstream from there. Central place foraging rules apply here with beavers as foraging intensity declines markedly beyond 500m from the center point (Fryxell, 1992; Nolet & Rosell, 1994; Fustec et al., 2001; Sidorovich, 2011). Standardizing this spatial unit allowed consistent comparison of habitat characteristics (water depth and woody vegetation availability) across sites (John & Kostkan, 2009; Šimůnková & Vorel, 2015; Ritter et al., 2020) and aligns with the spatial modelling approach by Graham et al (2022).

The territory center was defined by the presence of an active primary lodge, active burrows and key foraging signs (in order of importance) (Campbell-Palmer et al., 2021; McLaren et al., 2022). This hierarchical approach was used to prioritize the most reliable indicators of long-term occupancy and thus the most ecological impact. In cases where multiple lodges occurred within the same area, the largest or most active lodge was selected, or the middle one was taken when this activity wasn't known to best represent the core of activity. When no lodges were present, territories centers were based on the middle or most active burrow and lastly, if no burrows were present, a territory was based on the center of sections with 5 or more foraging signs.

River sections and distances followed the natural course of the waterway rather than in a straight-line (Rosell et al., 1998; Rosell & Hovde, 2001). When a river branched, the branch with the highest observed density of beaver activity signs was followed. If no signs were found after the branch or there was a similar density, the biggest river branch was followed. This ensured that the drawn river section represented the portion of the river that was influenced by beavers the strongest.

Non-beaver sections were also outlined as a control for comparison. These control sections consisted of one-kilometer segments located along the watercourses where no permanent beaver presence was observed. We assumed a section was unoccupied if it had no observable foraging signs or a maximum of one normal and one small foraging sign, assuming such infrequent foraging signs represented only occasional beaver presence. Control sections were spatially separated by at least 200m from occupied river sections and from each other, with a minimum gap of 100m between the last recorded foraging sign and the start of any control section to minimize the likelihood of beaver influence. All control sections were located along watercourses and streams accessible to beavers, ensuring that their absence reflected active non-use rather than physical inaccessibility.

All spatial analysis were conducted using QGIS version 3.40.15 (Bratislava) (QGIS Development Team, 2024). The coordinate reference system used throughout the analysis was Amersfoort / RD New (EPSG:28992) to ensure accurate distance measurements in meters.

## **Statistical analysis**

River section presence-absence was defined as a binary response variable, with sections classified as either occupied (1) or unoccupied (0). Of the 72 sections analyzed, 44 were occupied and 28 were not. The first of the two predictor variables included in this analysis was water depth category (categorical: deep  $\geq 50$ cm and shallow  $< 50$ cm). This was made into a categorical variable because the binary classification reduces the influence of the temporal variation. The second predictor was woody vegetation availability, which was continuous: the proportion of cover within 60 meters on

either bank of the river section. This buffer was used to capture the riparian zone most relevant for beaver foraging and habitat use. This choice is supported by studies showing that beaver activity decreases rapidly with distance from water, with the majority of habitat use occurring within the first tens of meters from the shoreline (Jenkins, 1980; Donkor & Fryxell, 1999; John & Kostkan, 2009; Zwolicki et al., 2019).

Before modelling, the correlation between water depth and woody vegetation availability was tested with a point biserial correlation test to assess multicollinearity. If the predictors showed a strong correlation, separate models would be constructed for each predictor. If the correlation was not strong, both predictors would be included in a single model.

To model the probability of river section presence-absence, a Generalized Linear Model (GLM) with a binomial error distribution and logit link function was used, as the response variable was binary. This makes logistic regression the most appropriate approach for modelling presence-absence probability. River section presence-absence was modelled as a function of woody vegetation availability and water depth category.

Model results are presented as regression coefficients ( $\beta$ ), standard errors (SE), z-values, and p-values. Statistical significance was assessed at  $\alpha = 0.05$ . To improve interpretation, coefficients were also converted to odds ratios with 95% confidence intervals.

Assumptions made in the model were checked with the DHARMA package (Hartig, 2025), which simulates residuals to evaluate model fit. A Kolmogorov-Smirnov test was conducted for the distribution of residuals, a dispersion test for overdispersion, and an outlier test.

For the statistical analysis R (version 4.5.2 2025-10-31 ucrt; R Core Team, 2025) was used with the package DHARMA for validating model assumptions (Hartig, 2025). Plots were made with ggplot2 (Wickham, 2016). The generalized linear model (GLMs) was fitted in R using the glm() function from the base stats package (R Core Team, 2025).

## Results

For this study, we analyzed 72, 1km long river sections with 44 being occupied by beavers and 28 unoccupied. We have measured two predictors across the sections: water depth and woody vegetation availability. Of the 72 sections, 52 are classified as “deep” ( $\geq 50\text{cm}$ ) and 20 as “shallow” ( $< 50\text{cm}$ ). The woody vegetation availability within 60 meters on either bank ranged between a cover of 0.06% to 41.30%, with a mean of 13.29% (SD = 10.45%). Occupied sections showed a higher mean woody vegetation availability (mean = 15.31%, SD = 10.56%) compared to unoccupied sections (mean = 10.11%, SD = 9.61%).

There was no significant correlation between woody vegetation availability and water depth ( $r = 0.08$ ,  $p = 0.50$ ). I modeled beaver presence-absence using a generalized linear model with a binomial error distribution and logit link function. Water depth was a significant predictor of beaver presence-absence (Fig. 2) in the river sections ( $\beta = -2.26$ ,  $SE = 0.64$ ,  $z = -3.52$ ,  $p < 0.001$ ). Beaver occurrence was significantly higher in river sections with water depth  $\geq 50\text{cm}$  than in shallower sections, with shallow areas showing about 90% lower odds of beaver presence (odds ratio = 0.10, 95% CI: 0.03–0.34). Predicted occurrence was considerably higher in deep-water sections (75.95%) than in shallow ones (24.78%), highlighting the strong influence of water depth on beaver river section presence-absence (Fig. 2).

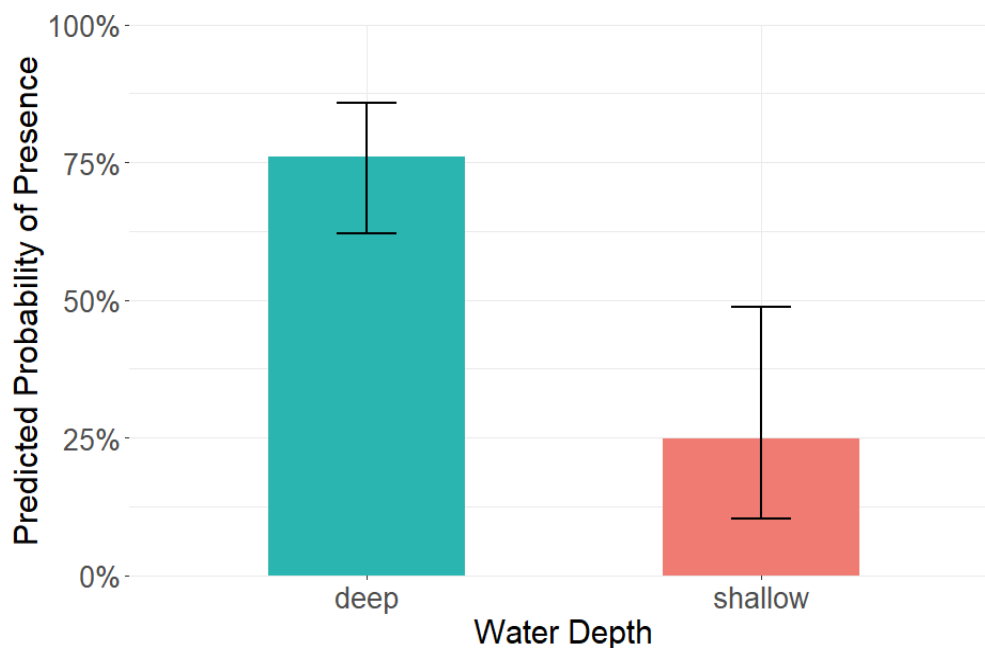


Fig. 2: The predicted probability of beaver river section occupancy for deep ( $\geq 50\text{ cm}$ ) and shallow ( $< 50\text{cm}$ ) water depth categories, based on a binomial GLM ( $n = 72$ ). Error bars represent the 95% confidence intervals.

Woody vegetation availability showed a positive association with beaver presence (Fig. 3) ( $\beta = 0.06$ ,  $SE = 0.03$ ,  $z = 1.93$ ,  $p = 0.054$ ) but did not reach statistical significance. The odds of river section

occupation increase by approximately 6% for each 1% increase in woody vegetation availability (odds ratio = 1.06, 95% CI: 1.00–1.13). Figure 3 shows that deep river sections consistently have a higher presence-absence probability across all vegetation levels.

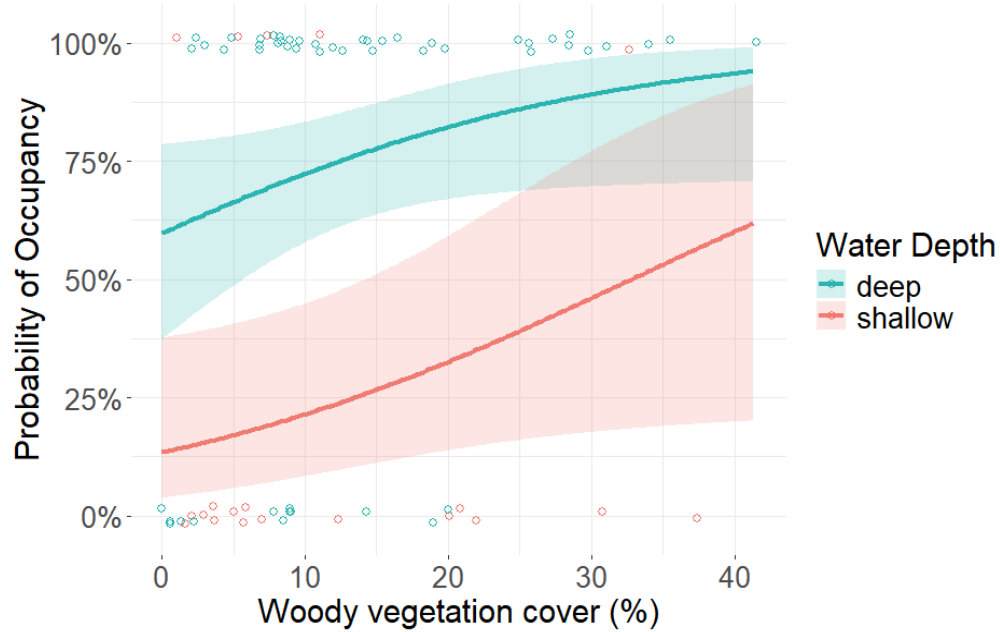


Fig. 3: The predicted probability of beaver river section occupancy in relation to woody vegetation availability (%), separated by water depth category (deep = blue, shallow = pink), based on a binomial GLM ( $n = 72$ ). The gray shaded areas indicate the 95% confidence intervals.

DHARMA residual diagnostics showed no significant deviation from expected distribution (KS test:  $p = 0.60$ ), no overdispersion ( $p = 0.874$ ), and no outliers ( $p = 1.0$ ). No significant problems were detected in the residuals vs. predicted plot.

## Discussion

This study gains insight into beaver occurrence in relation to water depth and woody vegetation availability. The findings are relevant as management practices may affect beaver recolonization, creating a conflict between conservation goals that requires a broader management perspective. This study shows that water depth is a significant factor determining beaver river section presence-absence in the Drentsche Aa, with deep water significantly increasing the likelihood of occupation. With large-scale mowing reducing woody vegetation along riverbanks, woody vegetation availability showed a positive relationship with beaver presence, although this effect was not significant. These results suggest that water depth plays the most dominant role in habitat selection at the territory level and hydrological management might be more consequential than mowing for beaver recolonization in this system.

### **Predictors associated with beaver occurrence across the landscape**

The strong dependence on deep water sections is consistent with the known ecological requirements for habitat in literature for European beavers. Deep water provides beavers with access to underwater lodge entrances, refuge from predators and it facilitates easy movement (Collen & Gibson, 2000; Hartman & Tornlov, 2006; Raffel et al., 2009; Swinnen et al., 2019). In the Drentsche Aa, water depth is not always a freely varying habitat characteristic but rather a direct outcome of water management policy by using weirs, drains and removing dams (Wanders et al., 2011). Active dam removal in ditches and river sections (Seljee et al., 2025) prevents beavers from raising local water levels, effectively eliminating one of their primary solutions for shallow water (Brazier et al., 2020; Larsen et al., 2021). Because of this active management in the Drentsche Aa, shallow ditch- and river sections may remain structurally unsuitable for beaver settlement regardless of food availability or mowing. This explains the strong presence-absence pattern we observed in the data and may reflect policy-driven hydrological conditions, making it impossible to create deeper water. However, with the population increasing in the Drentsche Aa, individuals may be forced to occupy suboptimal habitats and exploit available resources more flexibly in the future.

Beavers are still in an early colonization stage; this could be the reason they are yet to expand into shallower watercourses and ditches. Recolonizing beaver populations are known to settle in optimal habitats first, with suboptimal areas only occupied as density increases and prime territories become saturated (Pinto et al., 2009; John et al., 2010). The strong water-depth effect may therefore partly reflect the selectivity of a still expanding population (Bos et al., 2020; NDFF Verspreidingsatlas Zoogdieren, 2026). Whether beavers will eventually colonize shallower sections depends on their ability to build dams. The fact that beavers only started building dams recently, in 2018, supports this statement and maybe beavers will continue their dam building and recolonize shallower watercourses in the next couple of years. This might be difficult for them if dams keep getting removed, perhaps in these Dutch settings beavers can only colonize optimal habitats. If beavers cannot settle in smaller watercourses and ditches and build dams, they also have very limited ecological functionality. Under EU law (EU Habitats Directive, Art. 6) it is a legal obligation to establish conservation measures corresponding to the ecological requirements of protected

species within Natura2000 sites like the Drentsche Aa, and to avoid deterioration of the habitats upon which those species depend (Council of the European Communities, 1992).

The non-significance of woody vegetation availability is surprising, as many studies suggest it is important (Janiszewski et al., 2017; Wang et al., 2019; Juhász et al., 2023; Pejstrup et al., 2023), but can likely be explained through the fact that even in heavily mowed areas, there may be small patches of vegetation beavers can use like hedgerows, trees on riverbanks or patches of shrubs. Woody vegetation availability may not be a limiting factor for beaver presence-absence for choosing territories in the Drentsche Aa National Park. Even river sections with relatively low shares woody vegetation may provide sufficient food and building resources through small patches that were not fully captured in the habitat assessment. This is a methodological restraint because of the 5-meter error margin in the vegetation data (Hazeu et al., 2025), potentially overestimating the impact of mowing regimes for beaver families. It is possible however, because of large scale mowing, beavers use larger territories needing 2km of river to acquire sufficient food. This raises the question of how much woody vegetation is required for a beaver family to maintain a territory in a river section.

### **Methodological considerations**

Despite the strong and consistent effect of water depth, several methodological and ecological limitations should be acknowledged. River sections were treated as independent observations, although nearby sections share the same river system. As a result, they may have similar hydrological and vegetation conditions, introducing potential spatial autocorrelation that could not be fully accounted for in this study. Spatial autocorrelation was minimized by separating control sections  $\geq 200\text{m}$  from sections with beaver presence. Field surveys were conducted during winter (November 2025 – February 2026) to maximize the visibility of beaver activity signs such as tree cuttings, foraging trails and lodge structures. This substantially reduces the likelihood of false absences compared to summer studies. However, the possibility of false absences cannot be fully excluded, especially because the data comes from different sources (own field surveys and existing data from the provinces of Drenthe & Groningen). Additionally, the assumption that absence of field signs indicates true absence may introduce detection bias. Control sections (non-beaver sections) may still have been used by low-activity individuals, meaning that “absence” may in some cases reflect low-intensity use rather than true absence. This was allowed in the study to increase the sample size of sections and sampling area, which outweighed the low-activity individuals as their ecological impact would be minimal.

The dataset showed an imbalance between deep ( $n = 52$ ) and shallow ( $n = 20$ ) river sections and on a less significant scale with beaver presence ( $n = 44$ ) or absence ( $n = 28$ ) as well. This may have influenced model performance and reduced statistical power, though the strong effect of water depth ( $p < 0.001$ ) suggests this did not influence the primary finding. A related methodological consideration was how river sections were defined. Delineation was based on lodges, burrows and foraging signs, while scent marks were not included even though several studies suggest that this is a good representation of functional section boundaries (Müller-Schwarze & Heckman, 1980; Rosell & Nolet, 1997; Rosell et al., 1998). This hierarchical basis of using the lodge or burrow as a center point is an ecologically constructed assumption and the fixed 1 km section length assumes a

standardized core activity range based on central place foraging theory (Fryxell, 1992; Fustec et al., 2001; Raffel et al., 2009; Sidorovich, 2011; Šimůnková & Vorel, 2015), but in reality this may vary substantially depending on habitat quality and population density. This standardized section length does, however, allow for direct and fair comparison of habitat characteristics between sections.

Woody vegetation availability was derived from the LGN 2023 dataset (Hazeu et al., 2025) which may not fully reflect seasonal or recent changes in vegetation due to mowing or local management. By reclassifying this data into woody / non-woody variables it loses the ability to capture variation in food quality, species composition and accessibility anymore. Finally, habitat conditions in the Drentsche Aa are partially shaped by active management practices such as mowing, dam removal and water regulation, meaning that key habitat variables might not be fully independent natural drivers. While this management influence is a limitation for isolating purely ecological drivers, it is also a key strength of the study. It reflects real-world conditions in a highly managed lowland river system, which not many studies have focused on.

### **Further research and broader implications**

Several questions raised by this study ask for further investigation. The dominant role of water depth in beaver occurrence, especially over woody vegetation, should be confirmed in other managed lowland river systems in the Netherlands and northwestern Europe and we do not know the role of water in areas where beavers cannot build dams and how they cope with this. If water depth consistently emerges as the primary habitat driver, this would strengthen the case for using hydrological management like weirs, drains or dam removal as a conservation tool for expanding or shrinking beaver populations. The non-significant but positive trend of woody vegetation availability and thus, the influence of mowing suggests a potential relationship that the current study was unable to detect. With a larger and more balanced sample size, controlling for water depth, it could be clarified whether mowing plays a meaningful role in habitat selection. Sampling areas with deep waterways and no woody vegetation or areas with low water depth and complete mowed banks without woody patches or hedgerows, would be very valuable to add to the current data. Hedgerows and small woody patches may provide an important alternative woody resource for beavers in otherwise mowed landscapes. This is an interesting thought for management and landscape design whether you want beavers in a certain area. Answering these questions become increasingly urgent as the beaver population in the Drentsche Aa continues to grow (Bos et al., 2020; NDFV Verspreidingsatlas Zoogdieren, 2026). We expect beavers to gradually colonize suboptimal habitats, including agricultural ditches, as optimal deep-water habitats may reach the carrying capacity soon (Pinto et al., 2009; John et al., 2010). Long-term monitoring is needed to determine whether beavers can successfully adapt to lower water depth conditions or modify these environments within existing management practices. Possibly, in a further recolonization stage, beavers do not need deep water in areas without wolves. In predator-free environments the survival cost of settling in shallow water is reduced, so this shift may happen more readily and successfully than in populations with predators elsewhere (Ripple & Beschta, 2004; Gable et al., 2023). Future studies could investigate whether beavers show different foraging patterns, have lower reproductive success or show different territorial behavior compared to those in deep-water sections. Understanding which habitat factors drive river section presence-absence becomes

increasingly relevant for predicting population growth and spatial distribution for management (Rosell et al., 2005; Wang et al., 2019). This raises a broader issue of when population growth will begin to level off, and whether this transition can be predicted.

The findings of this study have broader implications for beaver conservation and riparian management in the Netherlands. Our results suggest that hydrological management like dam removal possibly plays a big role in habitat selection for beavers in managed lowland river systems. This has direct management implications: current water and vegetation management aimed at maintaining open habitats and specific target species may conflict with recolonization of beavers, with hydrological conditions largely determining where such conflicts are likely to occur. Ultimately, this study shows that in actively managed lowland river systems such as the Drentsche Aa, policy-driven hydrological conditions rather than vegetation structure may be the primary factor determining where beavers can successfully establish themselves.

## Management implications and recommendations

This study shows that water depth is the most important factor determining where beavers occur in the Drentsche Aa. Woody vegetation was positively associated with beaver presence, but this effect was small and non-significant. This means that current (water) management strongly influences where beavers can live.

### **Influence of mowing on beaver occurrence**

The results suggest that annual mowing does not strongly limit beaver presence at the scale of whole territories (1 km river sections). Although areas with more woody vegetation tended to have a higher probability of beaver presence, this effect was weak.

This likely means that beavers are still able to find enough food and building materials, even in mowed landscapes. Small patches of shrubs, trees or hedgerows may already be enough to still occupy an area. Although the current mowing regime does not exclude beavers from river sections with extensive mowing, the literature suggests mowing may still lower the densities of beavers, and if woody vegetation is completely absent that may completely exclude beavers from certain parts of the national park (Wang et al., 2019; Juhász et al., 2023; Pejstrup et al., 2023).

However, mowing probably still affects habitat quality. Especially in winter, by removing woody vegetation, it reduces food availability (Ritter et al., 2020). So, while mowing does not completely prevent beavers from settling, it may reduce habitat quality or even carrying capacity. Lower habitat quality may translate into smaller family groups, reduced reproductive success or increased energetic costs as beavers need to travel further to find sufficient food. If mowing reduces the carrying capacity of the landscape, fewer beaver families can establish and maintain territories, ultimately limiting population growth.

### **Importance of water management**

Water depth turned out to be a key factor in beaver occurrence. Beavers were much more likely to be present in deeper water ( $\geq 50$ cm). Shallower sections were often not used.

In the Drentsche Aa, water depth is largely controlled by management. The removal of beaver dams in combination with controlled water levels by weirs prevents beavers from increasing the water levels themselves. This makes many areas unsuitable, even if enough food would be available. This means that current water management largely determines where beavers can and cannot live.

### **Steering beaver presence in the landscape**

Based on these findings, managers can actively influence where beavers occur in the Drentsche Aa. Beavers may be unwanted as they can cause conflicts like flooding of agricultural areas, hinder

fish migration or damage roads and infrastructure. Their presence may be desirable where managers seek to enhance biodiversity, restore wetland habitats or fulfil legal obligations under the EU Habitats Directive (article 6), which is a law that states that protected species within Natura2000 meet their ecological requirements (Council of the European Communities, 1992).

- To encourage beavers, it is important to allow deeper water. This could be done by reducing dam removal where possible and maintaining water depths of at least 50 cm. Keeping some woody vegetation like shrubs, trees or hedgerows along riverbanks will further improve habitat quality.

To fully support beaver ecological functionality, managers should consider designating more specific zones within the Drentsche Aa where beavers are permitted to build and maintain dams without interference. Dams are central to beaver ecology, as they raise local water levels to facilitate movement, lodge access and access to a wider foraging area, ultimately enabling beavers to function as ecosystem engineers across a larger part of the landscape (Brazier et al., 2020; Larsen et al., 2021). Formalizing and expanding zones where this is allowed would see more beavers able to recolonize suboptimal habitat. This would bring management in line with the obligations under Article 6 of the EU Habitats Directive while mitigating conflicts.

- To limit beavers, maintaining shallow water is likely the most effective measure. Continued dam removal will prevent beavers from raising water levels themselves and prevent them from settling (Butler & Malanson, 2005). Mowing can support this by reducing woody vegetation, but on its own it is probably not enough. When mowing it is important to remove all small patches of shrubs and trees as well.

### **Combining nature goals**

There may be conflicts between different management goals. Mowing is used to maintain open landscapes with high plant diversity, while beavers create wetter areas.

However, beavers can also be used as a natural management tool instead of a species that needs to be controlled. Their ability to slow down water flow and raise water levels can help maintain wet conditions in the landscape, which is especially valuable for wet grasslands (BIJ12, n.d.). Instead of relying only on technical water management, beavers can contribute to water retention in a more natural way.

By flooding areas, beavers can be used to create open wetlands together with mowing or grazing. Beavers maintain the wet conditions, while mowing or grazing keeps the vegetation open. Such combination could also help maintain species-rich wet hay meadows while reducing the need for intensive water management. Wet hay meadows depend on high groundwater levels and base-rich conditions, with desiccation being one of the main management challenges. Beavers could help address this naturally by raising local water levels through dam building, while mowing continues to maintain open vegetation (BIJ12, n.d.).

## Limitations and considerations

Although water depth clearly plays a major role in beaver presence, the effect of woody vegetation is less certain. This may be due to limitations in data or sample size. Because of this, it is important to apply these recommendations carefully. Management should be adjusted after more monitoring results and trail runs. Future studies may wish to explore how mowing effects beaver densities instead of occurrence.

## Monitoring and future research

To improve management in the future, long-term monitoring is important.

- Monitor
  - Whether beavers start colonizing shallower watercourses as the population grows (by building dams). Monitoring this process helps managers anticipate where new conflicts, such as flooding of agricultural land, may arise, and where proactive measures are needed. It also informs whether current dam removal policies are preventing beavers from accessing otherwise suitable habitat, and whether adjusting these policies could expand the area available for beaver settlement and associated ecological benefits.
  - How mowing affects food availability over time. This would help managers determine whether current mowing regimes are compatible with long-term beaver presence. This is valuable both for meeting conservation obligations and for using vegetation management to steer where beavers settle.
  - Where beavers are able to be ecologically functional. Knowing which parts of the landscape allow for this ecological functionality helps managers direct beaver presence to areas where society benefits most from their ecosystem engineering, while managing or discouraging their presence in conflict-prone areas.
- Test
  - More research is needed in extreme conditions, such as deep water without woody vegetation or fully mowed riverbanks, would help clarify the limits of beaver habitat use and inform management strategies for areas where beaver exclusion is desired but reducing water levels is not feasible.
  - Using beavers in combination with mowing as a management tool should be tested for practical use.
- Track
  - Differences in behavior and success in deep, optimal habitat and in shallow sub-optimal areas (reproduction, survival, ecosystem impact). This would help managers assess the true conservation value of beaver presence across various parts of the landscape. If beavers in shallow sections contribute little ecologically, while generating conflicts such as dam building near infrastructure, this would support targeted management decisions about where to facilitate or discourage settlement. It would also help predict population dynamics as beavers expand into less ideal habitats.

## Conclusions

Water depth emerged as the primary factor determining beaver presence in the Drentsche Aa. Deep water ( $\geq 50\text{cm}$ ) strongly increased the likelihood of occupation, indicating that hydrological conditions are the main driver of habitat suitability at the landscape level.

In contrast, woody vegetation availability showed only a weak and non-significant relationship with beaver presence. Although the effect was small compared to water depth, occupied sections did tend to contain more woody vegetation on average, but it does not suggest there being a strong limitation at the territory scale for beavers. This may suggest that remaining small patches of shrubs and trees within mowed landscapes are sufficient to meet beaver resource requirements.

These results highlight that habitat suitability in the Drentsche Aa is largely shaped by hydrological conditions rather than vegetation structure. Importantly, these hydrological conditions are strongly influenced by management, including water level regulation by weirs and dam removal.

This has direct implications for management of beaver recolonization in the area. Maintaining sufficient water depth ( $\geq 50\text{cm}$ ) is essential for supporting beaver presence, whereas shallow, actively managed sections are far less likely to be colonized. As a result, water management acts as the primary factor influencing where beavers can establish territories and have an ecological impact.

Vegetation management through mowing appears to play a secondary role. While mowing may reduce habitat quality by limiting woody vegetation availability, it does not appear to be a decisive factor preventing settlement. Its influence is therefore likely indirect, affecting carrying capacity rather than presence-absence of river sections.

Overall, these findings indicate that in managed lowland river systems, hydrological conditions are the primary determinant of beaver distribution, outweighing the influence of riparian vegetation availability. This highlights that in such landscapes; habitat suitability is largely shaped by human-controlled water regimes.

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## Appendix I

This appendix shows the classes used for woody vegetation of LGN2023.

*Table 1: Woody vegetation class of LGN 2023, that represents foraging and construction materials needed by beavers (Hazeu et al., 2025).*

<b>Class number</b>	<b>Description</b>
9	Orchards
11	Deciduous forest
12	Coniferous forest
20	Forest in primary urban area
22	Forest in secondary urban area
40	Forest in raised bog
43	Forest in marsh area
61	Tree nurseries
62	Fruit nurseries
321	Low shrub vegetation raised bog
322	Low shrub vegetation marsh
323	Other low shrub vegetation
331	High shrub vegetation raised bog
332	High shrub vegetation marsh
333	Other high shrub vegetation

## Appendix II

This appendix shows the DHARMA residual plots.

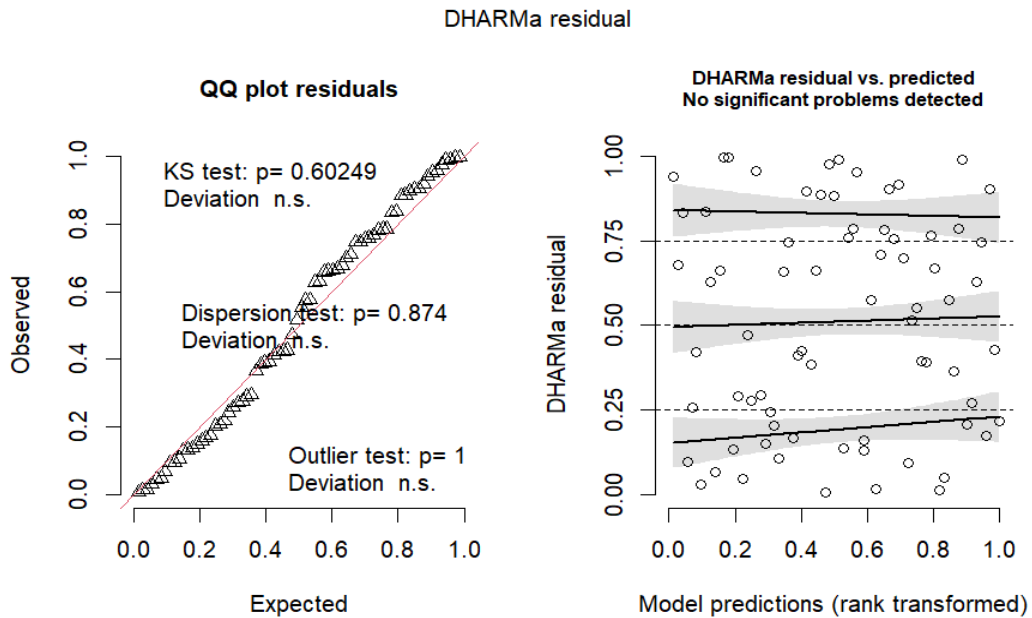


Fig 4: DHARMA residual test and residual vs. predicted test.

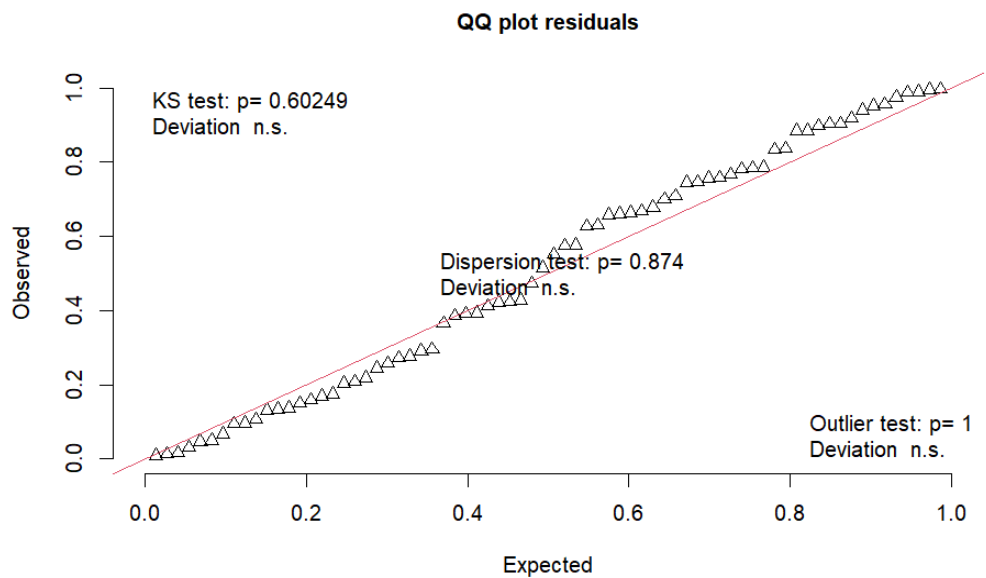


Fig 5: DHARMA plot residual test (bigger).

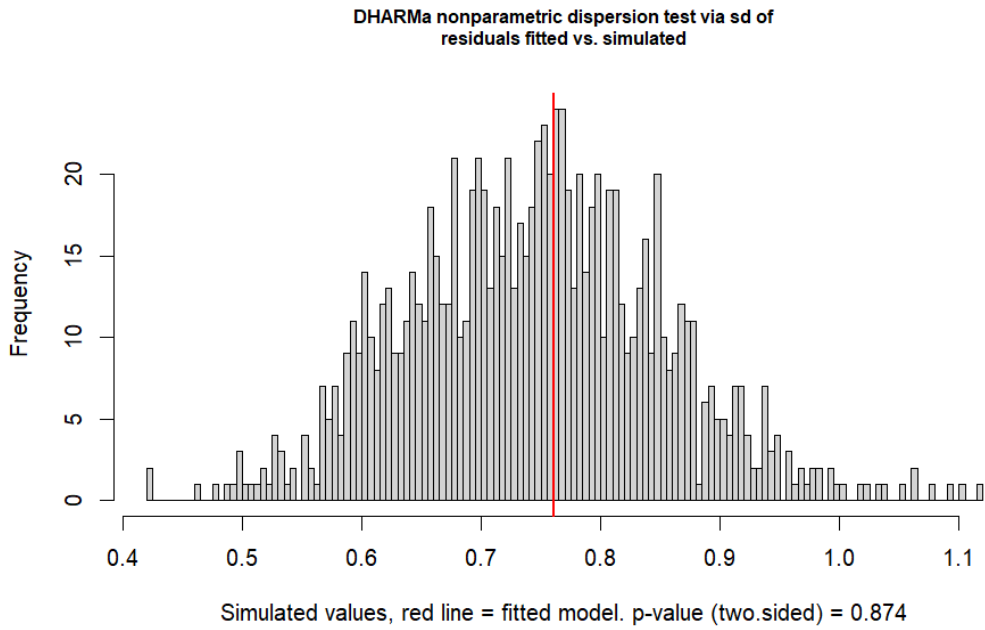


Fig 6: DHARMA nonparametric dispersion test.

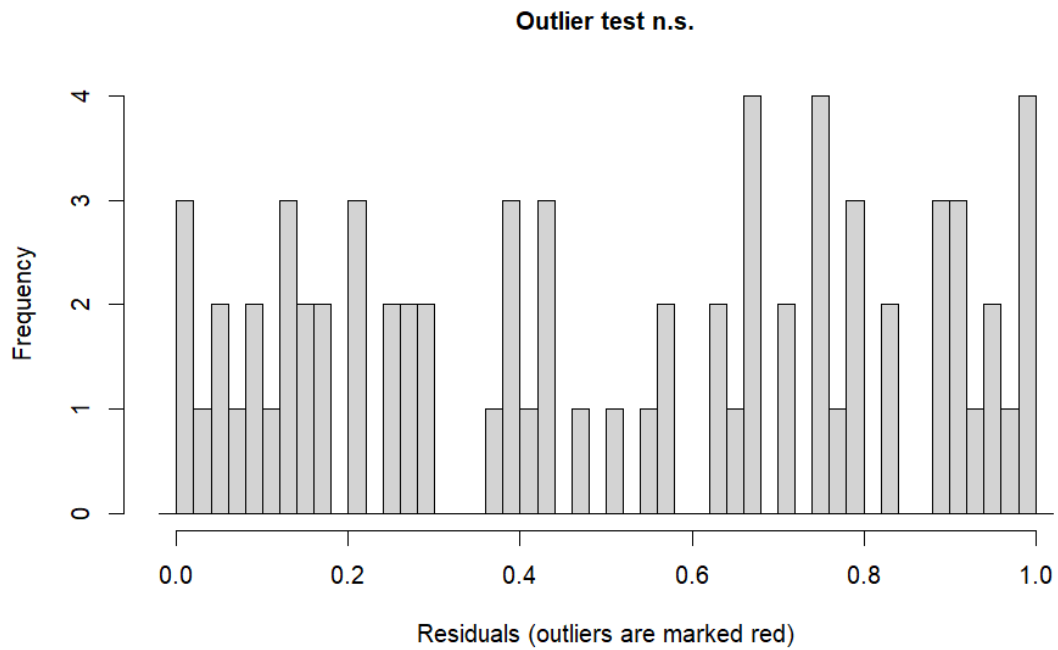


Fig 7: DHARMA outlier test.