

The potential impact of Beavers within the rare wetland habitats of the New Forest

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August 2025

A literature review identifies potential interactions between the colonisation of Southern England by Beavers *Castor fiber* and the internationally important wetlands for the New Forest National Park. The literature indicates potential risks and opportunities to habitats and species which will need to be addressed at a catchment level.

Wetlands are presented as some of the most valuable ecosystems and play a critical role in regulating the global climate (Dudgeon *et al.*, 2006). However, they are being lost at a rate that is three times faster than forests (UNFCCC, 2018). The United Nations Convention for Climate Change (2018) suggest that approximately a quarter of all plant and animal species that depend on wetlands are at risk of extinction, driven by pressures such as drainage for agriculture, invasive species, altered hydrology and increased sedimentation from soil erosion. Despite this, wetlands are often more resilient than commonly assumed.

A recent study by Jacob *et al.* (2025) demonstrated that much of the existing research focuses on the ability of wetlands to resist change and return to their original state and, emerging evidence shows that wetlands are capable of adaptive resilience by adjusting and transforming in response to change. This may involve shifts in dominant species or ecosystem structure, with the system retaining its essential functions and stabilising along a new trajectory or reaching an alternative stable state. From their research, they identify that wetland adaptive resilience only comprises about 9% of total studies on wetland resilience. This implies that change does not always negatively impact the functioning of wetlands. These adaptive qualities make many wetlands especially suitable for Beavers *Castor spp.*, which engineer such habitats to suit their requirements. However, research on some specific types of wetland systems, such as those found in the New Forest, remain relatively understudied in Beaver ecology.

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1. Importance of the New Forest's wetlands and trees

The New Forest is one of the most ecologically rich landscapes in Britain containing a rare mosaic of ancient woodlands, veteran trees, open pasture and wetland habitats including mires, peatlands, bogs, fens, ephemeral streams and ponds, spanning over 15,000 hectares (Tubbs, 1986., Chatters, 2024). These habitats are internationally significant for biodiversity and are protected under multiple conservation frameworks, including Sites of Special Scientific Interest, Special Areas of Conservation, a Special Protection Area, Wetlands of international importance under the Ramsar Convention along with both National and Local Nature Reserves (Forestry England, 2025; New Forest National Park Authority, 2007). Nowhere else in Europe do these habitats coexist across such a large and continuous area (Tubbs 1986., Chatters, 2024). A systematic account of the character and extent of Forest habitats forms part of the New Forest Special Area of Conservation Management Plan (Wright & Westerhoff 2001 & Weymouth & Wright 2024).

1.1 Mires and raised bogs

Mires are permanently wet habitats formed by the accumulation of organic matter, often dominated by *Sphagnum* moss (Wells, Hodgkinson & Huckerby, 2000). When soils become waterlogged, organic matter no longer breaks down but accumulates as peat. As the peat builds up, plants seen within bogs and mires begin to grow. Bogs are acidic, rain-fed peatlands with low nutrient availability (Karran, 2018). The term 'transition mire' relates to vegetation that in floristic composition and general ecological characteristics is transitional between acid bog and Alkaline fens, in which the surface conditions range from markedly acidic to slightly base-rich. The vegetation normally has intimate mixtures of species considered to be acidophile and others thought of as calciphile or basophile.

Peatlands are often described as self-regulating systems in terms of hydrology, with water tables maintained within narrow depth ranges (Karran, 2018). In contrast, fens receive water and nutrients from surrounding soils and groundwater, supporting a more diverse flora, but they are equally vulnerable to drainage and eutrophication (Mitchell & Niering, 1993).

According to Wells, Hodgkinson and Huckerby (2000), these wetland habitat types are sensitive to changes in hydrology and play a crucial role in carbon storage and water regulation.

The New Forest National Park has 75% of the valley mires in north-western Europe (90 out of 120). The permanently waterlogged soils along many of the valley sides and bottoms has led to the formation of the most important mire system in Western Europe supporting plants including mosses, Bog Asphodel *Narthecium ossifragum* and White Beaked-sedge *Rhynchospora alba*. In the New Forest most mires are found in valleys towards the south of the Park. A valley location means that water feeding the mire will have passed through the surrounding rocks and soils and be relatively rich in nutrients. The water movement through the mire creates complicated patterns of nutrients and vegetation.

At the outer edges of these mires, a plethora of species associated with nutrient poor soils are found including *Sphagnum* mosses alongside different orchid species, Cotton-grasses *Eriophorum* spp., Sundews *Drosera* spp. and Bladderworts *Utricularia* spp.. Plants such as Sundews and Bladderworts thrive here as both are adapted to low nutrients by being carnivorous on small insects. Purple Moor-grass *Molinia caerulea* and Bog Myrtle *Myrica gale* are found towards the middle of the mire along with areas colonised by Alder *Alnus glutinosa* and Birch trees *Betula* spp.. Mires are generally rich in plants with over 150 species being recorded on the better sites.

The New Forest is considered to hold the largest area in England of Depressions on peat substrates of the Rhynchosporion, in complex habitat mosaics associated primarily with extensive valley bogs. This habitat type is developed in three situations: in natural bog pools of patterned bog surfaces, in flushes on the margins of valley mires and in areas disturbed by peat-digging, footpaths, tracks, ditches etc. In places, this habitat is rich in brown mosses *Cratoneuron* spp. and *Scorpidium scorpioides*, suggesting flushing by mineral-rich waters. The mosaics in this habitat type occurs are important for Bog Orchid *Hammarbya paludosa*.

1.2 Ephemeral waterbodies and ponds

Ephemeral lakes are temporary water bodies that support highly specialised flora and fauna adapted to fluctuating conditions which often cannot persist in more stable aquatic systems (Bashinskiy, 2020). Temporary ponds occur throughout the Forest in depressions capable of holding water for part of the year. Most ponds are small (between 5-10m across) and, although great in number, amount to less than 10ha in total area. Rare vegetation of the *Littorelletea uniflorae* and/or of the *Isoëto-Nanojuncetea* occurs on the edge of large temporary ponds, shallow ephemeral pools and poached damp hollows in grassland, which support a number of specialist species in a zone with Toad Rush *Juncus bufonius*. These include the two nationally scarce species Coral-necklace *Illecebrum verticillatum* and Yellow Centaury *Cicendia filiformis*, often in association with Allseed *Radiola linoides* and Chaffweed *Anagallis minima*. Heavy grazing pressure is of prime importance in the maintenance of the outstanding flora of these temporary pond communities. Livestock maintain an open habitat, controlling scrub ingress, and trampling the surface. Commoners'

animals also transport seed in their hooves widely from pond to pond where suitable habitat exists.

Hatchet Pond in the New Forest is an example of an oligotrophic waterbody amidst wet and dry lowland heath developed over fluvial deposits. This type of waterbody is restricted to sandy plains that are acidic and low in nutrients and are therefore very scarce. The only known high-quality examples of this habitat type occur on fluvio-glacial deposits in the New Forest and on the Cheshire Plain, and on more recent sand deposits of marine origin in the Outer Hebrides. The water is typically very clear and moderately acid. It contains Shoreweed *Littorella uniflora* and isolated populations of northern species such as Bog Orchid and floating burreed *Sparganium angustifolium*, alongside rare southern species such as Hampshire purslane *Ludwigia palustris*.

1.3 Bog and floodplain woodlands

Within the New Forest, birch – willow (*Betula* – *Salix*) stands occur over valley bog vegetation, with fringing Alder (*Alnus*)– *Sphagnum* stands where there is some water movement. These stands appear to have persisted for long periods in stable association with the underlying *Sphagnum* bog-moss communities. The rich epiphytic lichen communities and pollen record provide evidence for the persistence of this association. The Bog Woodland occurs in association with a range of other wetland habitats.

Alluvial forests with Alder (*Alnus glutinosa*) and Ash (*Fraxinus excelsior*)

Many such woods are found on floodplains and are dynamic, being part of a successional series of habitats. Their structure and function are best maintained within a larger unit that includes the open communities, mainly fen and swamp, of earlier successional stages. The New Forest contains many streams and some small rivers that are less affected by drainage and canalisation than those in any other comparable area in the lowlands of England. Associated with many of the streams, particularly those with alkaline and neutral groundwater, are strips of Alder woodland which, collectively, form an extensive resource with a rich flora. In places there are examples of transitions from open water through reedswamp and fen to Alder woodland. The small rivers show natural meanders and debris dams, features that are otherwise rare in the lowlands, with fragmentary Ash *Fraxinus excelsior* stands as well as the Alder strips.

1.4 Southern Oceanic Woodland types

Atlantic acidophilous beech forests with *Ilex* and sometimes also *Taxus* in the shrublayer (*Quercion roburi-petraeae* or *Ilici-Fagenion*).

Found in the New Forest this woodland type comprises Beech *Fagus sylvatica* forests with Holly *Ilex*, growing on acid soils, in a humid Atlantic climate. Sites of this habitat type often are, or were, managed as wood-pasture systems, in which pollarding of Beech and Oak *Quercus* spp. was common. This is known to prolong the life of these trees.

Asperulo-Fagetum beech forests

The New Forest is the largest area of mature, semi-natural Beech woodland in Britain; The mosaic with other types of woodland and heath has allowed unique and varied assemblages of epiphytic lichens and saproxylic invertebrates to be sustained, particularly in situations where the woodlands are open and the tree trunks receive plenty of light. The traditional common grazing in the Forest by cattle and ponies provides opportunities to explore the impact of large herbivores on the woodland system.

Old acidophilous oak woods

The New Forest is the most extensive area of active wood-pasture with old Oak and Beech in north-west Europe and has outstanding invertebrate and lichen populations. The New Forest has been recognised as of international importance for its saproxylic invertebrate fauna by the Council of Europe (Nieto & Alexander 2010).

2. Beavers

Beavers are large semi-aquatic rodents recognized as herbivores, disturbance agents, ecosystem engineers, keystone species and facilitators. As herbivores, Nummi and Kuuluvainen (2013) note that they typically harvest herbaceous vegetation during the vegetative months and tree bark and cambium supplemented with aquatic vegetation in the winter months. This shapes riparian forest overstory structure and composition. Through felling trees, digging canals and constructing dams, Beavers are ecosystem engineers, altering water depth, sediment and the floodplain structure of their surrounding landscapes (Parker, Caudill & Hay, 2007). This constant disturbance can transform otherwise static terrestrial ecosystems into dynamic aquatic habitats (Nummi & Kuuluvainen, 2013). Their disproportionate effect on the environment drives landscape-scale changes and creates conditions that support a wide range of other species. They are both keystone species and facilitators that increase habitat heterogeneity (Parker, Caudill & Hay, 2007). Landscape-scale heterogeneity is typically enhanced by the dynamic mosaic of Beaver-engineered and

non-engineered habitats, along with the coexistence of sites at varying stages of succession (Law *et al.*, 2019).

The potential changes that Beavers may bring to the rare wetland habitats in the New Forest is largely unknown. The purpose of this literature review is to help inform discussions around how Eurasian Beavers (*Castor fiber*) may change these specialist freshwater habitats as they disperse into the catchment from where there are known wild living populations on the Hampshire Avon (see Figure 1 and 2).

Multiple systematic literature searches were conducted on Web of Science using ten key terms on mire, fen, peat, bog, wetland, woodland and forest as well as on grazing, herbivory and biodiversity. Initial searches returned 83 studies, which were then screened down to 45 papers as most existing research surrounding Beavers focuses on riverine or to a lesser extent, lake environments resulting in a limited number of relevant studies in these specific habitats (Karran, 2018). Furthermore, many papers that do examine temperate wetlands use the broad term “wetland” without specifying their particular type. Consequently, literature on the American Beaver (*Castor canadensis*) was included, as studies have emerged showing there is no difference in their dam-building behaviours compared to the Eurasian Beaver (Brazier *et al.*, 2020). Additionally, both Beavers have been observed to display, similar successional patterns caused by Beaver flooding (Zavyalov, Zueva & Petrosyan, 2024).

The term "ephemeral" and “woodland” yielded only one relevant paper, which addressed ephemeral ponds and ancient woodland in relation to Beavers. A total of 10 papers focused on fens, 3 on mires and 7 on bogs; these primarily examined herbivory with some attention to wetland habitats and to a lesser extent invertebrates. Studies predominantly originated from the United Kingdom, Poland, the United States, Germany, Sweden and Russia, with the majority published within the last 10 years. Overall, more research is needed to understand Beaver impacts within these specialist wetland systems.

2.1 The New Forest’s suitability for Beaver habitat

Beaver Habitat Suitability Modelling (BHS) is used to produce a continuous description of habitat suitability for Beaver over the landscape. First a vegetation suitability index is created using multiple high-resolution spatial datasets from Ordnance Survey, the UK Centre for Ecology and Hydrology, and Copernicus. These datasets are combined to provide detailed land cover and vegetation information which is classified based on empirical field observation of Beaver habitat and preference. Vegetation suitability is combined with additional parameters describing stream networks and water bodies. Whilst Beaver habitat suitability is primarily defined by vegetation suitability, Beavers also require water for security and movement. Therefore, accessibility to waterbodies (i.e. channels, ponds, and

lakes) will also determine the viability of Beaver occupancy and therefore are required to classify habitat accurately.

Examples of highly suitable land (graded 5) include broad-leaf woodland, mixed woodland and shrub; examples of suitable vegetation (graded 4) include shrub and marsh; examples of moderately suitable vegetation (graded 3) include coniferous woodland, marsh, shrub and unimproved grassland; examples of barely suitable vegetation (graded 2) include reeds, shrub and heathland and boulders, neutral grassland; examples of unsuitable vegetation (graded 1) include heather, acid grassland, unimproved grass and boulders, bog; examples of no accessible vegetation (graded 0) include shingle and sand, buildings, rock, urban, freshwater and saltwater habitats.

The New Forest has abundant broad-leaf woodland within the modelled 100m distance of the area's small watercourses and therefore out of 387.87km of river assessed for Beaver habitat suitability, 263.79km was classified as preferred habitat with only 35.71km being marked as low or unsuitable.

New Forest		
Category	Length (m)	Length (km)
Preferred	263793.07	263.79
High	61210.20	61.21
Moderate	27146.76	27.15
Low	26251.50	26.25
Unsuitable	9463.91	9.46
Total	387865.44	387.87

Figure 1: Table of Values for Beaver Habitat Suitability in the New Forest

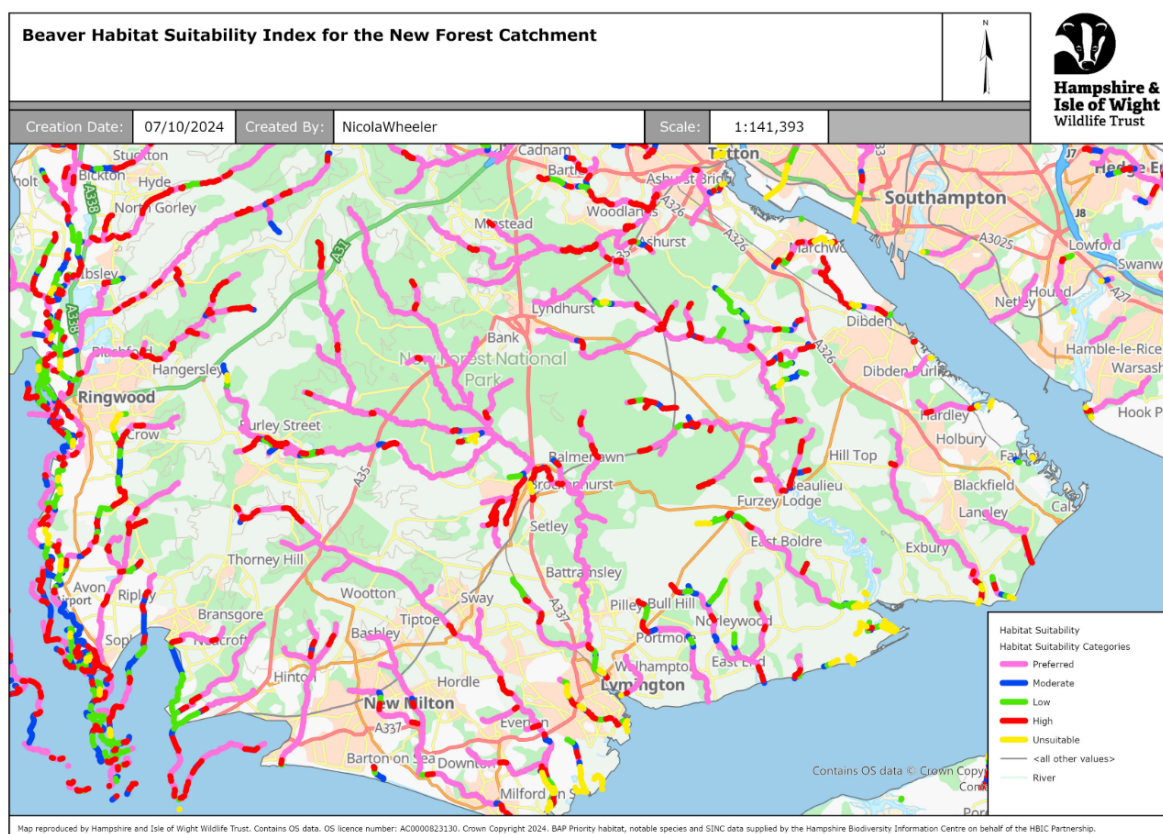


Figure 2: Habitat Suitability for Beavers (BHS) in the New Forest (Wheeler, 2025a)

BVI and BHI Values	Definition
0	Not suitable (no accessible vegetation)
1	Not suitable (unsuitable vegetation)
2	Barely Suitable
3	Moderately Suitable
4	Suitable
5	Highly Suitable

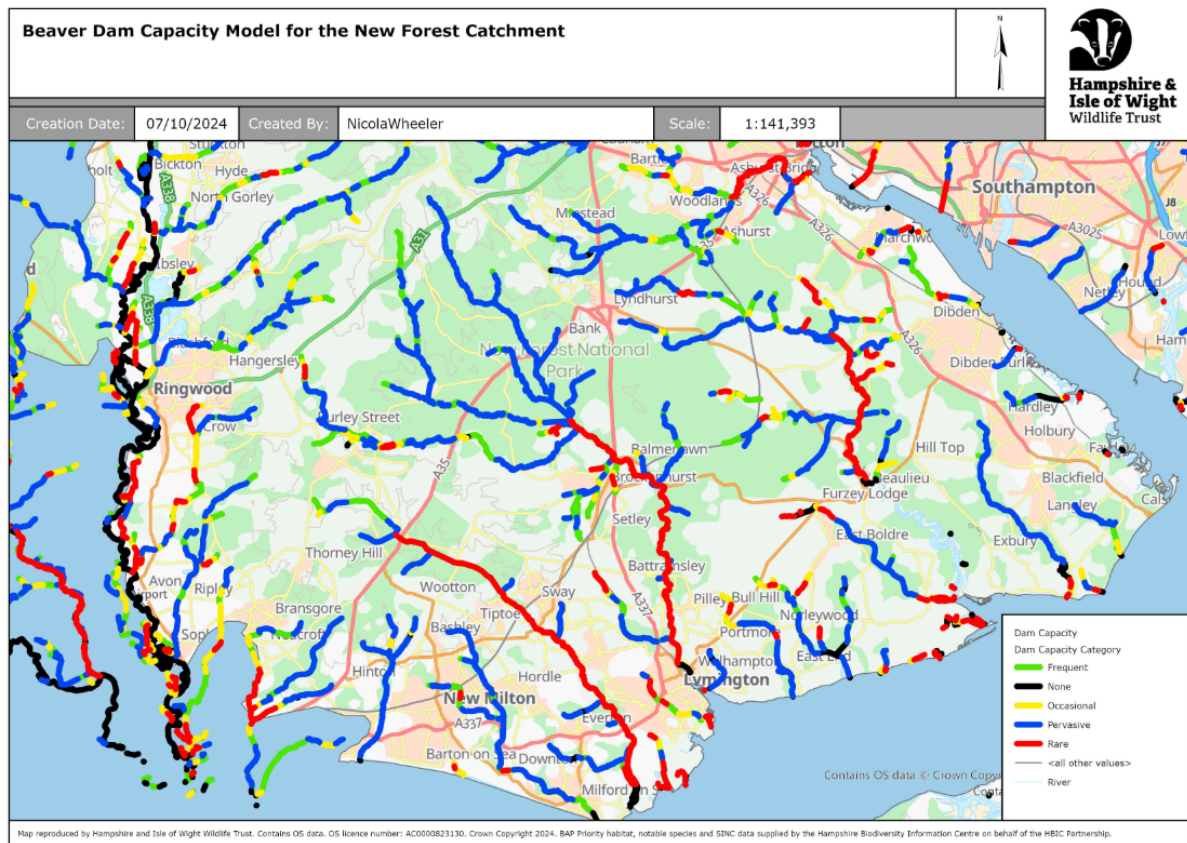


Figure 3: Dam Capacity for Beavers in the New Forest (Wheeler, 2025b)

Researchers at the University of Exeter tailored a Beaver Dam Capacity (BDC) model based on the Beaver Restoration Assessment Tool (BRAT), which was originally developed in North America (Gow *et al.*, 2020; Graham *et al.*, 2020). This map is designed to assess the potential of river systems to support Beaver dam construction by assessing the suitability of river reaches around 150m for dam building. It also identifies areas with a higher likelihood of dam construction and provides estimates of the number of dams that could be supported within a catchment if the Beaver population reached its ecological carrying capacity (Gow *et al.*, 2020).

BDC Classification	Definition
None	No capacity for damming
Rare	Max capacity for 0-1 dams/km
Occasional	Max capacity for 1-4 dams/km
Frequent	Max capacity for 5-15 dams/km
Pervasive	Max capacity for 16-40 dams/km

3. Beaver habitat interactions

3.1 Beavers as drivers of mire development

Beavers have been associated with wetland ecosystems across the northern hemisphere for thousands of years and their influence on wetland formation is being increasingly recognised (Karran, 2018). Nummi and Kuuluvainen (2013) suggest that the absence of Beavers, a key natural disturbance agent, has left many riparian landscapes in an unnatural state. Natural disturbances are essential for maintaining biodiversity and healthy ecosystem dynamics. Law *et al.* (2019) support this view, suggesting that the loss of Beavers may have contributed to current species extinctions, as these animals once played vital roles in spreading nutrients, shaping habitats, and regulating natural processes.

In Britain, Beavers have played a historical role in the development of mire habitats, with one of the earliest known examples identified at Briarfield's in Lancashire in a study by Wells, Hodgkinson and Huckerby (2000). Pollen analysis from boreholes indicated the formation of alder-sedge community and a decline in Birch which revealed that mire formation at this site was triggered by a sudden rise in the water table and the blockage of a slow-moving watercourse - likely caused by Beaver activity. At this site, during the Late Bronze Age (c. 1400–1000 BC), Beavers contributed to a shift in succession from a previously dry, Hazel-dominated landscape to a wetter environment with silty peat accumulation by the Early Iron Age (c. 800–500 BC). According to their study, Beavers likely played a crucial role in both creating and maintaining these landscapes by promoting ecological succession and facilitating the spread of wetland plant species through dam building and gnawing. However, the environment forming activities of Beavers is often density context and scale dependent (Zavyalov, Zueva & Petrosyan, 2024).

3.2 Suitability of rare wetland habitats for Beavers

The impact of Beavers on the habitat of bogs differs from their habitat-forming activities on small rivers (Zavyalov, Zueva & Petrosyan, 2024). Rebertus (1986) identified that Beavers displayed strong habitat selection in bogs, rather than utilising all available wetland areas within north-central Minnesota. In his study, Beavers showed a preference for areas with access to open water and a reliable supply of deciduous tree and shrub vegetation to support their construction and foraging needs. Furthermore, Zavyalov, Zueva & Petrosyan (2024) suggested that in Russia, Beavers constructed more dams in bogs compared to riverine habitats in Russia and they established a network of short channels that alternate with the beds of watercourses.

In a study on a fen habitat in Scotland, Law *et al.* (2017) noted that Beavers promote plant species associated with high moisture and light conditions through pond creation, lodge building and damming. However, their research highlighted that the impact of Beavers on bog vegetation depended largely on the dynamics of mineral and organic sediments. In mineral-rich bog environments, Beaver activity reduced the abundance of plants suited to nitrogen-rich conditions, due to nutrient leaching, uptake by aquatic vegetation, nutrient storage in sediments and reduced decomposition. Similarly, research on bog habitats in Connecticut by Mitchell and Niering (1993) found that Beaver flooding created a mineral gradient within these landscapes. Inundated areas developed into nutrient-rich zones and support minerotrophic fen vegetation, while the surrounding oligotrophic bog grew increasingly nutrient-poor. This gradient maintained a diverse range of bog-specific flora.

Perhaps the only long-term study on Beavers in large bogs is a 20-year research project within the Polistovo-Lovatskaya bog system, in the Rdeysky Nature Reserve, Northwest Russia. This study was conducted by Zavyalov, Zueva and Petrosyan (2024) in an area characterised by 100,000ha of relatively little disturbed raised bogs with wetland forests and agricultural lands. The bogginess of the area is more than 50% and large areas of secondary woodland comprising young Birch trees and Aspen are present. The Beavers located in this study were established 20 years prior to the investigation, and throughout that time period most of the Beavers resided on the edge of the bog system due to the dryer conditions.

Karran (2018) along with Zavyalov, Zueva and Petrosyan (2024) found that unlike fens, in peatland environments and bogs, Beaver ponds were not associated with a build-up of organic sediments – possibly due to the characteristics of the existing peat substrate and altered decomposition dynamics. They found that Beavers tended to create a series of 15-20 active dams where they primarily focused on excavating the peatland, changing its physical structure to increase habitat suitability. Longer periods of Beaver occupancy are associated with an increase in both the number and size of water bodies which was the most noticeable impact of Beaver colonisation (Zavyalov, Zueva & Petrosyan, 2024).

Zavyalov, Zueva and Petrosyan (2024) noted that Beavers can create channels formed under the peat termed “peat-pipes” which are covered by a layer of moss for them to move around short uninterrupted distances of 10-50m. For longer distances Beavers prefer trampling over sections of moss. The larger Beaver ponds and Beaver patches were located on the border of the bog system where there was an abundance of trees and shrubs and dead tree stands from flooding and inundation. Drained forest types such as Birch and Aspen forests, were especially affected. Their observations of the dynamics of vegetation in

“Beaver patches” and analysis of the structure of vegetation in them, made it possible to formulate general patterns of changes in vegetation under the influence of Beaver activity.

Dams on intra bog watercourses in the Polistovo-Lovatskaya bog system were shorter than dams along the edges. These were built from lumps of peat and woody debris no more than 30-40cm and were quickly destroyed on the river during floods. Extensive ponds were rarely formed, they did not last long. Often the Beavers built dams to store water in canals and the dam itself formed one of the banks of the canal. If the banks of these bog systems were relatively dry and dense this supported the construction of burrows.

In place of the dead tree stands, Zavyalov, Zueva and Petrosyan (2024) identified that both afforested and unforested lowland bogs had formed. Moreover, even in unforested lowland bogs, Beavers could find their required amount of food. On intra-bog watercourses or in poorer bog conditions within this study, Beavers were found to inhabit transitional bogs with Birch forests and a few Willow *Salix spp.* trees. Following the removal of these forests, and the partial destruction of Beaver dams made of peat, a rather long period began when these territories became unsuitable for Beaver habitat, and their reintroduction was only possible 10–20 years after the restoration of birch forests. They also found that where Beavers had extensively foraged along the banks of bog river, they extirpated the Birch and Willow completely and favoured thickets of Alder Buckthorn (*Frangula alnus*), which Beavers do not eat.

Instead of residing permanently in river or lake environments, Rebertus (1986) showed that Beavers could relocate to wetlands when these key resources become limited due to factors such as drought or over browsing and sometimes beavers were observed to remain in these wetlands preferentially over the long term. Notably, his work demonstrated that fens provided ideal conditions due to their high vegetation productivity and sustained input of groundwater in Minnesota. However, his work showed that Beavers were more likely to construct dams along existing watercourses where they widened, deepened and excavated canals rather than creating entirely new systems which may require more specialised behaviours.

Rebertus (1986) highlighted Beaver preferences varied within different wetland types, depending on water depth and substrate conditions. In areas where dam construction led to deep flooded areas due to high levels of groundwater seepage, Beavers tended to establish colonies in zones dominated by woody vegetation, which likely contributed to greater stability and offered a dependable food source. His work suggests that in naturally occurring shallow wetland margins, Beavers favoured sedge-moss habitats. This preference was likely due to the ease of excavation in these areas, as the absence of deep-rooted vegetation reduced obstruction to movement and simplified the transport of woody materials. Additionally, he discovered that dispersing juvenile Beavers often constructed dams in

habitats in which they were raised. In woodland habitats within Scotland containing stores of ancient and veteran trees, Jones *et al.*, (2009) further recorded that Beaver dams served a purpose of allowing Beavers to forage whilst minimising the time spent out of water at risk of predation.

3.3 Alterations to wetland hydrology

At the watershed level, Beavers can also have a pronounced effect on hydrology. In Finnish forest environments, research by Nummi and Kuuluvainen (2013) found that Beaver dams are capable of storing between 30% and 60% of the total water during periods of low base flow. In regions that experience seasonal water scarcity, this retained water, which is released gradually over time, plays a vital role in sustaining groundwater levels, supporting minimum downstream flows and boosting late-season water availability.

Beaver activity helps to restore dynamic fluvial processes where they have been largely absent. In England, the University of Exeter (2020) studied the River Otter Beaver Trial (2015–2020) within a forested landscape where the river channel had previously been artificially deepened and straightened. Within this landscape, Beavers encouraged natural re-meandering and raised the bed through gravel and sediment buildup. These materials settle behind the dams and are redistributed as these structures gradually erode, contributing to the development of features like sediment bars and riffles, while also creating pockets of erosion and scour.

Karran (2018), along with Zavyalov, Zueva and Petrosyan (2024) found that Beaver dams in peatlands and bogs can raise and stabilize shallow groundwater tables by connecting streams to surrounding wetlands, a process vital to peat formation through its support of vegetation succession and carbon sequestration. Karran's (2018) study in Alberta, Canada demonstrated that these dams formed connections between the stream and the peat aquifer through "large berm-like structures" extending up to 150 m, a feature unique to peatland and bog environments. Due to the flat terrain, he noted that these structures flooded much larger areas than is typically observed in mineral soil settings.

Karran (2018) reported that dams present in peatlands can lower the upstream hydraulic gradient while increasing it downstream, altering flow paths without changing the overall direction of groundwater movement - a pattern also reported in bogs and mineral soil environments. By increasing hydraulic head and connectivity, Beavers within his study acted as focal points for groundwater recharge, enhancing peatland resilience to hydrological fluctuations. This is especially important in limiting vegetation shifts under external pressures such as climate change, which typically drives warmer and drier conditions that favour increased shrub cover over moss, as well as during storm flow events that affect plant species sensitive to changes in water depth (Goud, Watt & Moore, 2018; Karran,

2018). Karran (2018) and Zavyalov, Zueva and Petrosyan (2024) highlight that Beavers increase both surface and groundwater storage in peatlands and bogs, with important implications for regional water balance. By raising the water table and thereby reducing grazing pressure, they help mitigate vegetation shifts and carbon loss during wildfires. Although Beaver ponds may release some methane, his paper emphasises that the net impact on carbon storage remained positive, as these emissions are minimal compared to the substantial carbon losses that can occur when peat is oxidised under lowered water tables.

The hydrological impacts of Beavers in these peatlands can be divided between the inundated zone and the surrounding area, with more pronounced changes occurring within the flooded zone (Zavyalov, Zueva & Petrosyan, 2024). Zavyalov, Zueva and Petrosyan (2024) highlight that the flooded zones within their study often expanded outward, affecting parts of the surrounding landscape. Similar studies conducted by Juhász et al. (2023) in Hungary and Nummi and Kuuluvainen (2013) in boreal forest landscapes identified that raising the water table through flooding often did not kill existing trees, instead it created new establishment sites for Willow shrubs and young Willow and *Populus* spp. trees. Furthermore, Karran (2018) together with Zavyalov, Zueva and Petrosyan (2024) note that the stability and low stream energy of Beaver dams allow them to persist for 40-70 years, maintaining function after abandonment and leaving a lasting hydrological legacy that enhances spatial and ecological complexity across the landscape.

In Canada, Karran (2018) found that peatlands did not trap sediment or organic material which means that the influence of Beaver dams on nutrient cycles and decomposition processes, water chemistry, and the transfer of energy and matter differs compared to other wetland systems. In addition, conditions between wetlands are influenced by small scale, local disturbances which are difficult to quantify including fluctuations in water levels, exposure of marginal habitat, selective herbivory, tree felling and lodge building or caching of woody material (Law *et al.*, 2019). Although such disturbances often contribute to the flooding of habitats through pond creation, in the long term Zavyalov, Zueva and Petrosyan (2024) suggest that Beaver abandonment can have a drying effect on bogs through channel formation and dam failure which may trigger erosion events.

Beaver territory occupancy typically lasts around 4.8 years and, during this time, their foraging activity can periodically extirpate certain species (McMaster & McMaster, 2001; Parker, Caudill & Hay, 2007). Following abandonment, Beavers may return and reflood the area by repairing old dams or building new ones once vegetation stocks have regenerated (Parker, Caudill & Hay, 2007). Short lived Beaver dams, termed ephemeral dams can reconnect the river with the floodplain, creating new flow pathways in times of flood which deposits nutrient-rich silts onto the floodplain and improves downstream water quality (University of Exeter, 2020).

Through their research, Parker, Caudill and Hay, (2007) identified that the likelihood of reflooding appears to depend on the topographic gradient, the size of the upstream watershed and the structural condition of the abandoned dam. In low gradient wetlands with intact Beaver dams, heavy rainfall events can trigger reflooding. Due to the consistent environmental conditions in low gradient wetlands, they suggest that distinct habitat zonation is often minimal or absent. This lack of spatial variation helps explain why, across various wetland types, hydrological factors such as the frequency, duration, and extent of flooding as well as nutrient availability, seed dispersal, and colonization potential, can play a more significant role in wetland vegetation succession than water table levels alone (Goud, Watt & Moore, 2018; McMaster & McMaster, 2001).

While general wetland studies often group habitats together, peatlands represent a distinct case due to their unique hydrological characteristics (Karran, 2018). Unlike other wetland types, peatlands have shallow water tables that are more spatiotemporally variable in response to climatic changes. This influences peat chemistry and in turn variations in pH which are responsible for differences in plant community composition between ombrotrophic (rain fed) and minerotrophic (groundwater fed) peatlands (McMaster & McMaster, 2001).

In central and southern Europe, Juhász *et al.* (2023) suggests that small streams and their surrounding areas are increasingly at risk from reduced flows and hydrological drought, driven by climate change, water extraction and land drainage. Rapid drops in the water table and altered soil moisture conditions can threaten the survival of Salicaceae species, particularly Willows, potentially shifting the composition of woody vegetation toward species better suited to drier environments. According to Goud, Watt and Moore (2018), if water levels remain consistently low, fen communities risk being replaced by either expanding bog vegetation or encroaching meadow and mudflat communities. Within these wetland systems, Sphagnum mosses contribute alongside Beaver-induced flooding to stabilise water levels. Their ability to retain moisture through capillary action helps maintain the saturated, low-oxygen conditions required for resilience and long-term stability.

3.4 Biodiversity

Most studies examining Beaver activity in wetlands report an increase in plant species richness associated with their presence (Misiukiewicz, Piętka & Olszewski, 2023). Beaver created wetlands can enhance plant species richness by generating unique habitat structures that go beyond the effects of natural succession producing novel habitat patch combinations that would otherwise not be found in the landscape (Willby *et al.*, 2018). Rather than being a subset of an existing landscape, these wetlands can create distinct environments that can be especially valuable for supporting endangered species (Nummi & Kuuluvainen, 2013).

A study by Wilby *et al.* (2018) describes Beavers as agents of 'within-habitat heterogeneity,' promoting high species turnover and increasing vegetation diversity in ponds over five years old in Sweden. Diversity gains were observed across multiple spatial scales, including a 15% increase at the plot (α) level, 17% between plots (β) and 33% at the landscape (γ) level, indicating a larger and more distinct species pool compared to other wetlands (Wilby *et al.*, 2018). A supporting study cited in this paper by Law *et al.* (2014) highlights that over a nine-year period in Perth in east Scotland, plant diversity increased more substantially in bogs than in swamps at both α and β scales. Specifically, β -diversity in bogs increased fivefold, while swamps saw a threefold increase, even in the absence of hydrological changes. Law *et al.* (2017) reported that fen habitats in east Scotland experienced the greatest increase in diversity at the landscape (γ) scale, with a 148% gain, compared to a 46% increase at the β scale. This deviates from the succession seen in other wetlands (Wilby *et al.*, 2018). Wilby *et al.* (2018) suggests that Beavers do more than alter existing conditions. Their presence creates a unique type of habitat, a "Beaver wetland", that has distinct effects on plant diversity, independent of just soil or water chemistry.

A 23-year study in Evo, Southern Finland, found that while Beavers had little impact on alpha and beta diversity at individual sites, their influence on community composition was the most significant, leading to a 1.3-fold increase in landscape-level species richness (Nummi & Kuuluvainen, 2013). In a separate study referenced by Zavyalov, Zueva and Petrosyan (2024), Ray *et al.* (2001) found that in peatland bogs in Minnesota, plant species richness increases with the age of Beaver created water bodies but tended to stabilize after 40 years as larger ponds allowed Beavers to "cultivate" their food. Goud, Watt and Moore (2018) found that flooding from Beaver ponds enriched the Mer Bleue peatlands in Canada with nutrients and major ions by prolonging the retention of soil and moisture runoff. This enrichment was identified as a key driver of increased plant richness at the plot and site scales, primarily by suppressing tall, dominant understorey species.

Compared to other wetlands, Wilby *et al.*, (2018) signifies that Beaver ponds typically exhibit lower water depths, more bare ground, shorter shrubs and reduced plant height and litter which supports species coexistence by lessening competition for light, space and nutrients. In his study he records that the number of species unique to Beaver ponds was 50% higher than those unique to other wetlands. Law *et al.* (2017) further demonstrated that small-scale disturbances, such as creating canals and lodges, can enhance habitat suitability for bog plants by increasing woody debris, exposing relict seed banks and creating variable water levels. Beavers often deliver more dynamic ecosystem services such as improved water quality and increased biodiversity by influencing ongoing ecological processes rather than producing fixed or predefined outcomes (Law *et al.* 2018). These factors influenced the plant composition in the Beaver ponds, whereas vegetation within other wetlands were primarily shaped by plant cover, height and leaf litter (Law *et al.* 2017).

This is consistent with Law *et al.* (2019), who characterised Beaver pond vegetation as being dominated by fast growing ruderal species like aster, while other wetland communities were shaped more by larger competitors and stress-tolerant species. These processes can generate a fine scale mosaic of interconnecting habitats subject to differing types and intensities of disturbance, contributing to greater ecological complexity.

Law *et al.* (2019) suggests that effects of Beavers on biodiversity are often context and taxon specific; while greater species richness and habitat heterogeneity are positive attributes, they do not guarantee the presence of rare, specialist or native taxa. Novel Beaver habitats do not always support novel biodiversity. Flooding in eutrophic (alkaline) moss bogs can alter plant communities, leading to the loss of characteristic moss bog species and the spread of widespread reed dominated vegetation (Zavyalov, Zueva & Petrosyan, 2024). In bog systems, the ability to accurately predict the consequences is rare, however, this concern is more applicable to regions where Beavers are considered invasive and native Beaver reintroductions tend to yield positive ecological outcomes (Law *et al.*, 2019; Zavyalov, Zueva & Petrosyan, 2024).

Historically, Beavers were believed to facilitate invasive species spread by preferentially feeding on native vegetation (Law *et al.*, 2019). However, a study conducted over 2 years in the Chattahoochee river in the United States found their activities such as flooding, bioturbation and grazing, suppressed the establishment of invasive species like Parrot's-feather (*Myriophyllum aquaticum*), reducing recruitment by up to 90% and thereby offering a form of biotic resistance to invasion (Parker, Caudill & Hay, 2007). Hence resistance to invasive species is likely moderated by factors other than herbivory such as the population size and the seasonality of resource supply particularly in supporting the recovery of freshwater biodiversity, especially for plant communities (Parker, Caudill & Hay, 2007; Law *et al.*, 2019). Parker, Caudill and Hay, (2007) recorded that Parrots-feather decreased because it grew alongside less palatable neighbouring plants making it susceptible to herbivory. Since native plant recolonisation did not directly contribute to its decline, this suggests that exotic plants can often persist despite herbivory from native consumers.

Grazing by Beavers and livestock can add to the cumulative species richness in wetlands across plot, site and landscape scales by reducing competition from large rhizomatous and mesic plants over small hydric and aquatic species that would dominate under rewetting alone (Law *et al.*, 2018; Mitchell & Niering, 1993). Although, the influence of livestock may be limited due to routine exclusion by fencing suggesting that beavers exhibit a more consistent influence (Law *et al.*, 2019). For example Parker, Caudill and Hay (2007) identified that Beaver activity reduced aquatic plant biomass by 60% and plant litter by 75% in comparison to separated areas in the Chattahoochee river which more than doubled in vegetation. Law *et al.* (2018) further demonstrated that the combined effects of flooding and grazing can enhance habitat heterogeneity, particularly in agriculturally degraded systems. They suggest the extent that Beavers succeed as ecosystem engineers depends on

the availability of preferred woody tree species (e.g. Willow, Birch, Aspen *Populus tremula*), which is in turn shaped by livestock grazing intensity and wider land management practices. In already species rich wetlands, Beaver activity may have less pronounced effects and within drained areas, historic fen vegetation may not be restored (Law *et al.*, 2018).

Aquatic herbivores are often underappreciated, however as Beavers become more common, their effects on the ecology and evolution of freshwater plant species is likely to increase (Nummi & Kuuluvainen, 2013). Beaver activity may help buffer or reverse the impacts of generalist vertebrate herbivores which can significantly affect aquatic plant communities (Parker, Caudill & Hay, 2007). By creating a spatiotemporal mosaic of habitats with different successional pathways and stages, this can support an increased diversity of aquatic species, including fish (Nummi & Kuuluvainen, 2013). These habitats often take time to develop; for example, Law *et al.* (2017) saw a lag in response, with an initial decrease in plant diversity in the first 1–2 years following Beaver reintroduction, followed by a continued increase in diversity after eight years. Law *et al.* (2017) suggests that the length of this lag time likely depends on factors such as geographic location, connectivity to propagule sources, site productivity, Beaver occupation time and population density. The effectiveness of Beavers as a restoration tool often depends on these conditions. Although, when predicting the changes to community composition in Beaver habitats, Law *et al.* (2019) demonstrated that wetland type was more significant than the effects of dam induced inundation.

3.5 Succession

Goud, Watt and Moore (2018) highlighted that Beavers within their study promoted an alternative successional pathway that departs from Clements' classical model of unidirectional hydrarch succession, which progresses through fixed seral stages toward a single climax community. Traditionally, fixed seral stages in wetlands detail pioneer species like *Sphagnum* mosses were thought to progress to tall vascular plants and eventually tall scrub or bog forest within active Beaver ponds. However, their paper suggests that the colonisation of Beavers in wetlands can initiate a continuous feedback cycle of alternate succession, allowing ecosystems to shift between different stable states without a definitive endpoint. This pattern is consistent with Slayter's model of succession, where species composition depends on individual species' tolerances rather than a predetermined sequence (Pulsford, Lindenmayer & Driscoll, 2014). Mitchell and Niering (1993) similarly found that vegetation in a Beaver pond in northwest Connecticut responded to nutrient and acidity gradients rather than following a rigid successional pathway.

In addition, Goud, Watt and Moore (2018) demonstrated that Beaver induced changes can influence the direction of species shifts in response to different wetland types and their successional stages (e.g., bogs, fens and mires). The study documented two alternative pathways of succession, one encouraging bog development through *Sphagnum* moss and bog expansion and another supporting meadow and mudflats following the collapse of a Beaver pond. The moss *Sphagnum cuspidatum* may play a key role in early successional stages due to its broad tolerance range and its ability to acidify local conditions (Karran, 2018). This acidification can promote the establishment of peatland species such as *S. fallax* and *S. papillosum*, which in turn support bog development (Karran, 2018). To achieve the conservation outcome of a bog rather than a meadow or mudflat, they show that understanding how these shifts occur requires a study of these specific habitat types and the mechanisms behind the changes in their succession which is increasingly relevant given that global change drivers such as climate and disturbance can push ecosystems into alternate states (Goud, Watt & Moore, 2018).

A previous study conducted by McMaster and McMaster (2001) further documented these alternative successional pathways in abandoned Beaver wetlands. Within their research, they identified the pathway leading to the formation of a Beaver meadow was caused by frequent re-floodings. This formed a low diversity habitat promoting the dominance of graminoid and tussock plant species which were resistant to change even with subsequent re-floodings. Another pathway they identified involved the persistence of flood tolerant woody species, particularly *Spiraea*, *Alnus* and *Viburnum*, which could survive inundation and continue to grow 2-3 years following dam abandonment (Nummi & Kuuluvainen, 2013). Additionally, species such as Willows (*Salicaceae*) and poplars are often among the first to recover. Their roots tolerate low-oxygen (anaerobic) conditions, and seed germination increases in saturated soils (Nummi & Kuuluvainen, 2013). In contrast, they found that conifers were generally less flood-tolerant. These surviving and recolonizing trees may be further supported by Beaver herbivory which can stimulate adventitious root formation from non-root tissues, although these effects are highly site-specific (Jones *et al.*, 2009). This suggests that successional trajectories following dam abandonment can vary considerably.

Within the study conducted by McMaster and McMaster (2001) they also discovered that in areas with low spring and autumn runoff, a Beaver dam and the flooding it causes, may persist long after the site is no longer maintained, delaying terrestrial recolonisation. During this extended period of inundation, saturated conditions can encourage the colonization of peatland vegetation. Whilst Beavers can cause scrub growth, it should not be seen as a negative impact as it only becomes problematic when not shaped by natural or human processes that maintain a dynamic habitat mosaic (University of Exeter, 2020). Although, Beaver activity in bogs creates a “landscape inertia” which can make it difficult to return to its original state (Zavyalov, Zueva & Petrosyan, 2024).

Around the outer zones of bogs, Goud, Watt and Moore (2018) identified that vegetation changes were more evident compared to its interior. This formed a transition zone where fen and bog characteristics overlap. Within rain fed (ombrotrophic) bogs, the outer edge provided a key role acting as a barrier to mineral-enriched inputs and helped to sustain higher water levels. Their research demonstrated these marginal zones frequently attracted Beaver activity. Through repeated damming and recolonisation, Beavers create disturbance cycles that can reset vegetation to earlier, submerged successional stages. In temperate bogs, they show that declining water levels and intermittent exposure of pond margins tend to support the spread of “bog specialist” species such as dwarf shrubs, sedges and Sphagnum rather than fen or marsh plants, which require mineral-rich, inundated conditions. Nonetheless they suggested that vegetation remained varied across a range of moisture levels, likely due to the influence of the Beaver pond.

Interestingly, Goud, Watt and Moore (2018) noted that while the water table declined in most vegetation zones during the second year, bog habitats remained relatively unaffected. Despite this hydrological change, plant diversity showed weak correlation with water table depth during the first one to two years after Beaver return. This is supported by research from Mitchell and Niering (1993), who found that long term Beaver disturbance at a bog margin did not reduce species richness in adjacent bog communities. Contrary to human interventions, Beavers alter environments both at a broad scale and at fine scales too intricate to replicate. This creates a unique mosaic of habitat heterogeneity with intrinsic ecological value (Law et al., 2018). In degraded bog ecosystems, studies assessing Beaver impacts are limited and often rely on remote sensing, which requires ground verification and offers no insight into Beaver population characteristics (Zavyalov, Zueva & Petrosyan, 2024).

3.6 Feeding preferences of Beavers

Eurasian Beavers are often seen as a generalist herbivore feeding on Grass and forbs, aquatic and woody plants (Vorel *et al.*, 2015). Evidence from Parker, Caudill, and Hay (2006) shows that Beaver tend to adopt a central place foraging strategy, which largely confines them around their lodges and nearby wetlands due to the high energy investment required for building and maintaining their habitats and potential threats posed by predators. Foraging ranges can extend 15–20m from the water’s edge depending on the presence of a dam, the availability of preferred species, and the stage of habitat establishment, with Beavers in less established areas traveling further (Juhász *et al.*, 2023; Misiukiewicz, Piętka & Olszewski, 2023; Vorel *et al.*, 2015). Rather than relocating when food becomes scarce or suboptimal, Beavers within the study produced by Parker, Caudill and Hay (2007) shifted to consuming less preferred species, which may account for their increased reliance on sedges later in the season. During the growing season, Beavers primarily fed on herbaceous plants, while cutting trees and shrubs for winter food stores. Foraging preferences can change

seasonally and between years depending on the rate of exploitation and the rate of regeneration of food supply but Beavers studied in Hungary had a general preference for the following 6 genera: *Populus Salix*, *Corylus*, *Crataegus*, *Prunus* and *Sorbus* depending on what is available in the landscape (Janiszewski, Kolasa & Strychalski, 2017; Juhász *et al.*, 2023).

Janiszewski, Kolasa, and Strychalski (2017) highlight that *Alnus* was not generally used as a food source due to its high content in tannins as a juvenile, but it provides a good resource in construction as structural elements in making lodges or dykes. Furthermore, Elder *Sambucus nigra* was typically avoided as a food source due to its content of cyanogenic glycosides. By cutting down trees Beavers can significantly affect the biomass structure and species composition within their habitat (Janiszewski, 2017). A study by the University of Exeter (2020) supports this finding based on data from the River Otter Beaver Trial, which saw a reduction in canopy height and an increase in canopy variability, with a wider range of tree shapes and sizes following Beaver reintroduction. These changes improved light conditions, supporting new tree growth (Juhász *et al.*, 2023). Jones *et al.* (2009) found that Willows and other trees felled during dormancy in autumn and winter typically regenerated more vigorously, while those cut in active growing seasons showed weaker regrowth. In a comparable study, Juhász *et al.* (2023) reported that native softwood trees in Hungary were among the most susceptible to Beaver activity, regardless of trunk diameter. However, their ability to survive and regenerate was aided by rising water tables and improved hydrological conditions from Beaver damming.

Felling trees can create space for smaller trees and shrubs, such as Hazel *Coryllus avellana*, to establish, however, cutting large-diameter trees often requires significantly more energy (Janiszewski, Kolasa & Strychalski, 2017). Although many studies have examined the relationship between tree diameter and beaver damage, most - including Ważna *et al.*'s (2018) four-year study in western Poland, have concluded that trees with larger breast height diameters are less likely to be felled. Wood cutting is a key behaviour that drives habitat change and plant succession, with Willow, Alder, and Aspen frequently cited as preferentially foraged species (Janiszewski, Kolasa & Strychalski, 2017). In a study in Hungary by Juhász *et al.* (2023) comparing Willow and Poplar, stems measuring 5 to 9cm in diameter were most frequently utilised. Thicker trees were less commonly felled; they were often only damaged by Beavers or disappeared over time due to flooding-driven succession along the stream corridor. Nevertheless, larger stems tended to resprout effectively when hydrological conditions were favourable (Juhász *et al.*, 2023; Misiukiewicz, Piętka, & Olszewski, 2023).

This preference for intermediate-sized stems is echoed in other studies. A two-year investigation conducted by Ważna *et al.* (2018) identified that in a riparian zone in western Poland, encompassing meadows, non-forested tree and shrub communities, Willow (*Salix triandra* and *Salix dasyclados*) was a preferred genus where it was readily abundant in

lowland habitats and accounted for 92% of all cut stems, reinforcing the selection for smaller to medium-sized individuals. Notably, Willows with a diameter of less than 10cm made up 81% of all cut trees. While very small shoots (≤ 2 cm) are typically avoided, Beavers have still been observed cutting them under certain conditions (Jones *et al.*, 2009). Beavers may favour smaller-diameter stems so they can spend less time on land to avoid predator or human disturbance, with trees over 20cm often left unfelled (Genney, 2015; Misiukiewicz, Piętka & Olszewski, 2023).

Willow proved to be the most influential in foraging decisions (Juhász *et al.*, 2023). Within Scotland, Jones *et al.* (2009) found that by cutting Willow, Beavers prolonged its growing season, with newly sprouted stems showing earlier spring growth and delayed autumn dormancy. Beavers also positively selected Poplars and Aspens (Ważna *et al.*, 2018). Within Wigry National Park in Poland, a study by Misiukiewicz, Piętka, and Olszewski (2023) discovered Beavers were willing to travel up to 62 metres to reach their preferred food source, which was Poplar, depending on local plant availability.

In the USA, Parker, Caudill, & Hay, (2006) show that Beavers have even been observed travelling up to 700 metres along river channels to forage for aspen. Although, they suggest that species Beavers do not favour, such as Alder, are rarely felled. Beavers tended to damage rather than cut these trees and were less willing to travel far to access them. Janiszewski, Kolasa and Strychalski (2017) provide evidence for these findings in the Poleise National Park in eastern Poland noting that moderately palatable plants were usually ignored until more preferred neighbouring species have been selectively removed, an effect known as associational resistance. In some cases, they show that highly preferred species can gain refuge from herbivory by growing near less palatable plants that physically or chemically deter feeding. Beavers are known to gradually eliminate palatable species from a floodplain in a preference hierarchy and once only unpalatable vegetation remains, they may abandon the site altogether (Parker, Caudill & Hay, 2006). Ważna *et al.* (2018) also linked tree palatability to factors such as species, age, and habitat.

Aquatic macrophytes can have strong direct and indirect effects on ecosystem level processes including productivity, biogeochemical fluxes, and water flow (Parker, Caudill & Hay, 2006). Through selective feeding, Parker, Caudill and Hay (2006) suggest that Beavers significantly reduced plant biomass and altered species composition within wetlands in the Chattahoochee River National Recreation Area. Plants growing among sedges or tussocks showed a 73–93% increase in foliage, which could indicate that a protective effect like silica-rich stems supports plant diversity by deterring herbivory. Although this lasted until more palatable plants were extrapolated. Beaver activity also led to lower plant litter, as leaf litter from both internal and external sources contributes to freshwater carbon pools, these changes may impact carbon cycling, detritus breakdown, and nutrient availability. In turn,

this can influence food web productivity and ecological processes downstream of Beaver-modified habitats.

Contrary to many studies, Vorel *et al.* (2015) describe Beavers as selective generalist herbivores rather than opportunistic feeders. Their consistent preference for Willow and Poplar in the Czech Republic was recorded regardless of the surrounding riparian species composition, with demand for these species increasing as they became less abundant. In diverse habitats Beavers consume the prevailing species of Willow. Beavers can also vary their use of trees based on trunk diameter rather than species, with thicker stems more often debarked or carved rather than fully felled (Juhász *et al.*, 2023). As Willow species are highly preferred, their utilisation did not always decline with increasing trunk diameter; instead, the type of use shifted (Juhász *et al.*, 2023; Vorel *et al.*, 2015). The three-year study carried out in the Czech Republic on 500 Beavers in 5 diverse populations by Vorel *et al.* (2015) showed that to a lesser extent Hawthorns and Hazel were also positively selected, although there was a distinct preference for Willows and Poplars which made up 80% of foraged trees and was a major portion of the total volume of consumed biomass. Beavers hence tended to occupy localities where these species were dominant, demonstrating a co-evolutionary relationship between Beavers and certain tree species. The greater diversity in Beaver inhabited areas may be both a result of Beaver activity and the selection of more attractive areas for dam construction (Misiukiewicz, Piętka & Olszewski, 2023).

In an enclosed Beaver study set within ancient woodland in eastern Scotland, Jones *et al.* (2009) demonstrated that Willows that were not fully felled accounted for a small fraction of Beaver activity but added significantly to the biomass of woodlands. This supported the development of layered riparian habitats. Of these partially felled trees, 92% had a diameter of at least 11 cm. Many regenerated both from the base and along the leaning trunk, with this regeneration particularly evident at lake-edge sites where flooding was more frequent. Regrowth was more substantial on incompletely felled trees than on those fully cut, leading to denser low-level vegetation. This may offer improved ground-level cover for Beavers while foraging away from water.

In addition to tree species and diameter, Beavers foraging preferences are also affected by distance to the shoreline of a waterbody (Janiszewski, Kolasa & Strychalski, 2017). A Polish study by Misiukiewicz, Piętka and Olszewski, (2023) identified that around 95% of felled trees were located within 50m of a watercourse in the Wigry National Park, with 50% of cutting activity occurring within 10m. Beavers generally avoided travelling further during early habitat colonisation but could extend their range up to 60m or more for preferred food sources or to gather construction materials in more established sites. In this study, dam volume was positively correlated with watercourse width and negatively correlated with Beaver foraging distance. In a review of Beaver foraging behaviour, Juhász *et al.* (2023) suggested that Beavers may include a variety of tree species in their diet to balance nutrient

intake. While Willow and Poplar are favoured for their digestibility and high phosphorus content, Beavers also consumed Hazel and Ash, likely to acquire dietary sodium which may reduce the risk of nutrient deficiencies in European Beavers.

According to optimal foraging theory, the energy gained from a food source must outweigh the energy and time required to obtain it. For Beavers, this means the size and distance of trees from water bodies can influence foraging decisions. As the distance from the shoreline increases, Juhász *et al.* (2023) suggests that Beavers can become more selective, aiming to maximise energy intake while minimising the effort needed to forage, process, and transport tree material. This distance-related selectivity was also associated with a reduction in grazing intensity and a decrease in the diameter of trees utilised further from water (Ważna *et al.*, 2018; Juhász *et al.*, 2023; Misiukiewicz, Piętka & Olszewski, 2023). In support of central place foraging theory, Juhász *et al.* (2023) found that Beavers in temperate environments reduce their foraging intensity with increasing distance from water, while other research finds no clear correlation. However, Misiukiewicz, Piętka & Olszewski (2023) observed a negative relationship between distance and tree size, indicating that Beavers were more likely to forage on thicker trees farther from the water's edge, especially in more fertile habitats where these trees may be abundant.

When preferred food sources are abundant, a study by Vorel *et al.* (2015) in the within the Czech Republic highlights that Beavers tend to be more selective and may forage further from water, as the trade-off between energy expenditure and foraging yield is reduced. This resulted in a higher proportion of less desirable species remaining in the landscape. If these primary food sources vary in abundance, Beavers may be forced to turn into an opportunistic generalist in order to meet their energy requirements depending on the proximity and accessibility of trees. In addition, Janiszewski, Kolasa, and Strychalski (2017) found that Beavers do not appear to select tree or shrub species based on their suitability for dam construction.

When herbage is scarce in winter, Beavers can supplement their diet with aquatic plants to meet increased nitrogen and phosphorus needs during breeding and nursing (Vorel *et al.*, 2015; Ważna *et al.*, 2018). It is also suggested by Ważna *et al.* (2018) that Beavers feed on species like Hazel, Ash, Blackthorn *Prunus spinosa* and *Populus* to avoid macronutrient deficiencies. On average, their research shows that in western Poland Beavers consume only about 30% of the vegetation they harvest, leaving the remainder to decompose. This reduced the abundance of preferred species but created space and resources for other plants to establish. Within their study, there was therefore a strong influence of location, habitat type, and plant species composition on Beaver foraging strategies. The selective foraging of Beavers can significantly reshape species composition and forest structure, with notable ecological impacts (Juhász *et al.*, 2023). A 9-year study by Law, Jones and Willby (2014) in Scotland found that persistent selective Beaver grazing on macrophytes led to a

threefold increase in species richness and notable shifts in composition and increased turnover, driven by reduced dominance of preferred species like Bogbean *Menyanthes trifoliata*. A constant and significant removal of macrophyte biomass was observed. While short-term impacts were minimal, sustained herbivory significantly boosted alpha and beta diversity, though effects may vary by site.

Research by Vorel *et al.* (2015) shows that Beavers typically avoided the thinnest shoots, which may contain anti-herbivore compounds. In response to repeated browsing, woody plants adapted by increasing sprout production and produced phytochemicals that deter further grazing. They suggest that these plant–herbivore dynamics likely evolved alongside long-term co-existence with grazers and predators. Willow species, though highly palatable, regenerate with bitter-tasting sprouts that reduce overgrazing. Beavers in their study also demonstrated selectivity among populus age classes, often avoiding young resprouts rich in deterrent secondary metabolites. To support Beaver populations and associated aquatic biodiversity, they suggest riparian zones should maintain a continuous supply of native tree species at varying stages of growth. Natural regeneration is key for maintaining both food availability and hydrological stability. These zones are better viewed as ecological corridors than sites for forest production.

3.7 Beaver and herbivory

Through herbivory, Beavers and deer both exert their own unique influence on wetlands (Law *et al.* 2019; Wilson, 2023). Law *et al.* (2019) suggests that Beaver grazing can support the recovery of riparian forests and contribute to structural habitat complexity through the development of both mature and multi-stemmed coppice trees. In south-central Sweden, their study found that tree grazing by beavers stimulated coppiced secondary shoots which were nutrient-rich, easily accessible, and had a favourable distribution and density for browsing deer. This can influence the distribution of deer across riparian forests and together they can create a Beaver-deer impact – an indirect interspecific interaction through a change in resource availability (Jones *et al.*, 2009; Wilson, 2023).

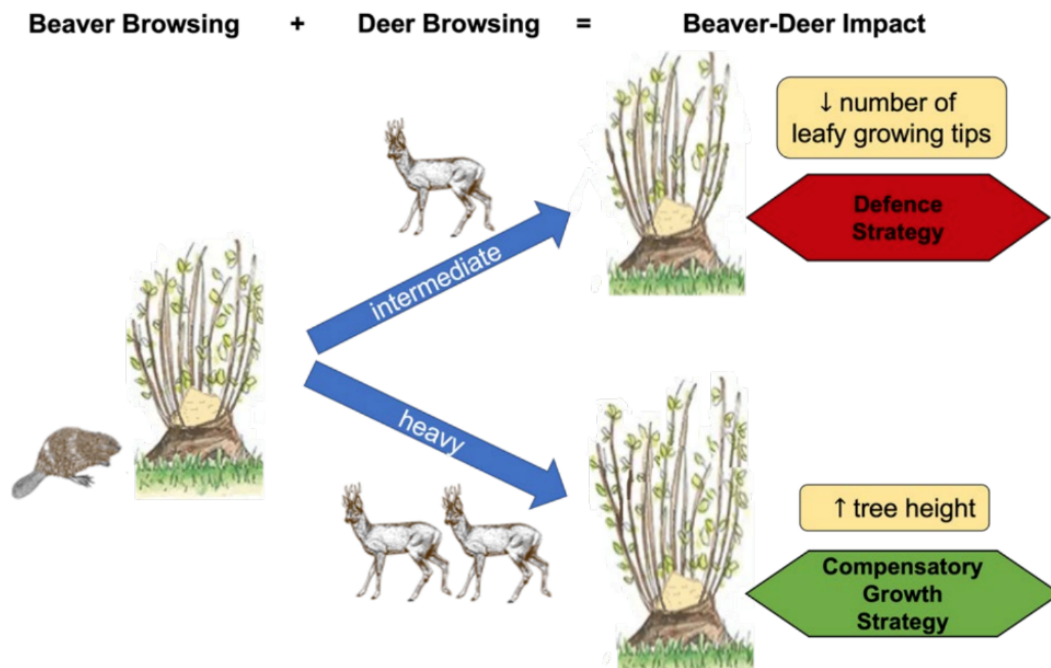


Figure 4: Beaver-Deer browsing interactions

Research by Wilson (2023) identified that Beaver and deer do not compete for the same resource, deer prefer the smaller growth of saplings and twigs several millimetres in diameter, whereas Beavers favour stems above 3 cm. Similarly, a study produced by Jones *et al.* (2009) noted that species like Willow and Aspen are especially favoured by both Beavers and deer, including roe and red deer.

By tracking the growth of Willow (*Salix cinerea*) stands in Perthshire, Scotland, Wilson (2023) showed that deer browsing can alter tree structure and resource allocation over time depending on the density of deer. Intermediate browsing by lower levels of deer encouraged a defence response in trees which led to thick shrubby growth with a decrease in leafy growing tips. High deer pressure drove plants to grow vertically, which may have an influence on woodland structure and future habitat use by both herbivores and other species. Additionally, a study conducted by Jones *et al.* (2009) 25 miles northeast of Perth in Blairgowrie, Scotland identified that changes in soil moisture due to damming may play a role in tree responses to Beaver deer interactions. As a result, Increased flooding caused by Beaver damming inundated sections of forest making them less accessible to grazing deer, these flooded stands were also rarely harvested by Beavers.

Beaver activity can supply deer with novel, nitrogen-rich forage by stimulating coppice regrowth absent in undisturbed woodland (Wilson, 2023). Wilson suggests that Beaver-occupied woodlands can show greater herb cover and more nutritious secondary shoots. When this occurs near farmland, it may divert deer from crops and nearby managed forestry, reducing browsing damage. Observed Willow stands were more susceptible to deer grazing at the trunk rather than the stump of felled trees because the exposed surface

provided easier access and led to more frequent damage to regrowing logs. Partially felled trees were also more heavily browsed than fully felled ones and deer appeared to favour the accessible stumps. Although deer can damage coppicing, Jones *et al.* (2009) found that by stripping bark, consuming twigs, leaves, and buds, and uprooting seedlings, their browsing pressure was not sufficient to prevent Willow coppices from successfully re-establishing through regrowth.

Studies in Canada provide further insight into this interaction. Hood and Bayley (2008), as cited by Wilson (2023), reported that in degraded or species-poor riparian habitats, lacking a diverse age structure, intense deer browsing can suppress the regrowth of tree species preferred by Beavers. This can force Beavers to alter their foraging behaviour and lead to conditions approaching competitive exclusion. However, they found that this effect may be mitigated in high-quality, diverse riparian woodlands, where both species are able to coexist without one excluding the other. When deer browsing pressure was low, partially felled trees produced substantially more new growth than intact branches of the same length, reflecting a higher growth rate. These shoots reached an average of approximately 1 m after one growing season and 2.5 m after two years. This suggests that in mature diverse riparian environments, Beavers and deer typically occupy two distinct browsing niches and Beaver–deer interactions can enhance vegetation regrowth and, in turn, promote greater biodiversity. A process-oriented model developed by Baker *et al.* (2012), as cited by Wilson (2023), demonstrated that Beavers in the USA tolerate deer browsing only up to a site-specific ecological threshold of ungulate density. Beyond this threshold, food limitation may lead to the local exclusion of Beavers. If deer browsing pressures displace Beavers from riparian woodlands, the animals may be forced into more human-dominated landscapes, increasing the potential for Human–Beaver conflict (Wilson, 2023).

Jones *et al.* (2009) highlighted that a similar pattern was observed in Aspen regrowth, where felling stimulated substantial shoot production. Within two years, 11 felled Aspen trees produced around 85 new suckers, averaging over 2m in height, and these young shoots remained largely untouched by deer, which was considered to be due to their chemical defences. Willow regrowth, in contrast, was browsed more frequently, though deer foraging tended to occur in clumped patches rather than evenly across the stand. Combined with Beaver felling, this patchy browsing created a structurally diverse mosaic of tree ages and forms, supporting a wide range of Aspen and Willow associated flora and fauna. Although, Wilson (2023), reported on a long-term monitoring in Knapdale Forest, Scotland, where he observed that whilst Beavers can cause marked localised changes through highly selective foraging; the woodland structure, composition, and regeneration showed little overall change at the woodland scale over the 11-year study, based on field surveys.

3.8 Lichen

In a note produced on the Management of lichen rich woodland for the British Lichen Society, Sanderson (2022) suggests that slow colonising lichen and bryophyte species require undisturbed environments and occupy very narrow ecological niches. He suggested that old woodland lichens typically require continuity (e.g. a succession of veteran trees and bushes), within sheltered but well-lit habitats, with a ground flora / understory that is open and relatively clear of invasive native species (e.g. ivy, bramble and dense thickets of holly) as well as invasive exotic species such as rhododendron. Ideal conditions can be found in sustainably grazed old growth woodlands, grazed by either managed domestic or wild herbivores (Genney, 2015). Sanderson (2022) highlights that the best sites have a long continuity back into the deep past.

These ideal conditions for woodland lichen assemblages are typically found in extensively grazed old growth pasture woodland with a mixture of open canopied high forest, glades and savanna like stands (Sanderson & Wolseley, 2001). Within the New Forest these conditions are maintained by browsing animals.

Sanderson (2022) emphasises that the main positive features appear to be:

- Many trees surviving to senescence.
- Varying, but generally good light levels (with different lichen species having widely different tolerances).
- Shelter producing humid conditions.
- Slow woodland dynamics.

The basic mechanism driving this is a varying browsing pressure on tree regeneration that suppresses regeneration for long periods (Sanderson and Wolseley, 2001). A key interaction occurs between the shrub layer and browsers, which can rapidly and drastically alter light and humidity levels without immediately affecting the canopy (Coppins & Coppins, 1998, cited in Sanderson, 2022). Interactions between browsers and the canopy are much more long term, but frequent glades are required. Glades need to be dynamic but permanent features and slow dynamics are crucial. As an initial guide, Coppins and Coppins (1998) suggest a requirement for at least 30% glades within the canopy of lichen rich woodlands and that the glades have a permanence of at least 30 years, but there will be a lot of variation around these figures.

3.8.1 Beaver influence on lichen communities

Although there are almost no studies of Beaver impacts on lichen communities, a lichen impact assessment written by Genney (2015) on the Scottish beaver trial provided some indication about the impact to Atlantic Hazel. Beaver activity within this study opened up the canopy near watercourses and the increased light shifted lichen communities. He suggests that the magnitude of impact at the lichen community scale will be related to the proportion of habitat affected and the degree to which micro-habitat continuity can be maintained through replacement of young and old Hazel stems. Recovery likely depended on: Firstly, whether lichen micro-habitats are able to recover and secondly on the health and abundance of adjacent unaffected Atlantic Hazel lichen communities.

Genney (2015) highlights that riparian woodland types are likely to be subject to the greatest impacts e.g. Willow carr, Birch carr and Alder woodland. Many sites of high lichen importance were typified by trees on river-banks, or low-lying strips of alluvial ground where humidity is high. In Scotland, the report notes the main tree species with important lichen assemblages in such places is Ash, but Willow (*Salix caprea*) and Hazel are also important, and the report recommended catchment level assessments where water bodies run through SSSIs notified for their lichen interest. Such an approach could be adopted in the New Forest.

Atlantic Hazel provides a habitat for diverse oceanic lichens. His research found that young, smooth-barked stems support a community of crust-like lichens called the Graphidion while older, rougher stems support a community dominated by larger, leafy lichens called the Lobarion. Under natural conditions, Hazel is a multi-stemmed shrub. As limbs can break off, shoots regenerate and through this natural process many Hazel trees persist and become ancient. This regeneration ensures the continuity of young, smooth barked and rough barked stems.

The Scotland Beaver trial lost species from both communities but there was no indication that they were any better or worse developed. According to Genney (2015) Graphidion-community lichens were more abundant on stems < 10cm in diameter while Lobarion-community lichen were more prevalent on larger stems. Smaller and hence normally younger, smooth barked stems were preferentially felled by Beaver over larger, rough-barked older stems. This means that lichens associated with the Graphidion community (typically occupying the smooth bark micro-habitat) will have been impacted to a greater extent relative to species typical of the Lobarion community. Many of the larger and some of the smaller, older, felled stems did however support luxuriant populations of Lobarion species. It was postulated that if the Beavers continue to utilise stems up to 5 and 10cm diameter at a rate close to 5 % per annum, it seems likely that few stems will survive more than 20 years if there were no mitigation measures in place.

The Scottish study identified a significant overlap between Atlantic Hazel lichen habitat and potential Beaver habitat and proposed that there is a risk to the long-term viability of Hazel in habitat occupied by Beavers. They recorded deer browsing of sun-shoots may prevent recovery of Hazel stools. This represents an important interaction between Beavers and other herbivores that will require careful monitoring and management.

Aspen is an important habitat for lichens, Genney (2015) reported it is one of the few tree species able to support lichens that require trees with a high bark pH. Three hundred and eighty species of lichen and lichenicolous fungi have been recorded from Aspen, including 14 species assessed as Endangered, ten as Vulnerable and 15 as Near Threatened against IUCN Red Listing criteria. Britain is considered to have international responsibility for 42 of these ICUN species because of the relatively high proportion of their global population that occurs here. Lichen diversity on Aspen is related to a number of factors but tends to be higher in areas with high historic woodland cover and a range of tree ages. However, Aspen is highly favoured by European Beavers and Genney (2015) suggests the observations of Beaver activity in Sweden demonstrate that Beaver will fell even mature trees in order to access the nutrient-rich bark.

In an ecosystem model called SAVANNA using field data from the Rocky Mountain National Park, Colorado, USA, Baker (2012) suggested three options to mitigate risks to Aspen, fence off, exclude or plant new stands of Aspen. Fencing was not recommended as the primary protection for lichen. Long term absence of grazing was identified to be just as damaging as overgrazing due to the light and shade requirements of lichens. He suggests that compensatory expansion of affected woodland lichen habitat is an essential mitigation measure. However, expanding important lichen habitat is a slow solution as it would take many years and is therefore more of a longer-term strategy, preceding beaver expansion by a number of decades.

Genney (2015) concludes that Beavers have the potential to negatively impact nationally and internationally important lichen populations by felling individual trees within ancient woodland or by breaking the ecological continuity of important lichen microhabitats. However, the risk varies greatly between lichen habitat types, mainly due to differential overlap with potential or occupied Beaver habitat. The Scottish Beaver Trial found that the activity of Beavers was almost always within 50m of a watercourse and the selection of trees for foraging or felling also depend on the species growing within the riparian zone. Beavers can alter the riparian woodland zone in the short to medium term and shift it to a more permanent, wetter woodland habitat type and this will present both opportunities and threats for lichen communities.

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Acknowledgements

Sasha Oubykine is a second-year student at the University of Southampton reading Physical Geography Bsc. This report forms the output of an internship with Hampshire and Isle of Wight Wildlife Trust, managed by Nicola Wheeler (the Trust's Senior Beaver Recovery Officer) and supported by Clive Chatters of the New Forest Association.

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