Interactive Effects of Beaver and Deer on Scotland's Riparian Woodlands

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Declaration of Authorship

I, Kelsey A. Wilson, declare that I have composed this thesis and that it embodies the results of my own research.

Where appropriate, I have acknowledged the nature and the extent of work carried out in collaboration with others.

All research material has been duly acknowledged and cited.

Signed: Kelsey Wilson

Date: 22nd of December 2022

General Abstract

Restoring lost interspecific interactions through reintroductions is a key aim in some habitat restoration projects, but few focus on the interspecific interactions specifically between herbivores. As a result, herbivore interactions are rarely considered in species management policies or woodland expansion targets, despite their potentially important role in shaping ecosystem function. The Eurasian beaver (*Castor fiber*) is an ecosystem engineer that is expanding across Scotland, following a long absence, into riparian woodlands already being structurally altered by deer (Cervidae). Riparian woodlands are high value habitats in terms of biodiversity and mitigation of climate change impacts, but their quality and extent have dramatically declined due to anthropogenic pressures. Beavers and deer both exert their own unique influence on riparian woodlands through browsing, yet no published research in Europe has so far investigated the relationship between beaver and deer browsing and how it could impact woodland structure, composition, and regeneration processes.

This thesis examined beaver-deer interactions in riparian woodlands through a combination of field-based surveys and experiments in Scotland. The foundation of beaver-deer interactions was firstly examined by studying beaver tree foraging preferences and their temporal effects on woodland composition and structure (Chapter 2). While beavers can alter their habitat drastically at a small patch-scale over a short period through highly selective foraging, it was found that woodland composition or structure did not significantly change over an 11-year period. The second field-based survey (Chapter 3) confirmed that beaver herbivory can promote riparian woodland regeneration and habitat complexity by creating a mosaic of mature and multi-stemmed, coppiced trees. In addition, the secondary shoots from resprouted beaver-felled trees were found to be readily available, nutritious, and morphologically appealing in terms of their distribution and density, which could enhance resources for browsing deer and influence deer distribution. Finally, the mechanistic elements of beaver-deer interactions were explored by tracking the growth of experimental riparian willow (*Salix cinerea)* stands (Chapter 4). This demonstrated that deer browsing on resprouted beaver-felled trees is likely to alter tree structure and resource allocation over time, but effects will depend on deer density. It also revealed that changes in soil moisture (caused by beaver damming) may play a role in tree responses to beaver-deer interactions.

As beaver and deer continue to expand into intensely-modified, populated landscapes throughout Europe, their interactions in riparian woodlands are likely to become increasingly commonplace. The research presented in this thesis highlights that nationwide riparian planting/enhancement, coupled with standardised monitoring of the impacts of herbivore interactions, should be considered a preventative priority in future beaver/deer management plans and woodland expansion targets.

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CHAPTER 1: GENERAL INTRODUCTION

Riparian woodlands play a fundamental role in connecting freshwater and terrestrial ecosystems. They have been described as far more important proportionally than their areal extent (Ogilvy et al., 2022). Eurasian beaver (*Castor fiber*) are spreading naturally or being reintroduced into riparian woodlands throughout Europe, often after long absences. The ability to transform their habitat through tree-felling and dam-building has led to the status of beavers as 'ecosystem engineers' (Jones et al., 1994) and placed them at the forefront of riparian habitat and stream restoration projects (Pollock et al., 2014; Brown et al., 2018). However, beaver are recolonising areas of their former distribution which have become highly populated and intensely-modified since their absence (Wróbel, 2020). They have also been returned to riparian woodlands that are already profoundly altered by other large herbivores, which have undergone pronounced expansions during the beavers' absence (Apollonio et al., 2010).

A major threat to natural woodland regeneration is the excessive browsing of young trees by deer species (Cervidae) (Reimoser & Reimoser, 2010). Observations in Scotland indicate that deer readily exploit the regenerative secondary shoots that sprout from beaver-felled trees (Iason et al., 2014). By providing a novel resource of forage that would have otherwise been absent prior to the beaver's reintroduction, tree-felling by beaver may inadvertently exert an influence on the distribution of deer and attract them into riparian woodlands. However, if the regrowth from beaver-felled trees is routinely removed by browsing deer, there could also be a simplification in the structure of riparian woodland, and potentially deterioration or even loss of the habitat.

Despite crucial implications that span wildlife and woodland management, beaver-deer interactions are largely unstudied in Europe. As beaver and deer populations continue to expand, interspecific interactions between beaver and deer in riparian woodlands will become increasingly commonplace. An understanding of beaver-deer interactions is therefore essential to predict potential ecological effects on the wider landscape. This introductory chapter firstly examines the conservation value of riparian woodlands before discussing in detail the role that beaver and deer play in shaping them.

1.1. The importance of riparian woodlands

1.1.1. Ecosystem services

Riparian woodlands are high value habitats that play an integral role in the transfer of energy between terrestrial and freshwater ecosystems (Cole et al., 2020). Riparian woodlands are biodiversity hotspots and are particularly valuable to; birds (Bennett et al., 2014; Yabuhara et al., 2019; Keten et al., 2020), mammals (Virgos, 2001; Matos et al., 2009), amphibians and reptiles (Bateman & Merritt, 2020). They can also support an increased abundance in invertebrates (Andersen & Hanssen, 2005; Halder et al., 2015) which in turn provide a food source for fish. Riparian woodlands also serve as effective wildlife corridors (Corbacho et al., 2003) and support an abundance of tree-related microhabitats which provide an array of niches occupied by specialist species (Przepióra & Ciach, 2022).

As well as biodiversity benefits, riparian woodlands can provide key abiotic ecosystem services. They can buffer the aquatic environment from the effects of agricultural diffuse pollution (Turunen et al., 2019), sequester carbon (Dybala et al., 2019) and facilitate nutrient cycling (Larson et al., 2018). Allochthonous inputs of leaf litter from riparian woodlands are also important drivers of basal energy flow in most small stream food webs with significant downstream effects (Erdozain et al., 2021). They also regulate sediment input which can improve habitat for endangered species such as the freshwater pearl mussel (*Margaritifera margaritifera*) (Pulley et al., 2019). Planting of riparian woodland is a feasible mitigation option for easing climate change effects by regulating rising water temperatures through increased shading (Justice et al., 2017; Turunen et al., 2021) which can benefit temperature-sensitive salmonids and other fish species (Jackson et al., 2018).

1.1.2. Current status & threats

Historically, most freshwater habitats in Europe were bordered by riparian woodlands (Brown et al., 2018). It is estimated that natural riparian woodland habitats across Europe and North America have declined by 80% since the 1700s (Naiman et al., 1993). Temperate hardwood riparian woodlands are considered ‘endangered’ and temperate softwood riparian woodlands are listed as ‘near-threatened’ in the European Red List of Habitats (Janssen et al., 2016). Furthermore, temperate alluvial forests dominated by alder and rowan are listed in Annex 1 of the EU Habitat Directive which includes priority habitats ‘in danger of disappearance.’ In Scotland, a 2015-2016 study of its river baseline network demonstrated that 56% of riparian vegetation was in poor condition with no woody vegetation at all (Ogilvy et al., 2022).

Riparian woodlands are threatened by a range of anthropogenic pressures such as pollution, changes in land-use and forestry practises, as well as climate change (Hoppenreijs et al., 2022). One of the main current threats for woodlands is excessive mammalian herbivory and specifically the effects of large ungulates (hooved mammals) (Ramirez et al., 2018; Spake et al., 2020). Ungulates target the shoots, buds, and foliage of young saplings (Gill, 1992a). Although some degree of mammalian herbivory contributes to the natural dynamics of woodland ecosystems, unnaturally high levels of browsing can be damaging. Detrimental impacts of ungulate browsing on woodlands have been documented for decades (Gill, 1992b) and have generally raised concerns for woodland regeneration and conservation (Reimoser & Putman, 2011). The economic impacts of ungulate browsing are also a major concern to the forestry sector and excessive ungulate browsing has been shown to significantly reduce the yield and value of commercial stands (Gill et al., 2000; Ward et al., 2004).

Ungulate browsing is prevalent in woodlands and can affect relatively vast areas. For example, at least 10,000 km^2 of forest area in Austria is damaged per year by browsing ungulates (Reimoser & Reimoser, 2010). In Scotland, an assessment of the ecological condition of all Scottish native woodlands in 2010-2015 reported that herbivore browsing was recorded in around 60% of woodland transects (Forest Research, 2020). Woodland expansion is high on the agenda with aims to increase woodland cover from 18% to 23% by 2032 (Scottish Government, 2019). However, most literature focuses on the impacts of herbivores on woodland habitats in general rather than riparian woodlands specifically, highlighting an important knowledge gap. Riparian woodlands are unique in terms of their species assemblages and growing conditions which are subject to frequent, periodic inundation (Zaimes et al., 2010). However, it is unclear whether they respond differently to herbivory than non-riparian woodlands.

Although European deer populations have increased in recent decades (Apollonio et al., 2010; Carpio et al., 2021), most other large herbivores have faced drastic declines across the world over the last few centuries (Ripple et at., 2015). Historically, the European woodland herbivore assemblage and its impacts on vegetation would have been much more diverse, comprising myriad of species such as beaver, deer, moose (*Alces alces*), bison (*Bison bosanus*) and wild boar (*Sus scrofa*), as well as the extinct aurochs (*Bos primigenius*) and tarpan (*Equus ferus*) (Ripple et al., 2015; Németh et al. 2017). Presently, deer are arguably responsible for the majority of herbivore impacts in European woodlands (Putman et al., 2011), generally resulting in a single-species browsing pressure. Restoring diverse sources of vegetation disturbance through large herbivore reintroductions is often an aim in habitat restoration projects (Dvorský et al., 2021).

1.1.3. Plant responses to herbivory

Plants have co-evolved alongside herbivory for millions of years and plant-herbivore interactions are pivotal in driving ecosystem function (Del-Claro & Torezan-Silingardi, 2021). While the significance of insect herbivory is largely studied, partly for its relevance to agricultural production, the interactions between plants and mammalian herbivores are less well documented or understood. Large herbivores can influence vegetation through grazing, browsing, trampling, defecation, and seed dispersal. Impacts can span key environmental processes such carbon cycling (Leroux et al., 2020) or wildfire regimes (Rouet-Leduc et al., 2021) which can ultimately influence climate change (Ramsay et al., 2022).

Large herbivores can create and maintain patch heterogeneity in systems that would otherwise comprise continuous vegetation. For example, bison create wallows which are essentially localised patches of disturbance in typically vast areas of homogenous grassland (Nickell et al., 2018). Wild boar wallows can also create transitory pools which benefit amphibians (Baruzzi & Krofel, 2017). On a much larger scale, African elephants (*Loxodonta africana*) can transform woodlands into patchy grassland mosaics by trampling, digging and even uprooting entire trees to access browse (Haynes, 2012). This disturbance can ultimately influence the distribution of other herbivores. The pathways that elephants form in dense thicket allow black rhinoceros *(Diceros bicornis)* to exploit forage that would be otherwise inaccessible (Landman & Kerley, 2014). In Kenya, hippopotamus (*Hippopotamus amphibius*) grazing has also been suggested to facilitate other large herbivores. By bulk foraging on grasses, hippos enhance the heterogeneity of riverbank vegetation, which attracts other grazing herbivores to the rivers (Kanga et al., 2013).

Per unit area, large herbivores contribute to a disproportionately higher removal of plant biomass than small herbivores (Doughty et al., 2013). To avoid or reduce herbivory, plants can defend themselves physically using spines, thorns, trichomes or a waxy cuticle (Stamp, 2008). Alternatively, plants can chemically deter herbivory by accumulating metabolites such as terpenes and phenolics rendering them unpalatable to herbivores (Iason, 2005). Following herbivory, different plant groups respond in different ways, usually corresponding with their growth rate and woodiness (Crawley, 1984). Graminoids, and some deciduous shrubs, can recover quickly via their large belowground carbohydrate reserves, and higher rates of photosynthesis (Bryant et al., 1983). Their resource allocation is typically diverted into fast, compensatory growth to quickly recover biomass. This often results in plant material of higher palatability to insect herbivores (Shelton, 2000; Lind et al., 2012). On the other hand, woody species are generally less able to respond positively to herbivory than graminoids and trees often divert their resource allocation into the production of defence chemicals to deter future herbivory (Cornelissen et al., 2003). However, some fast-growing species such as willows (*Salix* spp.) can compensate moderate levels of browsing by producing longer shoots and more buds (Herder et al., 2009; Christie et al., 2014).

1.2. The return of the beaver

1.2.1. Animal reintroductions as nature-based solutions

Ecosystem restoration has been deemed ‘one of the most promising strategies for conservation in the Anthropocene’ (Genes & Dirzo, 2022) and the reintroduction of key extirpated flora or fauna can potentially help restore degraded ecosystems at relatively large scales (Menz et al., 2013). Reintroductions themselves can be viewed as an invaluable tool in conservation biology with the potential of bringing several species on the brink of extinction back to healthy, self-sustaining numbers (Seddon et al., 2007). A reintroduction is conventionally defined as “the intentional movement and release of an organism inside its indigenous range from which it has disappeared” (IUCN/SSC, 2013).

The earliest known deliberate movement and release of an animal dates back around 19,000 years ago with the grey cuscus (*Phalanger orientalis*) in Papa New Guinea (Grayson, 2001). Since then, many well-known reintroductions for conservation purposes have taken place throughout the world such as the Arabian oryx (*Oryx leucoryx*) in Oman (Stanley Price, 1989) the California condor (*Gymnogyps californianus*) in North America (Toone & Wallace, 1994) and the golden lion tamarin, (*Leontopithecus rosalia*) in Brazil (Kierulff et al., 2012). More recently, proposals for the reintroduction of the wolf (*Canis lupus*) and lynx (*Lynx lynx*) to Scotland have been discussed at length in the media and scientific community (Hovardas, 2018)

Reintroductions have traditionally been motivated by increasing the abundance or distribution of the species themselves (Seddon & Armstrong, 2019). However, there has recently been a greater emphasis on reintroducing extirpated species for their role in an ecosystem, as well as their interactions with other species (Perring et al., 2015; Tanentzap & Smith, 2018). Nonetheless, this nature-based solution is not a straightforward one. The reintroduction (or removal) of just one species can reshape the structure and functioning of ecosystems while potentially resulting in significant cascading effects. These effects can be particularly evident when the reintroduced species is an apex predator or ecosystem engineer (Wilmers et al., 2012; Ripple et al., 2014; Hunter et al., 2015). Cascading effects may also be significant when a species is reintroduced into a modern landscape that has undergone significant environmental changes since the historical baseline (Brown et al., 2018; Hewett et al., 2020). A broad understanding of the inter-specific interactions of reintroduced species is therefore imperative in order to predict any unwanted or unexpected effects that may be triggered following their return.

1.3.2. Beavers in Scotland: a history

The Eurasian beaver has made a remarkable recovery from its near extinction in the 1800s following centuries of persecution. They were hunted by humans for their fur pelts for hat-making, and their castoreum gland for perfumes and painkillers (Nolet & Rosell, 1998). Anecdotal evidence highlights that the Catholic church believed that the swimming abilities of the beaver, alongside its scaly fatty tail, was justification for its classification as fish. It could therefore be eaten on Fridays and religious days when meat-consumption was not normally permitted (Kitchener & Conroy, 1997). From around eight relict, scattered populations totalling around 1200 individuals, beavers have now recolonised most of their former European range with recent population estimates suggesting at least 1.5 million animals (Halley et al., 2021). Their rapid range expansion has been accomplished through protective regimes, translocations, and reintroductions, as well as natural recolonisation (Wróbel, 2020). The latest population distribution research states that beavers now occupy every European country within their natural range except for Italy, Portugal, and the Balkans (Halley et al., 2021). Beavers have since 'reappeared' in Italy, potentially following unauthorised releases (Pucci et al., 2021).

In Scotland, the history of the reintroduction of the beaver is arguably a long and convoluted one. It is estimated that beavers were eradicated from Scotland in the 1600s (Coles, 2006) and the last Scottish record refers to beavers in the Loch Ness area in 1526 (Kitchener & Conroy, 1997). It was not until 2009 that they returned as part of a formal, government-licensed reintroduction, but on a 'trial' basis only. The five-year scientifically monitored trial reintroduction (the Scottish Beaver Trial, hereafter SBT) took place in 2009-2014. Four beaver families (2-4 individuals) were translocated from a source population in Norway to a secluded peninsula in Knapdale Forest, Argyll. The trial was deemed a success and resulted in a small population of around 20 individuals (Harrington et al., 2015) which has been steadily maintained to date through natural expansion and supplementary translocations (Dowse et al., 2020).

Meanwhile, records of unlicensed beaver releases also began to appear in Tayside, eastern Scotland, in 2006, although anecdotal reports go back to 2002. Whether an intentional result of impatient beaver-enthusiasts, an accidental result of captive population escapees, or some combination of these, the source of these releases is still a highly controversial topic in Scottish media today. Tayside is dominated by low-lying prime agricultural land which has contributed to ongoing beaver-human conflict, exacerbated by the contentious way in which the beavers first arrived. This population was formally censused three times between 2012-2021 and appears to have expanded significantly (Figure 1.1). The most recent estimate is 251 active beaver territories (approximately 954 individuals) which represents a 550% increase from surveys in 2012 (Campbell-Palmer et al., 2021a). Health screening and genetic testing have revealed the population is healthy despite having a potentially low number of founding individuals (Campbell-Palmer et al., 2020, 2021b).

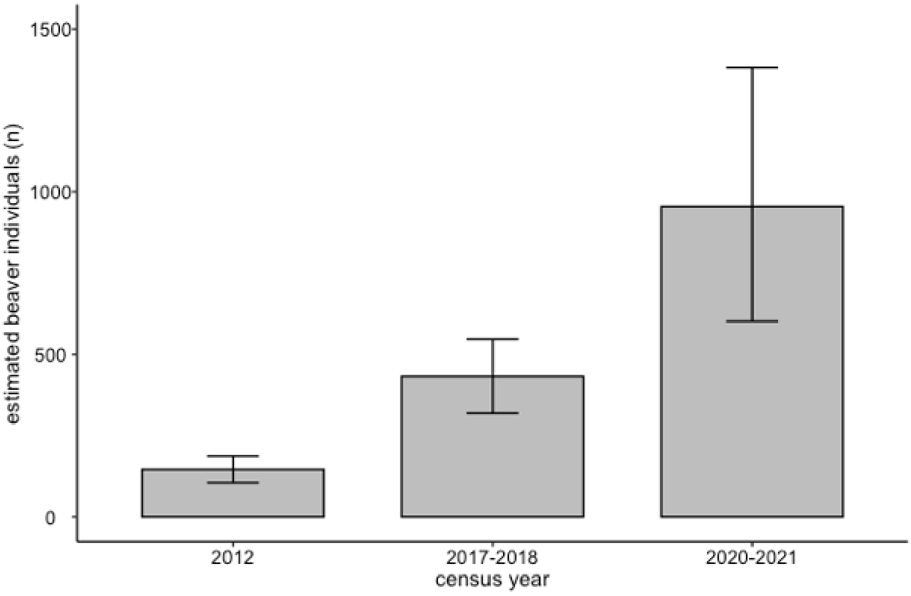


Figure 1.1. Number of estimated beaver individuals in Tayside, Scotland in 2012, 2017-2018, and 2020-2021. Error bars represent range. Data compiled from Campbell et al., (2012) and Campbell-Palmer et al., (2018, 2021a).

It was not until November 2016 that the Scottish Government announced their intention to allow the Knapdale and Tayside populations to remain, essentially formally approving the first (and since only) reintroduction of a mammal species in the UK. This news was not confirmed for another two and a half years when beavers in Scotland were listed as a European Protected Species (EPS) in May 2019. In summary, this legislation protects beavers from being killed or disturbed and permits their population to naturally expand. To ease human-beaver conflict, permits were issued to cull beavers in special cases where they were deemed to have significant impacts on prime agricultural land. Licence returns for 2021 show that 87 beavers were killed under licence. Translocations of 33 animals were permitted, but only to Knapdale Forest or enclosed projects in England (IUCN/CPSG, 2022).

More recently, the Scottish Government announced a shift in policy to allow problem beavers to be moved to new release sites within Scotland where conflict is minimal i.e., restoration projects by private estate owners with ample ground (IUCN/CPSG, 2022). This policy-change (November 2021) facilitated the first beaver release in

Scotland outside of Knapdale. Public consultations have just concluded (November 2022) to inform feasibility plans to translocate beavers into the River Leven and River Forth catchments (IUCN/CPSG, 2022). Elsewhere in Britain, there are wild beaver populations (all much smaller than that on Tayside) in around seven areas of southern England and Wales, mostly in the south-west, in addition to numerous enclosed projects (often comprising expatriated ‘problem beavers’ from Scotland) (Figure 1.2).

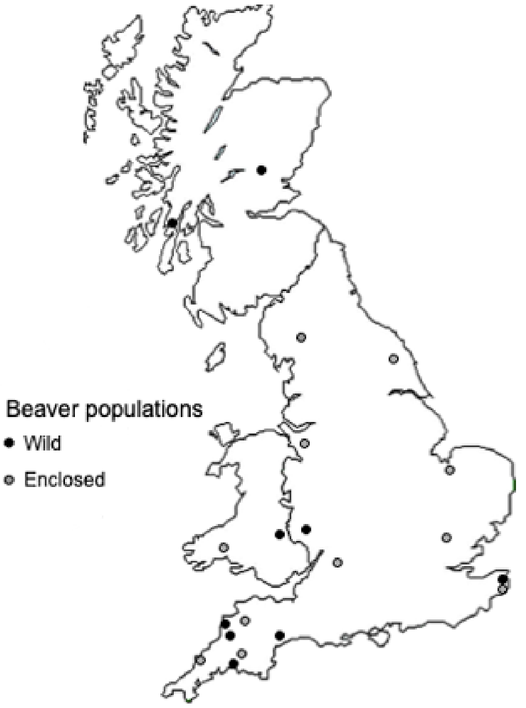


Figure 1.2. Distribution of the primary wild and enclosed beaver populations in Britain as of November 2022. Data sourced from Beaver Trust (2022).

1.2.2. Beaver ecology

Beavers are large, semi-aquatic, crepuscular rodents. There are two extant species: the Eurasian beaver and the North American beaver (*C. canadensis)*. Minimal differences are noted in their biology and behaviour, however comparative studies have generally found that the Eurasian beaver has a lower fertility rate, producing fewer kits per year than the North American species (Rosell et al., 2005). Recent research has demonstrated the use of pet dogs (*Canis familiaris*) in distinguishing the two species through olfactory cues in beaver castoreum glands (Rosell et al., 2020). Unless specified, this thesis focuses on the Eurasian beaver, but most observations are also applicable to the North American beaver.

Beavers occupy a range of freshwater habitats, ranging from lakes and ponds to narrow drainage ditches and wide rivers. Mean territory size is assessed in terms of an occupied stretch of river length and typically ranges from 1.8 to 4.7km in Scotland (Campbell et al., 2012; Harrington et al., 2015). One family will generally occupy a pond or lake, with large lakes being able to support several territories depending on the habitat quality (Wazna et al., 2018). They live in ‘family’ units (or ‘colonies’ in North American literature). Beavers breed once per year and a family typically comprises one adult breeding pair, and up to four kits, as well as the last years’ kits (named ‘sub-adults/yearlings’). Sub-adults generally tend to disperse and form their own territories when they are two-three years old (Wilsson, 1971).

The focal point of a typical beaver territory is their lodge. Lodges are typically constructed using mud and woody material on the shore bank, with an underwater entrance to evade terrestrial predators. Each family may build multiple lodges in a single territory and alternate their use in the summer and winter. At the SBT, each pair constructed one to three lodges (Harrington et al., 2015). Depending on the bank substrate and topography, beavers can alternatively live in burrows with a submerged underwater entrance that they dig into the riverbank. Beavers also build dams, allowing them to transform a largely terrestrial habitat into an aquatic one. Although beavers will always create a lodge/burrow, they will not always build a dam. Beavers construct dams to locally increase the water depth, mainly in order to improve access to foraging grounds and submerge lodge/burrow entrances thereby reducing predation (Figure 1.3) (Muller-Schwarze, 2011). Dams are typically constructed in small rivers that are <6 m wide, <0.7 m deep and in low gradients generally (Hartman & Törnlöv, 2006). Researchers have therefore been able to develop models to predict their location and density, with some sites in Britain being suggested to support up to 30 dams/km (Graham et al., 2020).

The main predators of the Eurasian beaver are humans and wolves (Rosell & Czech, 2000; Gable et al., 2018a). Research has documented that wolves can deviate from their typical hunting strategy to specifically ambush beavers (Gable et al., 2018b). Direct observations of beaver predation are rarely recorded. This is likely due to the timing (i.e., dawn/dusk) and the location of a kill (dense woodland), as well as the lack of evidence (a carcass). Other less frequent mammalian predators include lynx, otter, (*Lutra lutra*), red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) (Janiszewski et al., 2014). In Scotland, wolves have been extinct since the 18th century and lynx have also been absent since the late medieval period (Yalden, 1999). Although otters, fox and pine marten are all (relatively) common mammal species in Scotland, they are unable to predate adult beavers in such numbers that would regulate their population.

Figure 1.3. Photo of a typical active beaver pond, with lodge on the left bank and food cache/feeding station as a pale stick platform on the right. Localised dams have raised the water table and created a wetland (K Wilson, May 2021).

Beavers are strictly herbivorous and focus all of their terrestrial browsing along stretches of riparian woodland. They will readily select semi-aquatic and aquatic plants depending on their foraging environment, but primarily in the summer months when they are most abundant (Law et al., 2014). Species such as saw sedge (*Cladium mariscus),* common club-rush (*Schoenoplectus lacustris*) and white-water lily (*Nymphaea alba)* are commonly taken in Scotland (Willby et al., 2014). In autumn and winter, beavers will cut down or ‘fell’ trees using their strong incisors, leaving behind a characteristic conical stump marked with visible teeth marks, surrounded by tree shavings (Figure 1.4). The bark (including the phloem and cambium), twigs, shoots and leaves are then stripped from the wood to serve as their main food source. They will often cut up smaller branches and transport them into one area (often on/near the water's edge for an easy escape from terrestrial predators) to feed on – a behaviour which aligns with central place foraging theory (Haarberg & Rosell, 2006; Raffel et al., 2009). However, central place foraging does not always occur in every beaver territory, especially if a plentiful food resource is available within close proximity to the water (Law et al., 2014).

Beavers are highly selective in terms of the species and size of tree stems that they forage which leads to their label as 'choosy opportunistic generalists' (Vorel et al., 2015). A study by Haarberg and Rosell (2006) revealed that beavers fed on a total of 29 different tree species in Norway. Most studies have found willow to be strongly favoured (Vorel et al., 2015; Janiszewski et al., 2017; Wazna et al., 2018) but other regularly selected species include birch (*Betula* spp.), aspen (*Populus* spp.) and hazel, (*Corylus avellana)* (Janiszewski et al., 2017; Mikulka et al., 2022). Conifers tend to be avoided due to their unpalatable levels of plant metabolites (Johnston, 2017) but small numbers are often taken at some sites depending on local woodland composition. In areas where beaver territories border arable farmland, beavers can also supplement their diet with a variety of crop species such as wheat (*Triticum* spp.), oats (*Avena* spp.) and sugar beet (*Beta vulgaris*), although this behaviour is relatively rare (Mikulka et al., 2020; Lodberg-Holm et al., 2022)

Tree foraging preferences in beaver are thought to be based on nutritional quality and ease of handling (Doucet & Fryxell, 1993; Nolet et al., 1994). For example, willows are said to be favoured by beavers because their leaves and bark are more easily digested (Fryxell et al., 1994) - and not simply because these trees grow closest to the water's edge. Willow bark is also more easily stripped from its wood (Klich, 2017). Although willow was the most preferred species by beaver in the study by Haarberg and Rosell (2006), the majority of their diet actually comprised alder (*Alnus* spp.). The lower number of willow stems at the site had been completely utilised by beavers, leaving the more abundant, yet less digestible, alder. This pattern is consistent with other beaver foraging studies (Goryainova et al., 2014; Janiszewski et al., 2017; Wazna et al., 2018) and highlights that foraging preferences of beavers depend on the availability and diversity of the local riparian zone which could be highly site-specific.

As central-place foragers, they typically choose a higher number of smaller diameter tree stems closer to the water and fewer, larger diameter stems as distance from the water increases (Haarberg & Rosell, 2006). The majority of beaver browsing is therefore typically recorded within 10m of the water's edge (Janiszewski et al., 2012; Wazna et al., 2018; Jackowiak et al., 2020) and on trees stems <10cm in diameter (Misiukiewicz et al., 2016; Janiszewski et al., 2017). Studies have shown that foraging distance from the shore may be shorter in areas with predators and human disturbance (Jackowiak et al., 2020), but longer in areas of poor habitat quality where beavers have to venture further for their preferred species (Donkor & Fryxell, 1999; Wazna et al., 2018).

Figure 1.4. Fresh (<1 month) beaver-felling of alder, *Alnus* spp., trees showing typical conical shaped stump marked by teeth indentations and surrounded by wood shavings (K Wilson, November 2020).

1.2.3. Beavers as ecosystem engineers

Ecosystem engineers are species that can directly (or indirectly) influence the availability of resources for other species. As a result, they can modify, maintain and/or create habitats (Jones et al., 1994). For example, woodpeckers (Picidae) are considered ecosystem engineers due to their pecking behaviour which creates tree cavities that can be exploited by other birds, mammals, and invertebrates (Aitken & Martin, 2007). Beavers are recognised as ‘ecosystem engineers’ primarily due to their ability to structurally modify riparian woodlands through two main activities: the felling of trees and the construction of dams.

Beaver damming can inundate terrestrial habitats, including woodland, with tree-species-specific impacts, as well as, potentially, restricting access to other herbivores (Jones et al., 2009). Damming activity can lead to an improvement in both flow attenuation and downstream water quality due to fine sediment and nutrient storage (Puttock et al., 2017, 2018). Tree felling by beavers elicits regenerative responses, whereby secondary shoots grow from the beaver-cut stump as a natural form of coppicing (Figure 1.5). Studies in Scotland documented that 77-86% of beaver-felled willow trees resprouted secondary shoots (Jones et al., 2009; Iason et al., 2014). Beaver felling activity can have a thinning effect on woodlands. Gaps are created in otherwise relatively dense riparian woodlands, which can create localised well-lit patches that support tree seedling recruitment (Nummi & Kuuluvainen, 2013) and in turn can support significantly increased species richness of graminoid plants (Law et al., 2017)

Tree felling by beaver can also result in a higher abundance of deadwood in areas of active foraging, providing additional nutrient input (Thompson et al., 2016) and habitat for saprophytic invertebrates (Seibold et al., 2018). The combination of increased light availability to the ground layer, coupled with decreasing competition for soil nutrients as a result of deadwood inputs, could also increase net primary productivity of existing non-preferred woody species (Johnston & Naiman, 1990). Studies have offered snapshot insights or hypothesised how the selective foraging preferences of beavers could have cascading effects on riparian woodlands (Jones et al., 2009). By actively removing trees of specific species and diameter over time, and at particular distances from the shore, woodland composition may be altered (Johnston & Naiman, 1990; Stringer & Gaywood, 2016).

Figure 1.5. Resprouted willow (*Salix* spp.) tree following beaver felling in Knapdale Forest. Stump visible in lower centre of photograph (K Wilson, April 2021).

By creating natural and complex environments, opportunities are established for other species. Beaver-modified landscapes support higher biodiversity than areas which are uninhabited by beavers (Stringer & Gaywood, 2016). Beaver ponds that arise from dam building (Figure 1.6) are heterogeneous, shallow, standing water habitats that have been shown to benefit a diverse range of taxa (Nummi & Hahtola, 2008; Law et al., 2016; Nummi et al., 2019; Wathen et al., 2019; Dalbeck et al., 2020). These observations highlight the potential for beavers as providers and regulators of ecosystem services and explain their increasing use in ecological restoration projects across Europe and North America (Justice et al., 2017; Brown et al., 2018; Gorczyca et al., 2018). However, from an anthropogenic view, the engineering abilities of beavers are not always beneficial and can lead to human-beaver conflict (Auster et al., 2021). In populated and intensely-modified habitats, a dam can lead to flooded pathways, threats to transport infrastructure or impede drainage of agricultural land.

Tree felling can also result in large obstructions that block roads, or the damage of prized ornamental trees (Campbell-Palmer et al., 2016).

To date, no long-term studies (>10 years) have examined how the highly selective woody stem foraging of Eurasian beaver can influence riparian woodland composition, structure, and functioning. In North America, research has highlighted changes in tree species composition following prolonged selective beaver browsing (Johnston, 2017) Similar findings have been illustrated by a long-term beaver browsing model which predicted that selective foraging by beaver creates a more diverse plant structure over time (Peinetti et al., 2009). Studies of habitat modification by beavers in Scotland are relatively short (<10 years) when compared to the length of their extirpation (>400 years) leaving uncertainty over impacts and management needs. Current studies may therefore only be providing a snapshot of the primary effects their modification is having on their habitat. It is therefore essential to understand what long-term effects beaver modifications are having on woodland structure and composition in Scotland via further investigation before being able to predict any cascading ecosystem effects. This is particularly applicable in areas where human activities have led to significant landscape changes in the beavers' absence (Brown et al., 2018; Hewett et al., 2020).

Figure 1.6. Actively maintained beaver dam (12m wide, 1.5m tall) bordering agricultural grassland in Perthshire (K Wilson, November 2021).

1.3. Deer and vegetation dynamics

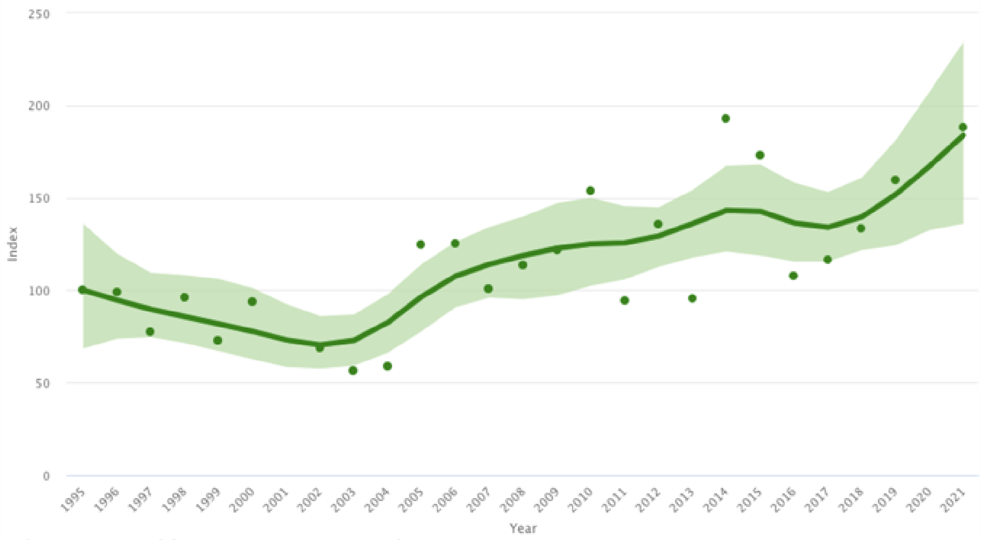
1.3.1. Deer population & distribution

Around 90% of Europe is inhabited by up to five species of native, wild ungulate including red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), reindeer (*Rangifer tarandus*), wild boar, and moose (Linnell et al., 2020). Roe deer are the most extensively distributed and the latest estimates suggest that they occupy 74% of the entire continent (Linnell et al., 2020). The extensive distribution of wild ungulates is paralleled by their abundance, which has undergone exponential growth since the 1960s (Apollonio et al., 2010). Red and roe deer are the most common European ungulate species (Linnell & Zachos, 2010) and are the two species that are the most overabundant in woodlands (Carpio et al., 2021). This overabundance has generally been attributed to a lack of large apex predators as well as changes in silvicultural practices (Carpio et al., 2021). Deer population sizes are notoriously difficult to assess (Morellet et al., 2010) especially in woodlands at a localised scale (Smart et al., 2004). Assessing population sizes can utilise direct methods such as visual counts, or indirect methods such as counting dung or tracks in snow (Mayle et al., 1999).

In Scotland, roe deer are the most common deer species in terms of their distribution, but red deer are the most common in terms of abundance. Two non-native deer species are also present in smaller numbers: fallow (*Dama dama*) and sika deer (*Cervus nippon*). Much like elsewhere in Europe, deer populations have experienced a steady increase in recent decades (Figure 1.7), which has been largely attributed to Scotland's increase in tree cover from 6.6% to 18% of total land area during 1947 to 2011 (Scottish Government, 2019). The exact number of wild deer in Scotland today is unknown, but the latest estimates suggest that there are 360,000-400,000 red deer and 200,000-350,000 roe deer (Pepper et al., 2020). General figures of 10 deer/km^2 (species unspecified) are reported (Albon et al., 2017).

Due to the lack of large predators, deer populations in Scotland (and elsewhere in Europe) are managed predominantly through culling. Cull records are reported to NatureScot annually and are compiled on a national basis in terms of three habitat types: open hill, agricultural and woodlands. Around 60% of annual roe deer culls are in woodlands whereas red deer are predominantly culled on the open hill (NatureScot, 2016) as reflects their main distribution. Although riparian woodlands have been specifically recognised as suitable deer habitat (Prior, 1995; NatureScot, 2016) there is very little data available on the deer populations that utilize it.

a) Red deer (*Cervus elaphus*)



b) Roe deer (*Capreolus capreolus*)

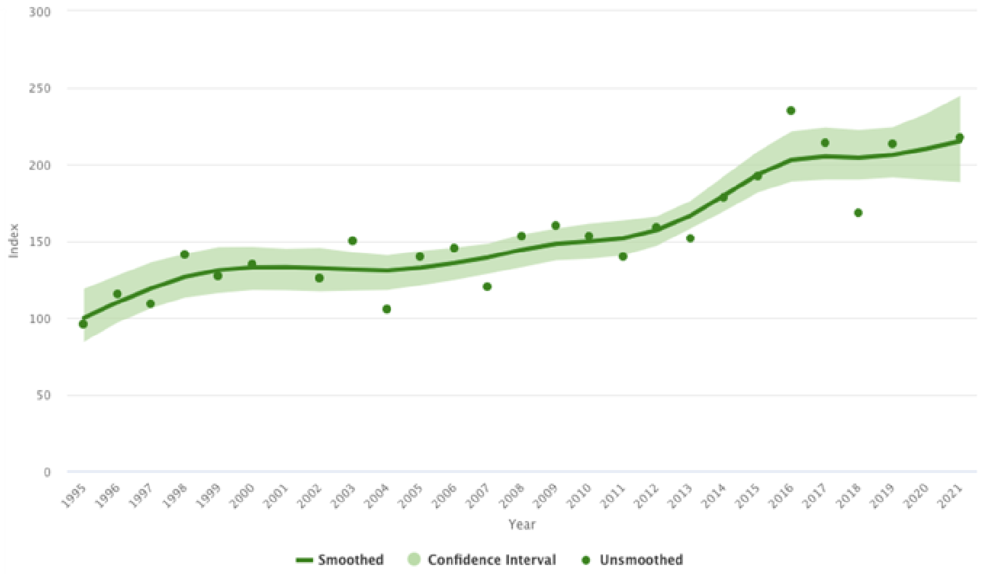


Figure 1.7. Index of a) red deer and b) roe deer sightings for 1995-2015 in Scotland from the British Trust Ornithology's annual breeding bird survey data. All values are indexed relative to the baseline year value of 100. Adapted from Harris et al., (2021).

1.3.2. Deer foraging ecology

Ungulates are generally classified into three groups based on their foraging ecology. These groups are (i) concentrate feeders (i.e., browsing species), (ii) grazers (species that mostly feed on grasses); and (iii) intermediate feeders (species that browse and graze) (Hofmann & Stewart, 1972). Roe deer are considered as 'concentrate selectors'

(Hofmann, 1985) since they focus their feeding on browsing plants of higher nutritional quality (Prior, 1995). Their diet encompasses a diverse variety of plant species but mainly the buds and leaves of trees and shrubs, as well as herbs (Ratcliffe & Mayle, 1992). Research has shown that roe deer prefer to browse plants around their shoulder height (typically 60-75cm) (Nichols et al., 2015). Most roe deer forage alone, or in groups of three-four individuals, within small home ranges typically no larger than a square kilometre (Lovari et al., 2007). They favour woodland gaps and edges but will also forage in open agricultural farmland, and even some urban areas (Putman et al., 2011). Riparian woodlands have been identified as optimal roe deer habitat due to their plant diversity (Barančeková, 2004) and connectivity to the wider landscape (Olson et al., 2004).

Red deer on the other hand are considered ‘intermediate grazers’ and rely on shrubs, grasses, sedges, and rushes, as well as tree shoots. Both red and roe deer increase the proportion of woody plants in their diet during winter when there is a lack of other fresh vegetation (Spitzer et al., 2020). Red deer are notably larger (1-1.5m shoulder height) and can browse material up to a height of 2.3m in the canopy (Nichols et al., 2015). Red deer graze in large single-sex groups for most of the year, favouring open hill moorland habitat, but also woodland edge (Clutton-Brock et al., 1982). The habitat use of red (and roe) deer is considered to be strongly determined by the availability of forage, shelter, and climate (Latham et al., 1997; Palmer & Truscott, 2003; Borkowski & Ukalska, 2008). Human disturbance can also play a role in red deer distribution (Marion et al., 2021). Although there are ample studies that detail red deer habitat use of woodlands (Krojerova-Prokesova et al., 2010; Heurich et al., 2015; Romportl et al., 2017), there is very little research on their use of riparian woodlands specifically, which remains largely unknown.

1.3.3. Deer effects on riparian woodland vegetation

Like beavers, ungulates are also considered ecosystem engineers due to their ability to modify woodland habitats (Smit & Putman, 2011; Ramirez et al., 2021). Deer play a role in seed dispersal (Iravani et al., 2011) and nutrient input (via urine and dung) (Riesch et al., 2022). Research has even demonstrated that changes in woodland vegetation density from deer browsing can improve sound transmission of woodland bird song (Boycott et al., 2019). Despite these benefits to other species, the impacts of deer browsing in woodlands are generally detrimental – both ecologically and economically (Putman et al., 2011).

Deer can shape the structure and dynamics of woodland vegetation through browsing, trampling, stripping, and fraying. The main concern is the browsing by deer on coppiced shoots, seedlings, and saplings of trees before they can naturally replace the loss of mature trees (Hester et al., 2010; Ramirez et al., 2018). Significant damage can occur in coppice woodlands from deer browsing on the fresh shoots that sprout after cutting (Joys et al., 2004; Kirby et al., 2017). Deer browsing can also lead to changes in woodland tree and ground vegetation species composition over time, shifting initially diverse woodlands towards a community dominated by browsing-tolerant species equipped with defence chemicals or thorns (Kuijper et al., 2010; Kirby et al., 2022).

The effects of deer browsing on individual plants are highly context dependent and vary with plant species, age and the parts that are browsed, in addition to the intensity and frequency of the browsing itself (Gill, 1992b; Hester et al., 2010). Generally, deer browsing of leader shoots can significantly reduce tree height and lead to shrub-like trees with stunted growth (Crawley, 1984; Kupferschmid, 2017). Alternatively, if vulnerable leader shoots can grow quickly out of deer reach, browsing of lateral shoots/foliage may produce taller trees with fewer leaves and side branches (Peinetti et al., 2001; Guillet & Bergström, 2006). These profound changes in individual tree stature arising from deer browsing can have long-lasting ecosystem-level impacts on woodland biodiversity, structure, and function (Gill & Fuller, 2007; Eichhorn et al., 2017; Ramirez et al., 2021) which are often difficult to reverse (Tanentzap et al., 2012).

Although the detrimental impacts of browsing by overabundant deer have been discussed at length in many European reviews (Gill, 1992b; Hester et al., 2010; Reimoser & Putman, 2011; Ramirez et al., 2018) there are few, if any, studies on deer impacts on specifically riparian vegetation in a European context. A few riparian studies in North America have found that elk (*Cervus canadensis*), and mule deer (*Odocoileus hemionus)*, substantially reduced the rate of tree growth in degraded riparian woodlands, impeding their restoration (Opperman & Merenlender, 2000; Brookshire et al., 2002; Averett et al., 2017). This research now needs applied to a

European context to assess the impacts of ungulate herbivory on riparian woodlands, and how this interacts with the effects of the other key herbivores that inhabit them.

1.4. Beaver-deer interactions

All native Scottish broadleaved trees are able to coppice or sucker following cuts or stress (Koop, 1987). High resprouting rates associated with beaver herbivory have been reported in a range of broadleaf species (Jones et al., 2009; Iason et al., 2014). Roe deer are also known to browse the nutritious, young shoots of many broadleaf species (Ratcliffe & Mayle, 1992). This forage may therefore offer an attractive resource for deer that would have been absent or scarce in un-coppiced woodlands prior to the beaver's reintroduction (Figure 1.8). Research from the five-year study at the SBT reported deer browsing on 68% of beaver-felled trees that had produced secondary shoots (Iason et al., 2014), inferring that deer will indeed readily utilise this resource. However, if the regrowth from beaver-felled tree stems is repeatedly eaten by deer, there could be a simplification in the structure of the woodland, and potentially deterioration or even long-term loss of the habitat.

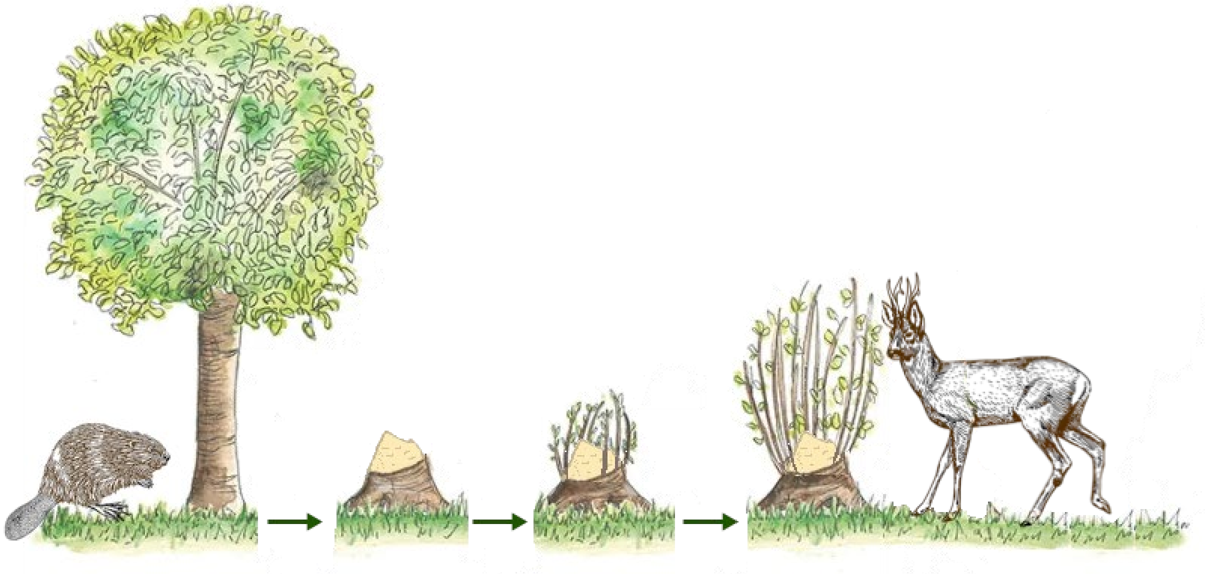


Figure 1.8. Diagram demonstrating how tree-felling by beaver (*Castor* spp.) can promote coppice-like regrowth over time, which can increase available leafy forage resources to browsing deer (Cervidae) (not to scale). Modified from illustration from Woodland Trust (2018).

Another hypothesis is that deer could exacerbate the structural and compositional changes that naturally occur in a beaver-modified forest. Research from the SBT demonstrated that tree felling by beaver influenced the structure of the woodland by encouraging gap and edge creation in a closed canopy (Iason et al., 2014). Red and roe deer prefer to forage along woodland edges and actively avoid closed woodland canopies (Clutton-Brock et al., 1982; Ratcliffe & Mayle, 1992). Furthermore, an increase in graminoids or herbs associated with higher light conditions may increase the abundance of forage for both red and roe deer. Therefore, beaver modification of some woodlands could potentially result in a habitat that is more suited to the habitat and feeding preferences of deer, ultimately influencing their distribution.

In North America, potential changes in forest structure and regeneration processes due to beaver-deer interactions have been illustrated. For example, Baker et al. (2012) developed a process-oriented model to investigate beaver-elk interactions in a willow woodland. They found that over time, intense elk browsing of beaver-cut willow produces smaller, shrub-like vegetation with a high percentage of dead stems over time. Another study observed that willow could recover 84% of its biomass after simulated beaver-felling, but only 6% when elk browsed the cut plants (Baker et al., 2005). Woodland stem density and regeneration processes have also been shown to be reduced by beaver-elk interactions (Hood & Bayley, 2008a; Loeb & Garner, 2022). However, very few studies have examined the overlap between beaver and deer in European riparian woodlands (Figure 1.9), highlighting a significant knowledge gap. As most woodlands in Scotland (and Europe) support large ungulate populations, plant-herbivore interactions are likely to be intensified. Closing this knowledge gap is particularly critical when one herbivore has been absent for centuries (beaver) and the other has undergone pronounced expansion (deer), and this scenario is set against the background of a general desire to expand woodland cover.

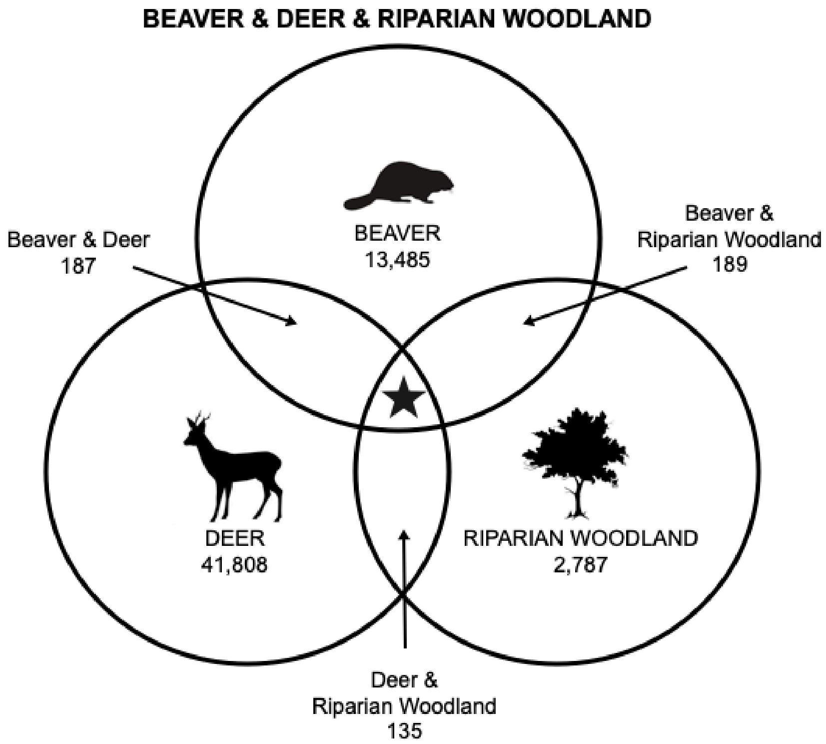


Figure 1.9. Venn diagram summarising the outputs of a literature search on Web of Knowledge for keywords “beaver”, “deer”, and “riparian woodlands/forests” in the last 20 years. Number denotes the number of studies returned in the search. Only two studies were found for an overlap between beaver, deer, and riparian woodlands.

1.5. Research overview

As discussed, riparian woodlands are high value habitats in terms of biodiversity support or mitigation of climate change impacts but can be dramatically altered by large browsing herbivores. Restoring lost interspecific interactions can offer a tool for repairing degraded habitats, however ecosystems can be highly sensitive to species reintroductions or removals. Beavers and deer both clearly exert their own unique influence on riparian woodlands through browsing, yet no published research in Europe has so far investigated the relationship between beaver and deer browsing and how it could impact woodland structure, composition, and regeneration processes. Closing this knowledge gap is increasingly important when beavers have been absent for centuries and deer have undergone pronounced expansion. A detailed understanding of this rekindled interspecific interaction is therefore essential to predict potential ecological effects on the wider landscape. It will also allow timely management intervention based around evidence of the nature of this interaction for the future.

The following chapters in this thesis outline research that examines beaver-deer interactions in Scottish riparian woodlands. Chapter 2 assesses the long-term (>10 years) effects of beaver activity on woodland vegetation composition and structure, including ground vegetation. Chapter 3 determines how tree felling by beavers affects resource availability for deer, by examining if tree felling by beaver can promote riparian woodland regeneration before investigating the nutritional and morphological qualities of the regrowth from beaver-felled trees. Chapter 4 assesses how beaver-deer interactions can affect the resource allocation, structure, and growth of riparian woodlands. Finally, Chapter 5 integrates these findings to provide predicted outcomes and management guidance for deer, riparian vegetation, and ecosystem services in the presence of beavers.

CHAPTER 2: EURASIAN BEAVER TREE FORAGING PREFERENCES & THEIR LONG TERM EFFECTS ON RIPARIAN WOODLAND

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2.0. Abstract

The Eurasian beaver (*Castor fiber*) is widely known for its ability to influence riparian woodlands through browsing trees and altering water levels via damming. However, research on the long-term effects of beaver browsing on woodlands is sparse, especially in Europe, leaving uncertainty over impacts and management needs. This study examined beaver tree foraging preferences and their temporal effects on composition, structure, deadwood, and ground vegetation across 28 woodland plots in Knapdale Forest, Scotland. Eleven years after their release, beavers had browsed (i.e., fully, partially felled or gnawed) 24% of tree stems in plots located within 30m of the shore, of which 80% survived (either due to incomplete felling, or resprouting of stems from the base). Birch (*Betula pubescens*) was browsed most frequently, reflecting its overall dominance in the resource, but hazel (*Corylus avellana*), was the most preferred relative to its availability. Browsed stems averaged 6.76 ± 6.24 cm in diameter which was significantly smaller than the overall resource average of 7.78 ± 7.27 cm. Strong spatial patterns of foraging were observed, with 90% of all browsed stems located <10m of the shore. Overall, beaver browsing had no significant effect on woodland species composition and structure over an 11-year period. The abundance of deadwood significantly increased over time and was likely attributed to beaver-induced flooding as opposed to browsing. Ground vegetation cover also increased over time, especially of herbs and graminoids, indicative of reduced shading in canopy gaps created by beaver browsing. Our findings suggest that while beavers can alter their habitat drastically at a small patch scale over a relatively short period through their selective foraging, this effect is not necessarily translated to the riparian woodland scale. These findings can inform both riparian woodland conservation and

beaver management practices, as well as decision making around beaver translocation policies.

2.1. Introduction

The Eurasian beaver (*Castor fiber*) has made a remarkable recovery from its near-extinction following centuries of persecution. From relict, scattered populations totalling around 1200 individuals, beavers have now recolonised most of their former European range with recent population estimates suggesting at least 1.5 million animals (Halley et al., 2021). Their rapid range expansion has been accomplished through protective regimes, reintroductions, and translocations, as well as natural recolonisation (Wróbel, 2020). However, after their long absence, beavers have returned to inhabit fundamentally different landscapes in some areas, including highly populated or intensively farmed regions such as southern England, the Netherlands and NW Germany (Halley et al., 2021).

Beavers can create, modify, and maintain habitats on a landscape scale resulting in their renowned status as ‘ecological engineers’ (Jones et al., 1994). Their process of dam and canal building can transform degraded habitats into a mosaic of complex wetlands by boosting biodiversity and habitat heterogeneity (Law et al., 2019; Willby et al., 2018). In addition to river restoration, beaver dam building can also facilitate flow attenuation, and improve downstream water quality due to fine-sediment and nutrient storage (Law et al., 2016; Puttock et al., 2021). These unique abilities are increasingly being harnessed in river restoration projects (Pollock et al., 2014; Dittbrenner et al., 2018).

As well as transforming the riparian zone through dam building, beavers can alter the structure and species composition of woody vegetation through browsing of trees (Johnston & Naiman, 1990). Tree browsing yields buds, leaves, and bark for consumption, but also the essential raw materials for dam and lodge construction. Beavers are highly selective in terms of the tree species they choose, often preferring willows (*Salix* spp.) and poplars such as aspen (*Populus tremula*) whilst generally avoiding conifers (Haarberg & Rosell, 2006; Vorel et al., 2015) due to their unfavourable levels of plant metabolites (Johnston, 2017). Their diet, however, also reflects the availability and diversity of species in the local habitat, which can be highly site-specific. Although willow may be preferred, local abundance or resource depletion may result in beavers resorting to less readily digestible alternatives such as birch (*Betula* spp.) or alder (*Alnus* spp.) (Haarberg & Rosell, 2006; O′Connell et al., 2008; Jackowiak et al., 2020).

In addition to species, beavers also select trees based on their size. Browsing intensity can therefore vary among different locations within the riparian zone depending on how trees of the preferred species and size are distributed. Beavers adopt a foraging strategy in line with central place foraging theory whereby they venture onto land to cut woody vegetation and transport it back to the safety of water which acts as their 'central place' (Haarberg & Rosell, 2006; Raffel et al., 2009). Therefore, their selection typically involves choosing a higher number of smaller stems closer to the shore and fewer, larger stems as distance from the shore increases (Haarberg & Rosell, 2006). This is thought to involve a trade-off between optimising energy consumption whilst minimising predation risks (Basey & Jenkins, 1995). Research has confirmed most beaver browsing to occur within 10m of the shore (Janiszewski et al., 2013; Iason et al., 2014; Wazna et al., 2018; Jackowiak et al., 2020) with stems <10cm diameter being generally preferred (Misiukiewicz et al., 2016; Janiszewski et al., 2017). However, sometimes central place foraging may not occur if a plentiful food resource is available in close proximity to the shore (Law et al., 2014).

Although beavers can physically alter their territory characteristics remarkably quickly, the ongoing active selection of tree stems of specific species and sizes, at specific distances from water, could drive habitat change over larger spatio-temporal scales. Studies have offered snapshot insights or hypothesised how the selective foraging preferences of beavers could have cascading effects on riparian woodlands over time. For example, diversification of woodland into mixed species, ages, heights, densities, and diameters has been suggested (Johnston & Naiman, 1990; Stringer & Gaywood, 2016). Structural changes such as canopy gap creation and density reduction are hypothesised to facilitate seedling recruitment or result in increasing ground cover of grasses and herbs due to the greater light availability (Rosell et al., 2005; Nummi & Kuuluvainen, 2013). Increases in abundance of fallen deadwood, now a scarce microhabitat in many modern woodlands, have also been highlighted (Nummi &

Kuuluvainen, 2013; Thompson et al., 2016). However, to date no long-term studies (>10 years) have examined how the highly selective woody stem foraging of Eurasian beaver can influence riparian woodland composition, structure, and functioning.

This study aims to investigate the long-term effects of beaver browsing on riparian woodlands by using archive tree survey data collected by Iason et al. (2014) between 2010-2013, and new data collected between 2018-2021, to monitor change over an 11-year period following beaver reintroduction to Knapdale Forest, Argyll, Scotland. In this study, the foraging preferences of Eurasian beaver were investigated by determining the characteristics of beaver-browsed trees in riparian woodland. The following hypotheses were then tested: long-term beaver herbivory i) alters tree composition and woodland structure, and ii) increases the abundance of deadwood and ground vegetation cover. We further hypothesised that observed effects of beaver browsing will diminish with increasing distance from the shore.

2.2. Methods

2.2.1. Study site

Fieldwork took place in a ~7km² area of Knapdale Forest, located in the west of Scotland (56°1′12″N, 5°31′12″W). The area comprises around 12 several small freshwater lochs (lakes) and their network of inflows and outflows which are bordered by well-established riparian woodlands. Prior to the beaver reintroduction in 2009, considerable areas of conifer plantation were cleared, particularly near the lochs, with downy birch regrowth taking their place in most areas (Moore et al., 2010). The riparian woodlands accessible to beavers typically extend up to 50m from the shoreline. They are now dominated by mature common alder (*Alnus glutinosa*) and mature/regenerating downy birch (*Betula pubescens*). Other less-common species in the riparian zone of Knapdale Forest include rowan (*Sorbus aucuparia)*, hazel (*Corylus avellana*), ash (*Fraxinus excelsior)* and goat willow (*Salix caprea*). Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) are also present in small numbers along the shorelines (Armstrong et al., 2004; Moore et al., 2010). Beyond the broadleaf riparian zone in Knapdale Forest lies large areas of mature, dense conifers which are generally inaccessible to beaver. These plantations are well-established and characterised by species including Norway spruce (*Picea abies*), Scot's pine (*Pinus sylvestris*) and Sitka spruce.

Knapdale Forest was the site of the Scottish Beaver Trial (SBT), a government-sanctioned trial reintroduction of Eurasian beavers imported from Norway whose population and its effects were formally monitored scientifically for five years between 2009-2014. In 2009-2010, a total of 16 beavers comprising five family units/pairs were released on Lochs Coille-Bharr, Linne, Creagmhor and Un-named loch (south)/Lochan Buic. At the end of the trial period, at least eight of the originally released animals remained, as well as one wild-born kit (Harrington et al., 2015). The next large-scale population survey was undertaken in 2016 and showed a minimum of eight animals occupying three lochs: Lochan Buic, Loch Coille-Bharr and Loch Losgunn. The reason as to why the population declined after the initial release is not fully understood. The decline is suspected to be a result of low reproductive success in a small population susceptible to stochastic events (Harrington et al., 2015). A reinforcement project then took place during 2017-2020 to supplement the Knapdale population with translocated beavers. These originated from Tayside, east Scotland, where a large population of Eurasian beavers has established since the early 2000s founded on escapees from private collections and unauthorised releases. In total, 21 beavers were released into Knapdale during this latter period and post-monitoring surveys showed all suitable lochs were occupied by the end of the project in 2020 (Dowse et al., 2020).

2.2.2. Study design

A total of nine woodland transects located in beaver territories on separate lakes throughout Knapdale forest were studied. All transects were perpendicular to the shoreline and comprised two to four 4m x 10m plots (32 plots in total), based on the available width of the riparian woodland (see plot details in Appendix 2.1). Plots were located at 0–4m, 6–10m, 16–20m and 26–30m from the loch shore. Loch shore positions can shift in relation to weather, season and localised beaver damming therefore plot locations were fixed using wooden set semi-permanent markers.

Five of the transects (comprising 16 plots) were selected from a wider set of 32 woodland transects established in 2009-2010 by Iason et al. (2014) as part of SBT monitoring research. These transects (herein referred to as ‘SBT transects/plots’) were chosen at random and included beaver territories on the following lochs that had remained active since their establishment: Linne, Creagmhor, Coillie-Bharr, Buic and Un-named loch (south). During the Iason et al. (2014) study, all woody stems with a diameter >1cm were labelled with uniquely numbered aluminium tags. We re-surveyed these SBT transects in 2018-2021 to track long-term changes in woodland composition and structure, as well as ground vegetation.

To incorporate areas of riparian woodland supporting more recently established beaver territories and investigate beaver foraging preferences, we established five new transects (comprising 16 plots) within the survey area using the same methodology in November 2018. These transects (herein referred to as ‘new transects/plots’) were located at Loch McKay, Loch Barnluasgan, Loch Losgunn, Faery Isles and Loch Laraiche (Figure 2.1). Since no beaver field signs were recorded on Laraiche following their release, this transect data (4 plots) was removed from data analyses. All other transects had nearby varying intensities and ages of beaver activity including browsing, damming, and digging (<100m) as well as an active lodge (<500m). New plot locations were fixed with wooden canes. Although there are no records that detail the exact year of every territory occupation after the SBT ended in 2013, the new transects included beaver territories that were not occupied by beavers at the end of the SBT. These territories were therefore estimated to be established sometime between 2014 and 2018 (i.e., short-term occupancy). The SBT transects included territories that had remained active since their establishment in 2009-2010 (long-term occupancy).

It was not always possible to access or identify the edge of the shore due to flooding therefore transect surveys were started at the closest point to the water that allowed safe working. Two plots (0-4m and 6-10m) in one SBT transect could not be surveyed at all during 2018-2021 due to complete inundation from localised beaver damming and are henceforth referred to as sunken plots. Records from 2013 archive data indicate there were 30 tree stems present. They could not be included in our statistical analyses due to lack of comparable data. However, they were represented in graphical analyses of tree mortality. Plots at 16-20m and 26-30m along this transect were surveyed and treated as 0-4m and 6-10m respectively in analyses when investigating effects of distance from water.

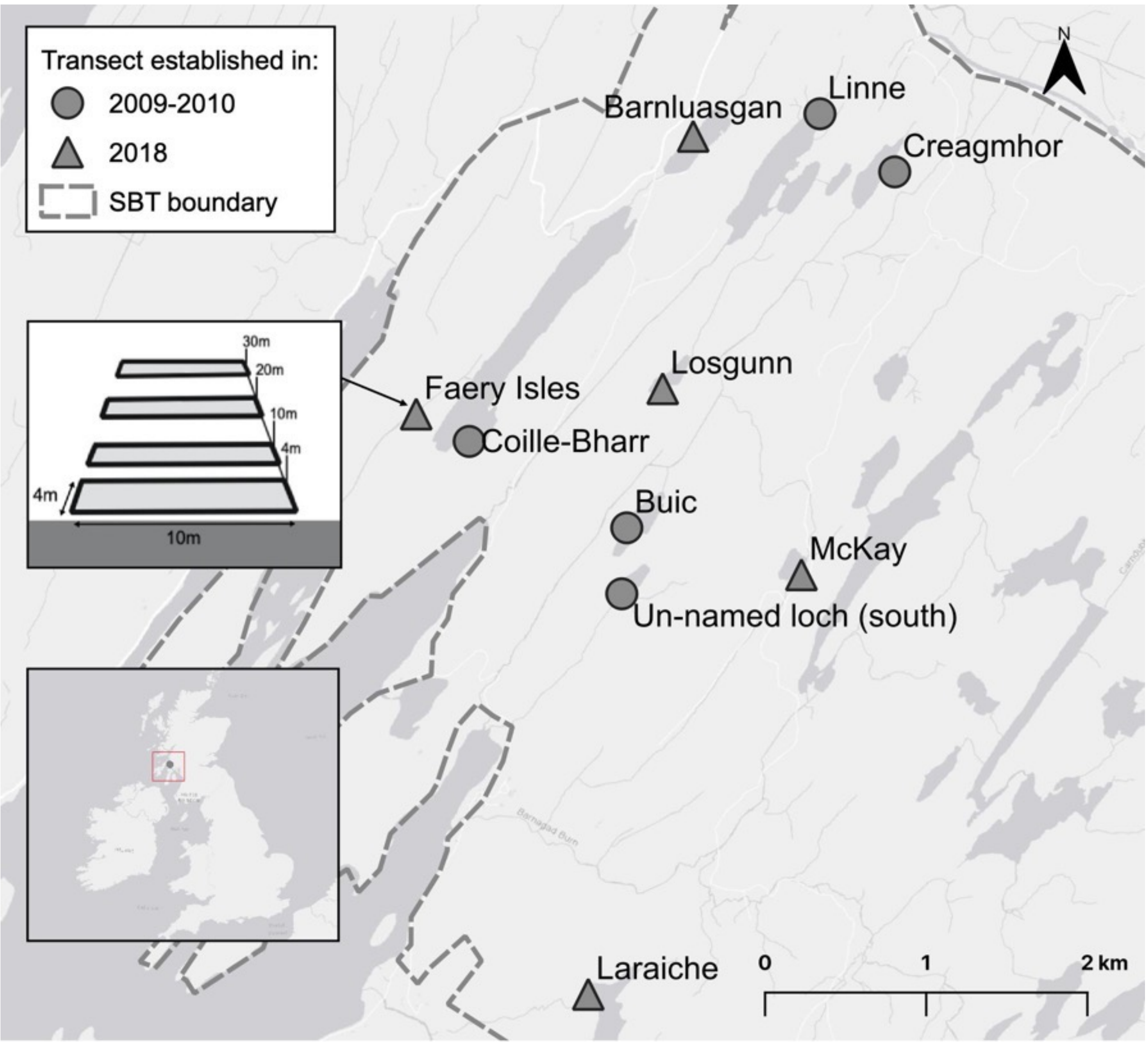

Figure 2.1. Location of ten transects surveyed: five SBT transects established in 2009-2010 and five new transects established in 2018. The ‘Laraiche’ transect was excluded from analyses due to lack of beaver activity. Middle left box denotes the plot layout within transects with dark grey representing water. Dashed grey line represents approximate Scottish Beaver Trial (SBT) boundary.

2.2.3. Woodland surveys

Woodland survey methodology was adapted from Iason et al. (2014) to allow a reliable temporal and spatial comparison of woodland across transects. We surveyed all transects (SBT and new) five times in total between 2018 and 2021. Surveys took place over one week and were carried out in Nov 2018, April 2019, Nov 2019, April 2021, and Nov 2021.

In woodland plots, every woody stem greater than 1.3m in height and 1cm in diameter was recorded as a tree stem. For each tree stem, a series of measurements were taken. Species identity and tree diameter (at 20cm height) were noted. Codes were assigned to species and are listed in Table 2.1. Tree stems were assigned to one of ten categories according to their 'status', primarily based on the type or presence/absence of beaver browsing (Table 2.2, Figure 2.2). Tree tag numbers were noted when possible (in the SBT plots only). A record was made as to whether a stem appeared to be alive, or dead. Upright, dead stems were classed as 'standing deadwood' in analyses and could be one of the following statuses: Up, B_up, B_p, and N_p (see descriptions in Table 2.2). Stems recorded as B_log or N_log were classed as 'fallen deadwood'.

If a tree stem had been browsed by beavers, the number of resprouted secondary shoots were counted. The mean and maximum length of these shoots (cm) were measured and if a shoot had grown >130cm in height and >1cm in diameter, it was recorded as a new tree stem. Height of cut (cm) from the ground was also noted for beaver-browsed trees. This included the highest part of a remaining stump, or the middle-point of the gnawing on any partially gnawed stems.

Ground vegetation cover was measured in SBT transects in two 2 x 2m quadrats (sub-plots) located in the top left and bottom right corner of each plot when facing the shore. Six categories of vegetation were recorded, each to the nearest 5% cover and included: graminoids (grasses, rushes, or sedges), bryophytes (mosses and liverworts), ferns, dwarf shrubs, and herbs. Plot ground cover values could exceed 100% as some categories of ground vegetation overlapped each other. Raw values were averaged across the two quadrats to generate a single value for each plot, to allow consistency with the 2010 dataset.

Table 2.1. Codes for recorded tree species, adapted from Iason et al. (2014).

Common Name	Scientific Name	Species Code
Sycamore	*Acer pseudoplatanus*	Acepse
Common alder	*Alnus glutinosa*	Alnus
Downy birch	*Betula pubescens*	Betpub
Hazel	*Corylus avellana*	Corave
Ash	*Fraxinus excelsior*	Fraexc
Sitka spruce	*Picea sitchensis*	Picsit
Willow	*Salix* spp.	Salix
Rowan	*Sorbus aucuparia*	Sorauc
Western hemlock	*Tsuga heterophylla*	Tsuhet

Table 2.2 Descriptions of tree status categories. Visual representation in Figure 2.2.

Status Code	Description
Up	Upright tree, unaffected by beaver browsing
B_up	Upright tree gnawed by beaver
B_stump	Stump of a tree felled by beaver
B_p	Tree partially felled by beaver
B_cut	Minor branch removed by beaver
B_tree	Coppice from beaver browsed tree that has grown to 1.3m
B_log	Log from tree felled by beaver
N_stump	Natural tree stump from windfall or decay
N_log	Naturally fallen log
N_p	Naturally partially fallen tree

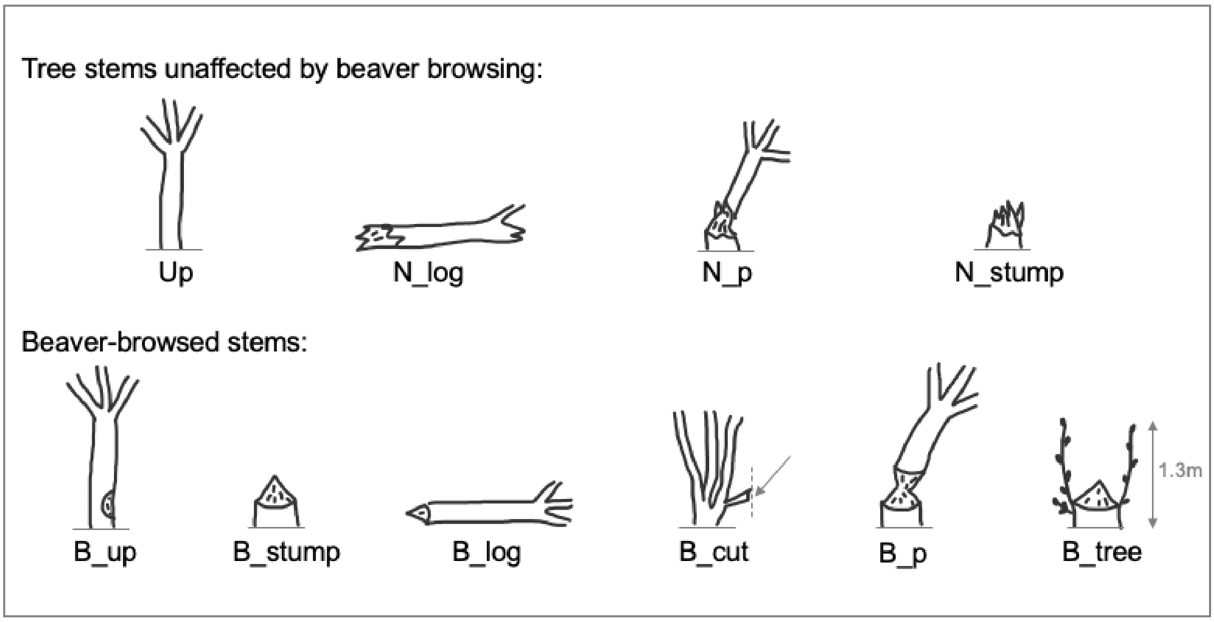

Figure 2.1. Visual representation of tree 'status' categories used to establish types of beaver tree modification. Adapted from Iason et al. (2014).

2.5. Data analyses

Statistical analyses were carried out in R Studio (version 1.4.1103) using packages lme4, vegan, sjPlot and ggplot2. All linear mixed models included a random effect of transect to account for site-specific variability between beaver territories. Response variables were transformed to normal distribution where required, and continuous predictors were mean and centre-scaled. Interactions were tested between explanatory variables and removed when non-significant. Models were selected for performance based on those with the lowest Akaike Information Criterion (AIC) scores. Residuals for all models were tested for normality and met model assumptions.

2.5.1. Foraging preferences

Foraging preferences were investigated across beaver territories that varied in short and long-term occupancy. Woodland survey data from spring 2021 from all nine transects was used in foraging preferences analyses. A Generalised Linear Mixed Model (GLMM) with binomial error distribution and a logit link was used to test whether beaver tree selection for preferred tree species or sizes (diameter; cm) changed with increasing distance from the shore (0-4m, 6-10m, 16-20m, 26-30m). The beaver browsing status (browsed/unbrowsed) of trees was used as the response variable. Whether a territory had a long-term (SBT transects) or short-term (new transects) duration of beaver occupancy was also included as a predictor.

Beaver foraging preferences were further investigated using Ivlev's electivity index (Ivlev, 1962). This entailed applying the following formula: ($E = (B - A) / (B + A)$), where B is the proportion of the trees browsed by beavers belonging to a given diameter class, and A is the proportion of all the trees available to beavers (browsed and unbrowsed in total) belonging within that diameter class. The index varies between -1 (complete avoidance) and +1 (maximum preference). A value around zero suggests a random, indifferent selection where consumption reflects availability. The electivity index (E) was calculated for each diameter class (<5cm, 5–10cm, 10-15cm, 15-20cm and >20cm) across all plots. Electivity analyses were then repeated for tree species where the formula was adapted to compare the species of trees utilised by beavers with the species available. An unpaired t-test was used to compare the diameter of trees browsed by beaver with the diameter of those available.

2.5.2. Woodland change 2010-2021

To determine temporal changes in woodland structure, composition, and ground vegetation, we compared archive data from 2010 with our survey data from 2021 in the five SBT transects only. As three of the SBT transects were first established in 2009 and two in 2010, the 2010 dataset was used as the common starting point. Only one stem across the 28 plots had been partially browsed by beaver in 2010 and was not included in the analyses. Analyses of tree mortality used data from 2010-2013, which was compared to data from 2019-2021. All analyses used data collected in spring unless specified otherwise.

Two paired t-tests were used to compare plot tree stem density (n trees per hectare; n=16) and mean stem diameter (cm; n=16) in 2010 and 2021. To further assess potential structural changes, the relative change in tree stem density (%) and mean stem diameter (%) between 2010 and 2021 were calculated for every plot. These variables were used as responses in two linear mixed models. Plot distance from shore (0-4m, 6-10m, 16-20m, 26-30m) and beaver browsing intensity (%) were included as explanatory variables. Beaver browsing intensity (%) was quantified as the proportion of the total number of available trees stems in a plot that had been browsed. When not acting as the response, the relative change in stem density and diameter were also included as explanatory variables to assess their relationship with each other. Relative change in diameter (%) and stem density (%), in addition to beaver browsing intensity (%), were mean-centred and scaled.

To quantify changes in woodland species diversity, Simpson's Diversity Index (SDI) was calculated for every plot based on the number of stems of each tree species. SDI considers both species richness and relative abundance, generating a value between 0-1 where a higher number indicates a more diverse composition. A paired t-test was then used to compare the SDI plot values between 2010 and 2021 (n=16 pairs).

To compare woodland species composition and stem diameters between 2010 and 2021, nonmetric multidimensional scaling (NMDS) with calculated Bray-Curtis dissimilarities was used. Live tree stems were sorted into three diameter classes of 0-10cm, 10-20cm and >20cm for every species. Stems of standing deadwood were included as a single category in the NMDS analyses (regardless of species or diameter). Permutational multivariate analysis of variance (999 permutations) was then carried out to test for differences in species and diameter composition between years, the effect of distance from the shore (0-4m, 6-10m, 16-20m and 26-30m), and transect (individual lochs).

Change in the abundance of deadwood (standing and fallen) between 2010 and 2021 was assessed using a paired t-test (n=16). Proportion of deadwood (%; square root transformed) was defined as the number of dead stems (including standing stems and fallen deadwood) as a proportion of the total number of both live and dead stems. Stems of fallen deadwood recorded in the woodland (both as result of beaver felling and natural causes) were excluded from all other analyses.

To assess woodland recruitment, the total number of young trees (stems of 1cm diameter) per plot were summed and compared in 2010 and 2021 using a paired t-test. Total tree basal area (expressed as m^2 per ha) is the area occupied by tree stems in a plot. The basal area of each stem was calculated using the formula (basal area = $\pi \times$ stem radius^2) and were summed to give a total stem basal area for each plot. A paired t-test was used to compare total stem basal area per plot (n=16) in 2010 and 2021 to assess change over time.

Finally, to investigate temporal change in ground vegetation cover (%), data were compared from 2011 to 2021. A paired t-test compared the summed abundance of the cover of all ground vegetation types per plot in 2010 and 2021. Five linear mixed models were then used to investigate each vegetation category in detail. The effects of year (2011 or 2021) and distance from the shore on each vegetation category were tested on the following response variables: graminoids, bryophytes, shrubs, ferns, and herbs (% ground cover per plot). Ground cover of ferns and herbs were square root transformed to meet model assumptions.

2.3. Results

2.3.1. Foraging preferences

In 2021, a total of 664 tree stems were recorded across the nine transects (28 plots). On average, beaver browsing was recorded on 19.9% (±21% SD) of the available tree stems across plots with plot-scale browsing intensity varying from 0% to 61%. At the riparian woodland-level, beaver had browsed 25.4% (n=169) of the total available tree stems across the 28 plots. Of browsed trees, the most common type of tree modification was B_stump (66.9%, n=113), followed by B_up (12.4%, n=21), B_cut (11.2%, n=19) and B_p (9.5%, n=16). Trees were browsed by beaver at a mean height of 38.5cm (±11.6 SD, 2–74 range).

Beaver browsing demonstrated strong spatial patterns where a total of 90% (n=152) of all beaver-browsed trees were recorded in plots situated within 10m of the shore (Figure 2.3a). This was further reflected in the proportion of the total available resource, where beaver-browsing intensity (%) was also highest in plots within 10m of the shore (Figure 2.3b). Furthermore, the likelihood of a tree being browsed by beaver significantly declined with distance from the shore ($P<0.05$). Tree selection by beaver was similar in plots regardless of how long the associated territory had been occupied ($P=0.9$) and beaver browsing intensity (%) in the short-term occupancy plots exceeded the long-term occupancy plots in their second and third year of survey (Table 2.3) (see Appendix 2.2 for full model output). Tree selection was also significantly affected by diameter ($P<0.001$). The mean diameter of beaver-browsed trees was significantly smaller (6.76cm ± 6.24 SD) than the mean diameter of all trees that were available to beaver (7.78cm ± 7.27 SD) ($t_{332}=-0.8$, $P=0.04$). Electivity analyses further indicated a decreasing preference for increasing diameter, with trees of 5-10cm diameter being selected the most in proportion to their availability (Figure 2.4).

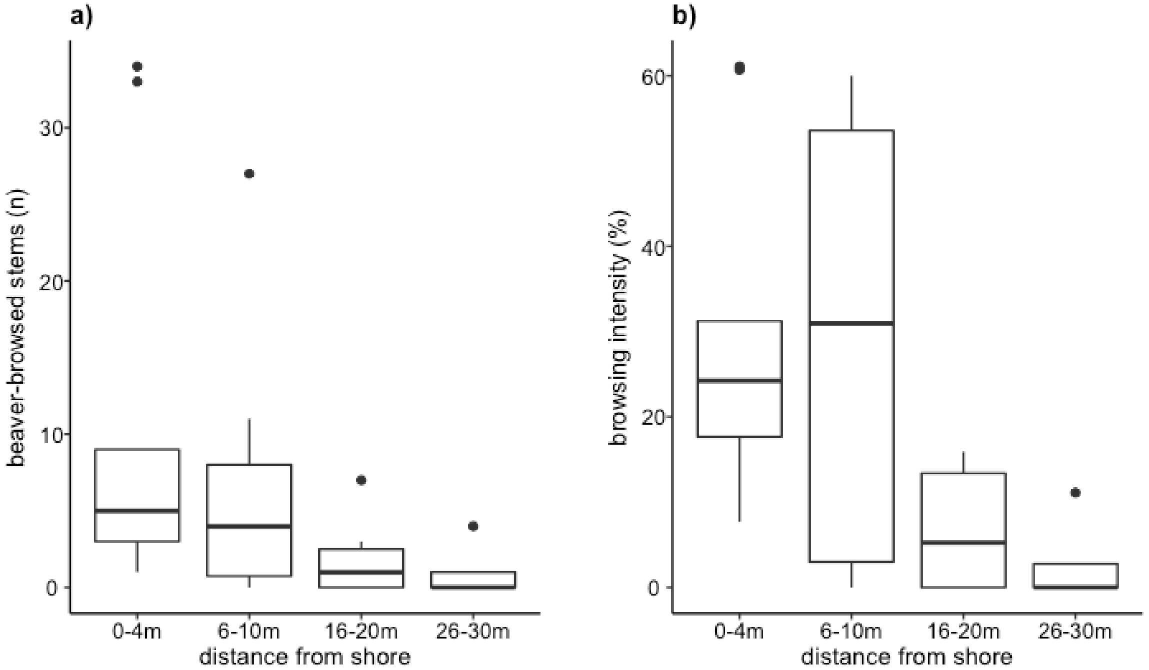

Figure 2.3. Spatial patterns of beaver browsing as a) the number of beaver-browsed tree stems and b) browsing intensity % (the proportion of beaver-browsed stems of all available stems) located in plots at 0-4m, 6-10m, 16-20m, and 26-30m from the shore.

Table 2.3. Browsing intensity (i.e., percentage of total tree stems browsed by beaver) in consecutive years from transects with short and long-term beaver occupancy using May (2019 and 2021) and November (2018) survey data.

Beaver Occupancy	Year	Tree stems (n)	Beaver browsed stems (n)	Browsing intensity (%)	Plots Surveyed (n)
Short-term[a]	2018*	182*	26*	14.3*	12*
	2019	211	37	18.5	12
	2021	250	69	27.6	12
Long-term[b]	2018*	398*	58*	14.5*	16*
	2019	408	73	17.9	16
	2021	414	100	24.2	16

[a] Short-term = beaver territories that were established after the final year of the SBT in 2014.
[b] Long-term = beaver territories that remain active since the beginning of the SBT in 2009/10.
**November survey data was used in calculations for 2018 browsing intensity.*

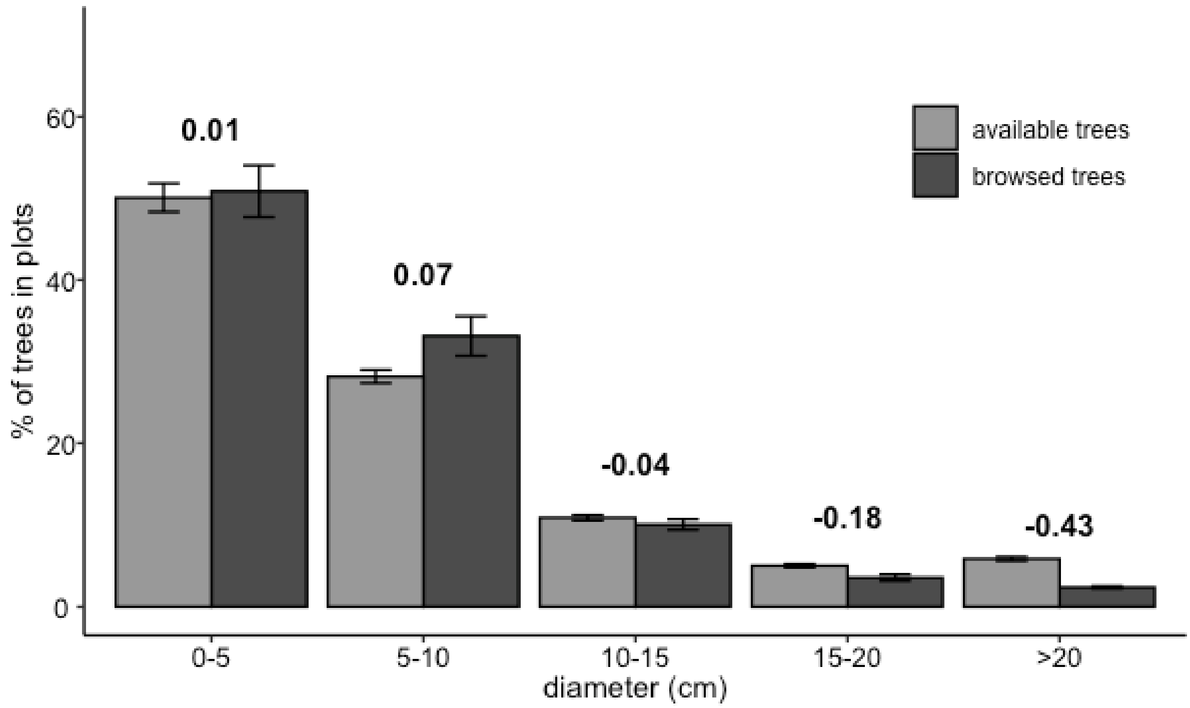

Figure 2.4. Proportion of trees available (light grey) and browsed by beaver (dark grey) per plot in five diameter categories (0-5, 5-10, 10-15, 15-20 and >20cm) with Ivlev's Electivity Index values for all transects. Error bars represent standard error.

Tree selection by beaver was significantly influenced by tree species. Willow ($P<0.001$), hazel ($P=0.01$) and rowan ($P<0.01$) were more likely to be browsed over alder. Downy birch accounted for 65.7% (n=111) of all beaver-browsed trees (n=169), followed by common alder (11.8%, n=20), hazel (8.9%, n=15) and willow (8.3%, n=14). Small numbers of rowan and Sitka spruce stems were also browsed (3.5%, n=6 and 1.8%, n=3, respectively). Although birch and alder were by far the most frequently browsed trees, their mean electivity values were close to zero (E = +0.02 and +0.06 respectively) suggesting indifference or a random selection. Hazel (E= +0.44), rowan (E= +0.21), and willow (E=+0.22) had positive electivity values indicating selection relative to their availability (Figure 2.5). All other species were either rarely exploited, e.g., Sitka spruce (E= -0.09) or avoided altogether, i.e., ash (E= -1.00) and western hemlock (E= -1.00).

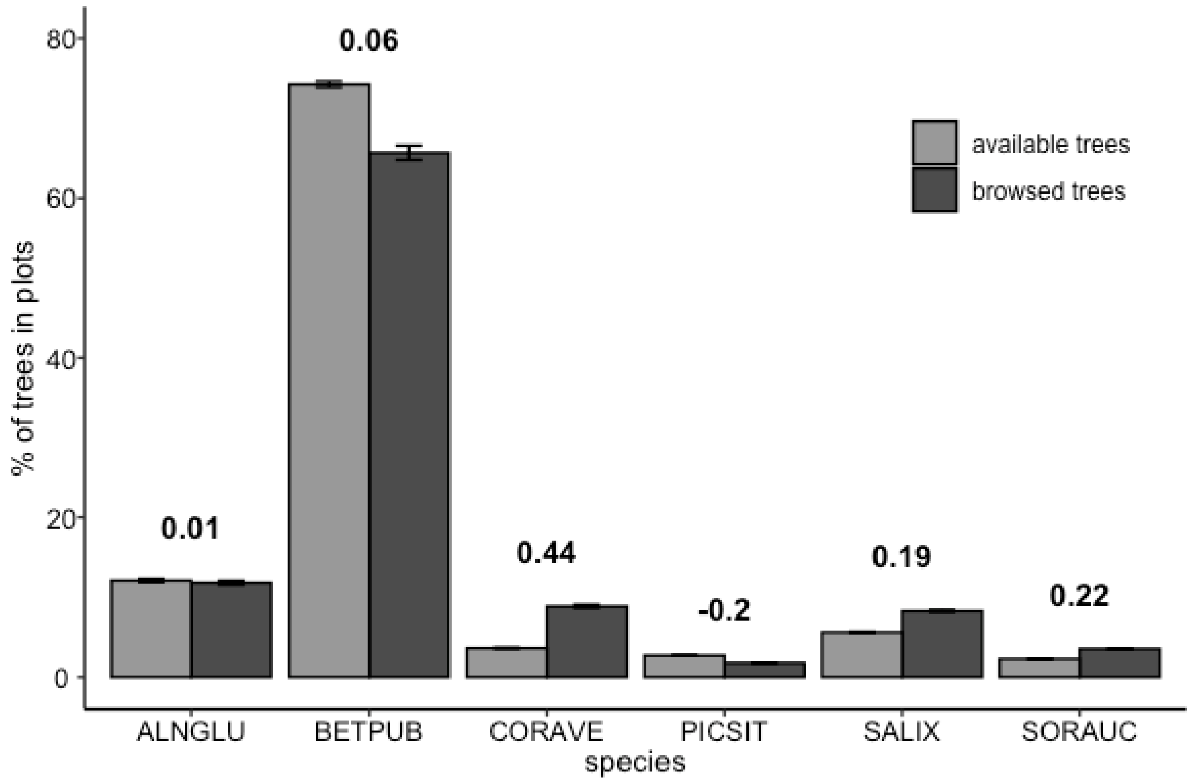

Figure 2.5. Proportion of the six tree species available (light grey) and browsed by beaver (dark grey) per plot with Ivlev's Electivity Index values for 16 plots. Species code abbreviations are detailed in Table 2.1. Only species browsed by beaver are included. Error bars represent standard error.

2.3.2. Woodland change 2010-2021

In the five SBT transects, the 2010 survey counted and tagged a total of 524 tree stems and 5 stems of fallen deadwood across their 16 plots. Eleven years later, 79% of trees with the original tree tags were recorded and measurements were taken for the remaining 415 tree stems and 31 stems of fallen deadwood across the same 16 plots.

Relative change in tree stem density and diameter

Over the 11-year period, stem density (trees per ha) showed a significant relative decrease (-21%) across the total plot resource (t_{15}=2.5, P=0.02) which was most readily evident in plots located furthest from the water's edge (Figure 2.6). Mean stem diameter (cm) per plot did not significantly differ between 2010 and 2021 (t_{15}=1.1, P=0.3).

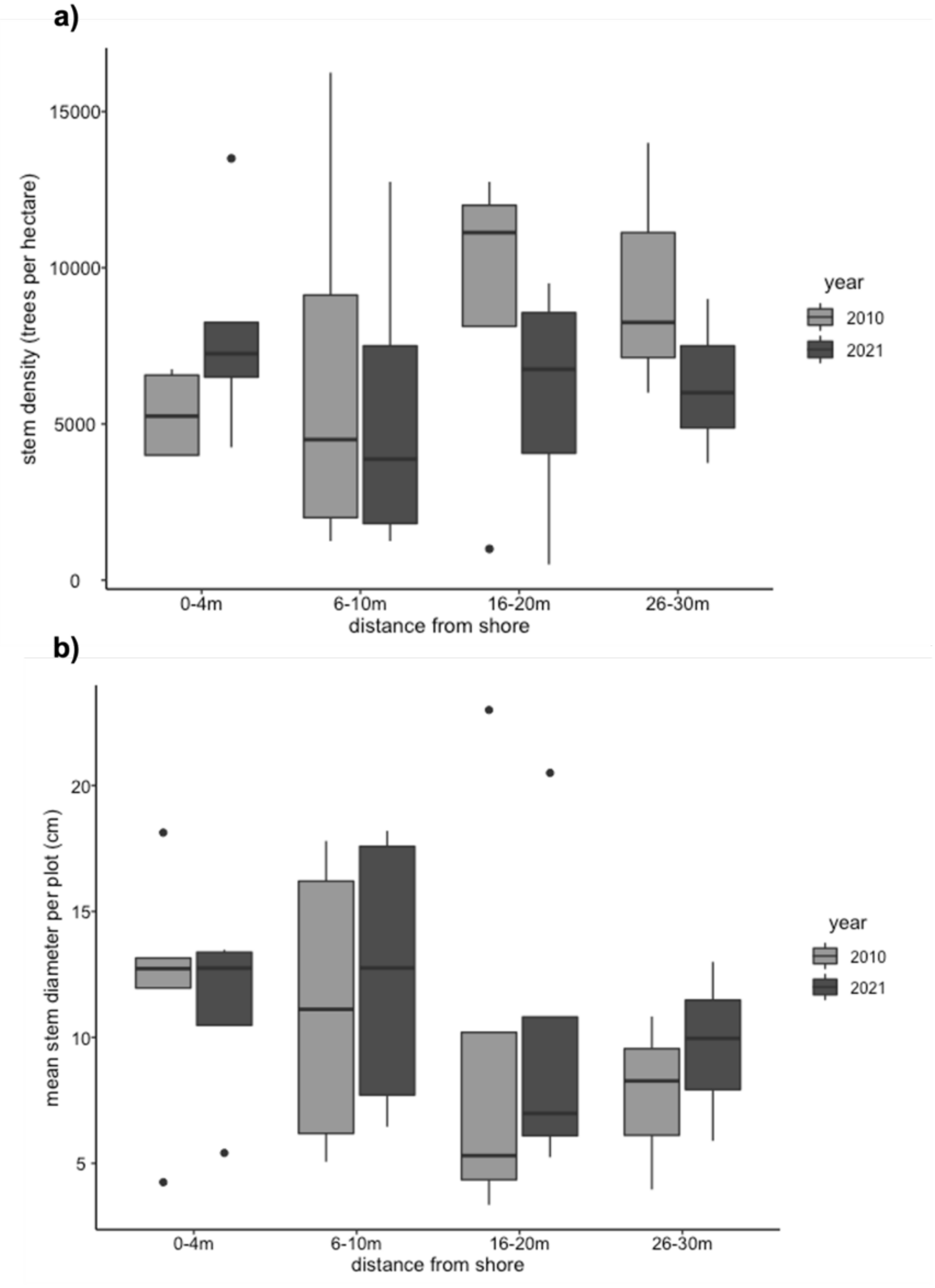

Figure 2.6. Boxplots of a) tree stem density (n trees per hectare) and b) mean stem diameter (cm) across plots in beaver territories in 2010 (light grey) vs 2021 (dark grey) (n=16).

Relative changes in tree stem density (*P*=0.7) and relative changes in mean plot diameter (*P*=0.1) were both independent of beaver browsing intensity (%). Distance from the shore had no effect on change in stem density (*P*>0.7). Change in diameter in plots located 16-20m from the shore was significantly higher than in 0-4m plots (*P*=0.03) (see Appendix 2.3 for full model output).

A significant, negative correlation between change in stem density and change in stem diameter was observed (*P*=0.01) and indicative of an overall shift in plot structure over time (to fewer, larger trees). After 11-years, most plots comprised a lower density of larger stems, with only those plots closest to the shore (0-4m) moving towards a higher density of smaller diameter stems (Figure 2.7).

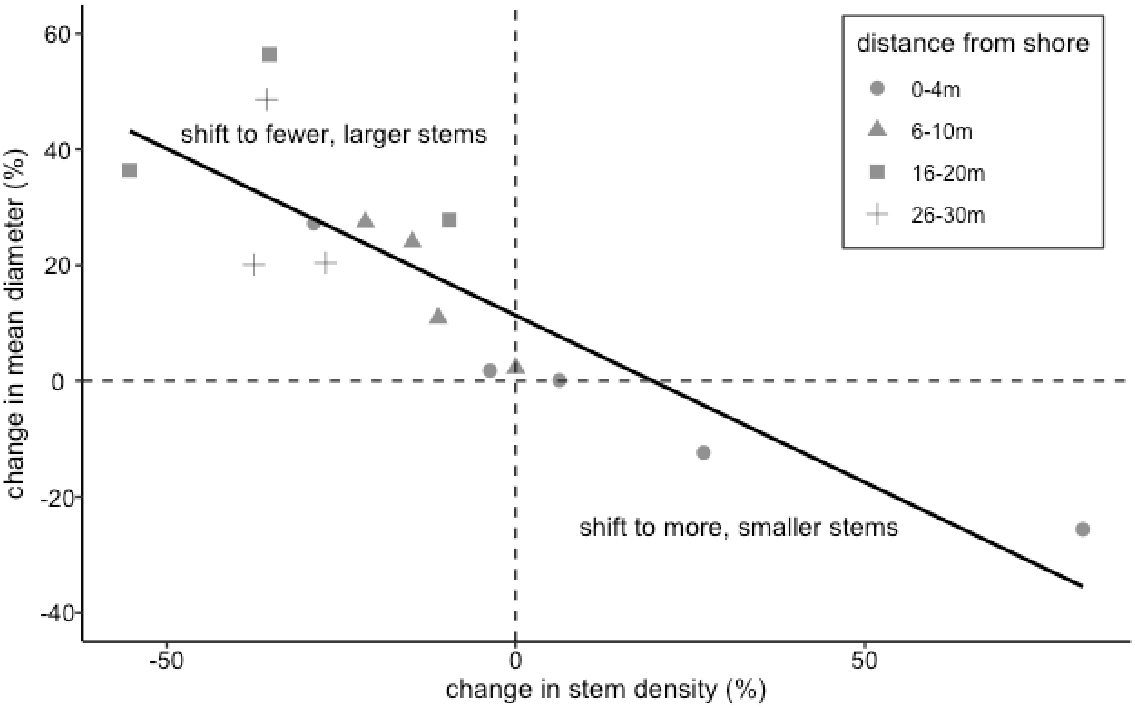

Figure 2.7. Observed change in mean stem diameter in relation to mean stem density of plots (n=15) in 2010 vs 2021. Top left quadrant of the graph indicates a structural shift to lower density, larger diameter tree stems. Bottom right quadrant of the graph indicates a structural shift of higher density, smaller diameter tree stems. One plot (at 16-20m) with <5 trees in total was excluded as an outlier.

Tree species diversity and composition

Tree species diversity per plot showed no significant change between 2010 (SDI=0.21) and 2021 (SDI=0.17) (t_{30}=0.66, *P*=0.5). Overall, tree species richness showed a low total relative change of -12.5% (range -50 to +50%) across the 16 plots from 2010-2021. Species richness averaged 2.25 (±0.93 SD) species per plot (range

1-4) in 2010, and 2.18 (±1.2 SD) species per plot (range 1-5) in 2021. The dominant tree species in plots (downy birch) remained the same over the 11-year period. There was an absolute increase in the share of alder (+4%), and an absolute decrease in birch (-27%) (Table 2.4) with most of the latter losses being converted to standing dead stems (B_up or Up). A deciduous shrub, bog myrtle (*Myrica gale)*, was also recorded during surveys and showed a relative increase of 125% over the 11-year period.

Table 2.4. Tree species composition based on live and dead[a] stems regardless of their beaver browsing status for 16 plots in 2010 (n=524 stems) and 2021 (n=415 stems) and their relative change in composition. Species codes are listed in Table 2.1.

species code	stems in 2010 (n)	stems in 2021 (n) live (dead)	2010 composition (%)	2021 composition (%)	change in stems % 2010-2021
Acepse	2	0 (0)	0.4	0.0	-0.4
Alnglu	37	46 (12)	7.1	13.9	+6.8
Betpub	446	243 (78)	85.1	77.3	-7.8
Fraexc	1	2 (0)	0.2	0.5	+0.3
Picsit	10	11(0)	1.9	2.7	+0.7
Salix	16	9 (0)	3.1	2.2	-0.9
Sorauc	12	10 (2)	2.3	2.9	+0.6
Tsuhet	0	2 (0)	0.0	0.5	+0.5
total	524	415			

dead stems[a] = includes standing trees recorded as dead at time of survey; stems of fallen deadwood (2010; n=5 and 2021; n=31) not included.

Tree species composition showed no significant change over the 11-year period as indicated by the overlapping ellipses in Figure 2.8. Tree species composition of the woodland did not differ between 2010 and 2021 (*P*=0.1). Woodland composition significantly varied with distance from the shore (*P*=0.01). Plots located at 0-4m from the water showed differences in their composition than those at 6-10m, 16-20m and 26-30m as shown by their isolated position in Figure 2.8. Transects were also significantly distinct from one another (*P*=0.01) indicating high variation in the woodland composition between beaver territories.

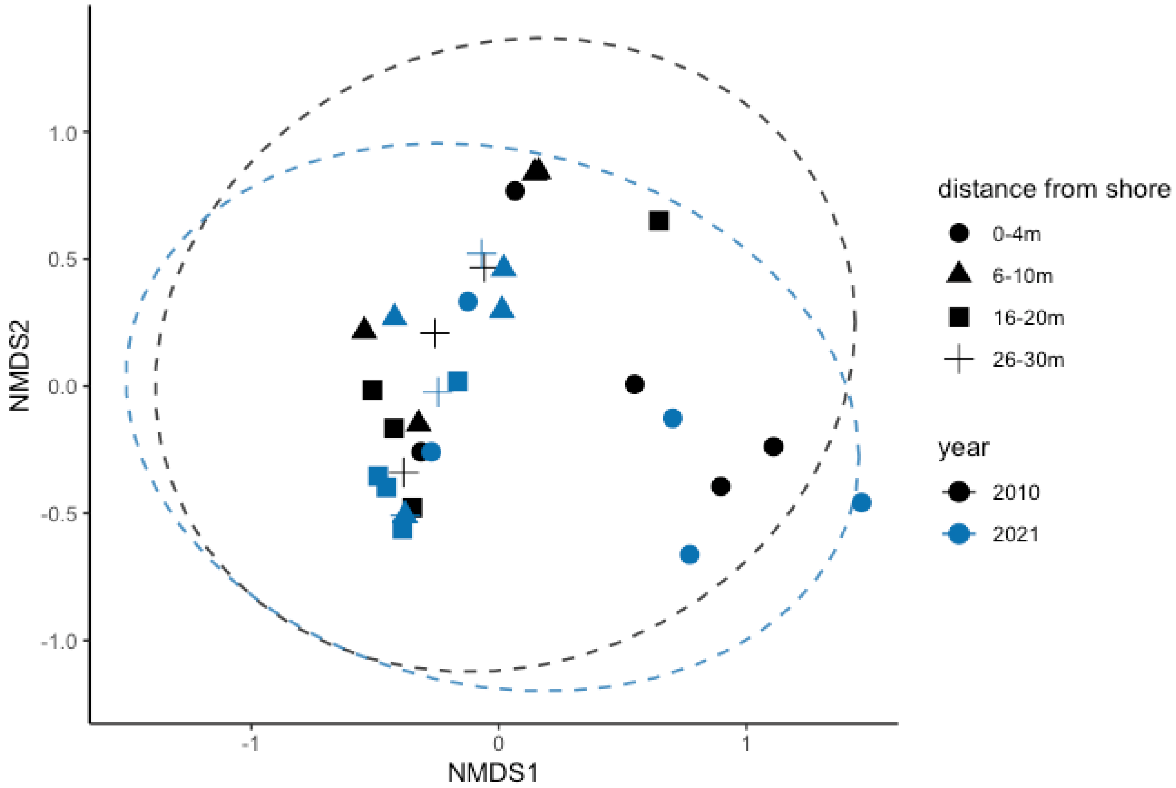

Figure 2.8. Non-metric multidimensional scaling ordination (NMDS) plot for tree species composition in 3 diameter categories (<10cm, 10-20cm, >20cm) for 2010 (black ellipses) and 2021 (blue ellipses). All stress values <0.1.

Standing and fallen deadwood

The proportion of deadwood (both standing and fallen) in plots significantly increased between 2010 and 2021 (t_{15}=-4.2, *P*<0.001; Figure 2.9). In 2010, no standing deadwood was recorded in the woodland across the five transects. After 11 years, a total of 27% (n=92) of available tree stems had been converted to standing deadwood. Most of the standing dead stems (79%, n=73) were not browsed by beaver and were located in the 0-4m plots (54%, n=50).

In 2010, fallen deadwood comprised 1% (n = 5) of all stems, increasing to 7% (n=31) in 2021. In 2021, a total of 58% (n=21) of the fallen deadwood could be directly attributed to beaver browsing (B_log status) with the remaining 42% (n=10) from other causes (N_log status). An additional 30 dead tree stems were identified in two sunken plots which suffered 100% mortality from beaver-induced flooding.

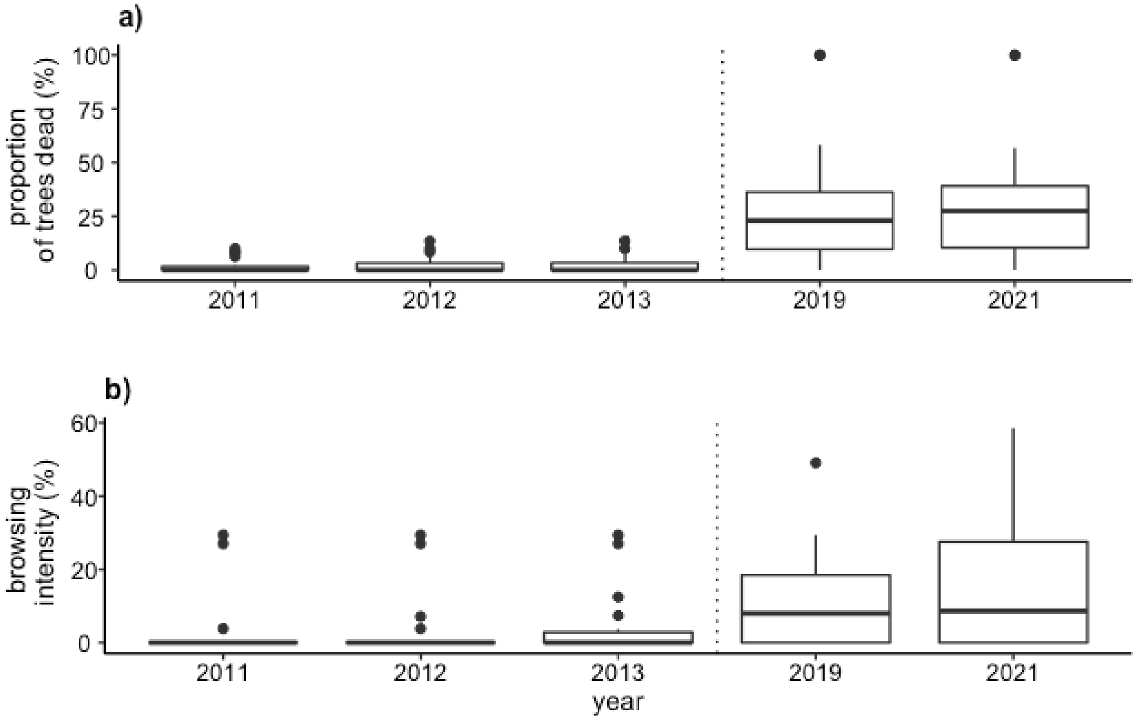

Figure 2.9. The proportion of stems existing as a) standing and fallen deadwood (including an additional n=30 stems from two fully submerged plots as a result of beaver damming) and b) tree stems browsed by beaver as a proportion of the available tree resource. Vertical, dotted line represents time gap in survey data.

Tree recruitment and regeneration

In 2010, 7.6% (n=40) of all recorded stems were young trees (stems of 1cm diameter). In 2021, this proportion significantly decreased to 2.4% (n=10) (t_8=3.5, P=0.007). Tree basal area per plot showed no significant change over the 11 years of beaver-browsing (t_{15}=-0.67, P=0.5). In total, 80% of beaver-browsed tree stems survived. At the end of the 11-year study period, a total of 48% of browsed trees had resprouted, producing on average 19.9 shoots per stump (±21.7 SD) which measured an average maximum length of 27.5cm (±24.9 SD). All beaver-browsed species resprouted, and downy birch accounted for 98% (n=937) of all resprouted shoots. Resprouting in this species was highly variable and ranged from 1 to 86 shoots per browsed tree.

Ground vegetation

A significant overall mean relative increase in abundance between 2011 and 2021 was observed for all non-woody ground vegetation combined (graminoids, bryophytes, ferns, shrubs, and herbs) (t_{67}=-4.83, P<0.001). However, the ground cover (%) of vegetation was highly variable across individual plots and transects (Figure 2.10). Year had a strong significant effect on herb ground cover (*P*<0.001) and a weak effect on graminoid cover (*P*=0.05), but no other vegetation categories. Ground cover of herbs and graminoids were 53% and 41% higher (respectively) in plots after 11 years. Distance from the shore had no significant influence on the ground cover of any of the other vegetation categories (*P*>0.1; see Appendix 2.4)

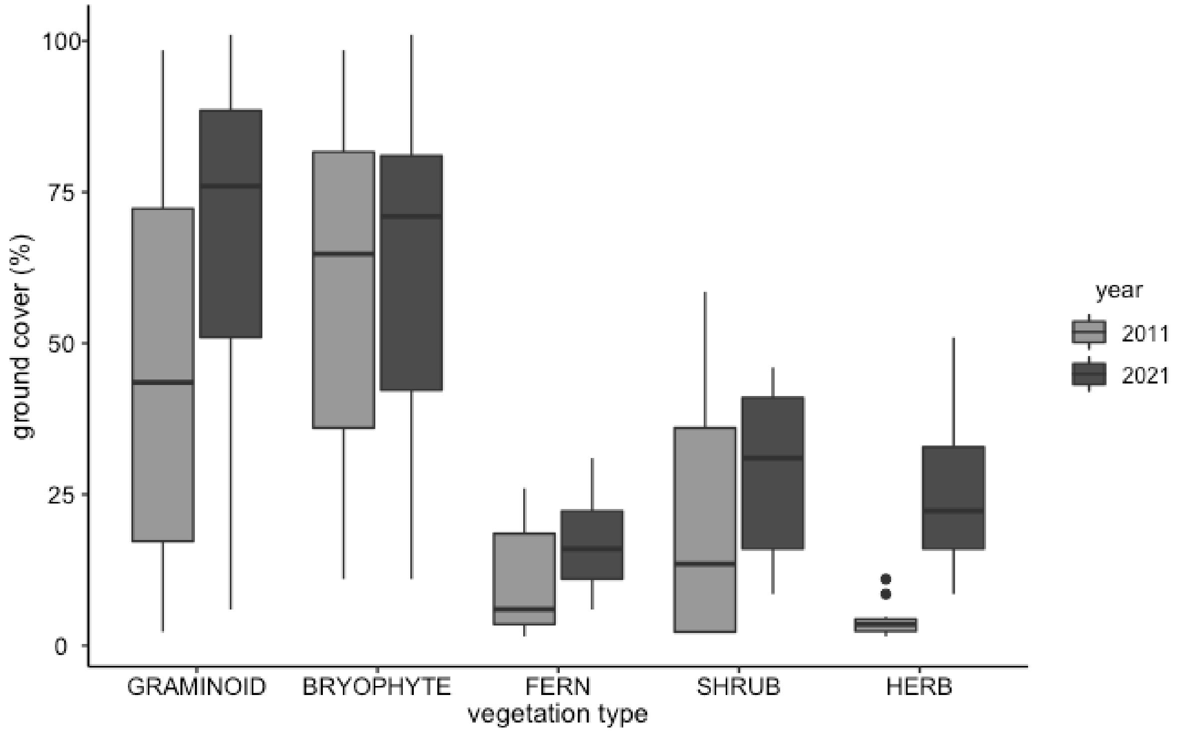

Figure 2.10. Mean plot ground cover of non-woody vegetation (%) of five categories: graminoids, bryophytes, ferns, shrubs, and herbs in 2011 (light grey) vs 2021 (dark grey) across 16 plots.

2.4. Discussion

Eurasian beaver continue to expand their distribution into highly populated and managed landscapes. A deeper understanding of beaver foraging preferences and their potential long-term impacts on woodland composition and structure is therefore crucial to inform both practical riparian woodland management and adaptive beaver mitigation. We present evidence that beaver foraging shows strong spatial patterns and is highly selective of tree species and diameter. Eleven years of selective foraging, however, had no significant effect on riparian woodland tree composition or structure. Relative change in stem density or diameter were not influenced by beaver browsing intensity. However, the observed significant association between relative change in stem density and diameter implies a structural shift in woodland plots towards fewer, but larger stems over time which is consistent with natural patterns of woodland development. There was also a significant increase in the abundance of deadwood and ground vegetation cover over time.

2.4.1. Foraging preferences

Tree species

Our finding that beaver foraging preference is strongly influenced by local availability of trees of specific species and sizes at an individual-site scale is consistent with our original hypothesis. In Knapdale Forest, birch (66%) and alder (20%) accounted for most of the browsed stems, but hazel was overall the most preferred species relative to its availability. In contrast, other studies have found willow species to be the primary preferred choice in a beavers' diet (Janiszewski et al., 2017; Jackowiak et al., 2020) with hazel only being considered the primary choice in habitats that are willow-deficient (Nolet et al., 1994; Vorel et al., 2015; Wazna et al., 2018). In our plots, willow and hazel represented only around 8% and 9% of all available tree stems, respectively. In stabilised beaver populations, long-term beaver foraging pressure can deplete the food base which results in beavers being compelled to select less attractive tree species (Misiukiewicz et al., 2016). Knapdale Forest was relatively willow-deficient prior to the beaver reintroduction (Moore et al., 2011). The available hazel stems may have been of a more suitable diameter, leading to the beavers' general preference over the predominantly larger stemmed willow.

Tree diameter

The utilisation and preference of smaller diameter trees (5-10cm) observed in our study is consistent with most beaver foraging research (Haarberg & Rosell, 2006; Janiszewski et al., 2012). One unique study on a 20ha fenced reserve in Flagham Fen, south-east England recorded preference of beavers for larger diameter trees (10–30cm), despite ready availability of smaller stems (O'Connell et al., 2008). Although beaver foraging decisions are primarily thought to be influenced by energy requirements, they have also been linked to predation risk (Salandre et al., 2017). Smaller stems are quicker to cut and are therefore presumed to carry less risk when feeding on land. Beaver territories in areas with a lower predation risk (i.e., within a small, fenced reserve) may therefore not accurately reflect the foraging preferences of the wider population. A survey of 32 beaver cadavers collected in Scotland attributed around 16% of deaths to suspected animal predation (Campbell-Palmer et al., 2021b). Although the main predators of Eurasian beavers (besides humans) such as wolves (*Canis lupus*) and lynx (*Lynx lynx*) have long been extirpated from Britain (Yalden, 1999), smaller predators such as red fox (*Vulpes vulpes*), otter (*Lutra lutra*), pike (*Esox lucius*) and birds of prey likely still pose a predation risk to beaver kits in our study area.

Another potential driver of beaver foraging preferences is anthropogenic disturbance. Beavers have been shown to choose smaller diameter trees in areas with higher human disturbance (Jackowiak et al., 2020). In North America, smaller diameter trees were preferred in urban areas when compared to rural habitats (England & Westbrook, 2021). Furthermore, human disturbance has also been shown to spatially limit beaver browsing (Loeb et al., 2014). Most beaver-occupied lochs in Knapdale Forest have low levels of human disturbance. Nonetheless, the potential effects of human disturbance (and predation) are increasingly relevant from a management perspective as beavers expand into more densely populated areas that lack large apex predators.

Browsing intensity

After 11 years of beaver occupancy in Knapdale forest, beavers had browsed around a quarter of trees (26%) located in 0-30m riparian woodland transects. After 75 years of beaver occupancy in Wigry Park, Poland, researchers reported a similar level of beaver browsing (24%) across their 0-30m riparian woodland transects (Misiukiewicz et al., 2016). In our study, the levels of beaver browsing intensity in long and short-term territories converged within a three-year period, implying that beavers carry out most felling activity within the initial period of their territory establishment. A study on a simulated riparian woodland estimated beavers to use 8% more willow stems during their first year of occupancy compared to subsequent years (Peinetti et al., 2009). Large differences in the woody biomass removed and consumed were also noted and thought to be a result of stems being stored in winter food caches (Peinetti et al., 2009). Although dam building activity at Knapdale has been relatively minor since beavers were reintroduced (Dowse et al., 2020; Willby et al., 2014), there have been ample food caches and, in some cases, multiple large lodges recorded for each beaver family (Harrington et al., 2015). The initial peak in browsing by beavers that we observed is presumably associated with the initial construction of primary lodges, dams, and caches, rather than to meet ongoing dietary requirements.

Distance from shore

Our findings of a concentrated beaver browsing area within 10m from the shore has also been highlighted in other research (Haarberg & Rosell, 2006; Janiszewski et al., 2012) and supports the strategy of central-place foraging theory (Raffel et al., 2009). Another study observed the focal area of beaver browsing extending up to 15m (Janiszewski et al., 2017). Although bank topography can be a limiting factor, foraging over further distances from the shore is generally required when preferred resources are poorer (Wazna et al., 2018) or have been depleted (Goryainova et al., 2014). When a territory borders arable farmland, beavers have been known to occasionally venture beyond riparian woodland to feed on cereal or vegetable crops (Mikulka et al., 2020). Beavers are recolonising areas of their former distribution which have become highly populated and intensely-modified since their absence (Wróbel, 2020). Moreover, riparian woodland condition in Scotland is generally poor (Ogilvy et al., 2022). A combined effect of more populated and extensively farmed landscapes coupled with low riparian woodland quality raises concerns that human-beaver conflict may become a more common occurrence.

One suggested mitigation method is to create a wide and attractive buffer zone of riparian woodland that would discourage beavers from venturing far from rivers in search of food (Gaywood et al., 2015). A recent study of 17 beaver territories in Norway found that beavers were significantly less likely to forage on cereal crops when there was a larger buffer of riparian woodland (Lodberg-Holm et al., 2022). As well as increasing the width of riparian woodlands, our findings suggest that increasing the availability of preferred trees (in terms of species and diameter) may help reduce conflict between beavers and humans.

2.4.2. Woodland change 2010-2021

Tree species composition

We demonstrated that beavers selectively browse trees in strong spatial patterns within a narrow strip of riparian woodland. Therefore, in these areas, compositional and structural changes would be expected at a riparian woodland-level over time.

Contradictory to this hypothesis, there was no significant change in riparian woodland tree species composition over the 11-year period. Most research has confirmed changes in tree species composition following prolonged selective beaver browsing (Johnston & Naiman, 1990; Nolet et al., 1994; Johnston, 2017). Alternatively, tree composition changes have been attributed to repeated flooding from localised beaver damming (Hyvönen & Nummi, 2008; Kivinen et al., 2020). Although our observed changes in tree species composition in Knapdale Forest were non-significant, the relative increases of woody species associated with wetter soil conditions (alder and bog myrtle) that were observed could have arisen from minor damming by beavers. Since certain tree species tolerate flooding better than others (Glenz et al., 2006), changes in riparian woodland tree composition may potentially be exacerbated at sites that experience more frequent or severe beaver-induced flooding.

Tree density and diameter

As well as changes in species composition, prolonged beaver browsing has been demonstrated to influence woodland structure in North America (Martell et al., 2006; Peinetti et al., 2009; Johnston, 2017). We reported a significant overall reduction in tree stem density after 11 years of beaver browsing, which is consistent with other studies (Johnston & Naiman, 1990; Peinetti et al., 2009). However, change in relative stem density was not significantly correlated with beaver browsing intensity. Plots located furthest from the shore (16-20m and 26-30m) featured the highest relative reductions in stem density over time. These observed temporal changes are generally consistent with the natural progression of woodland development over time. They may also partly be attributed to other natural environmental factors where storms created windblow shortly after plots were initially surveyed, leaving adequate time for decomposition. Additionally, stumps and fallen deadwood may have become hidden in the deep mossy undergrowth and missed during the meticulous surveys.

In contrast, the highest increases in mean tree stem density over time were observed in plots located closest to the shore (0-4m), despite being the focal area of beaver browsing. One explanation involves the high levels of browsing in plots closest to shore being counteracted by sapling recruitment. Shade-tolerant saplings can persist underneath the canopy for some time growing rapidly only once a canopy gap is created (Muscolo et al., 2014). The canopy gaps created by beaver felling are therefore believed to facilitate sapling recruitment, especially when combined with increased soil moisture from damming (Donkor & Fryxell, 1999). Although saplings (or soil moisture) were not recorded in this study, a significantly lower abundance of young trees (of 1cm diameter) was observed after 11 years. Saplings in our study may have established during the initial periods of beaver occupancy when trees were first felled, and canopy gaps were first created. This would explain higher stem densities being observed a few years later in plots closest to the shore, by which time saplings have grown into trees. These findings suggest that although beaver browsing intensity was not explicitly correlated with changes in stem density in this study, beaver browsing may play an indirect role in shifting woodland structure over time.

The strong relationship between relative change in density and diameter that we observed implied a structural shift in the riparian woodland over time. Similar findings have been illustrated by a long-term beaver browsing model which predicted that selective foraging creates a more diverse plant structure dominated by medium to large size trees (in terms of their biomass and height) (Peinetti et al., 2009). In our study, the structural shift to woodland comprising lower density, larger diameter tree stems was not universal. A small number of plots (n=3; 20%) shifted towards a structure of higher density, smaller diameter stems. This suggests that beaver browsing in our study plots was not widely counteracted by sapling recruitment. It is likely the result of the persistent removal of smaller, preferred stems, leaving behind only medium to large diameter stems.

Riparian deadwood

Deadwood is rare in managed woodlands due to commercial forestry practises despite its importance in woodland function (Keren & Diaci, 2018; Bujoczek et al., 2021). Our finding of an increased abundance of deadwood in beaver-browsed woodland plots is not unique (Nummi & Kuuluvainen, 2013). A short-term study in Finland compared deadwood abundance in beaver ponds to control sites and found beaver ponds had significantly higher levels of deadwood (Thompson et al., 2016). Surprisingly, most (79%) of the standing deadwood in our study had not been browsed by beaver. It was largely located in the plots closest to the shore (54%) which were susceptible to repeated flooding from beaver damming. It was not possible to distinguish the cause of tree death in this study. However, we suspect that indirect effects of beaver-flooding, as opposed to direct beaver browsing, were the main contributor to tree mortality. The implications of an increase in deadwood, whether a result of beaver browsing or beaver-induced flooding, span riparian woodland nutrient cycling and biodiversity (Radu, 2006). Standing deadwood in particular can act as crucial habitat for saproxylic invertebrates that survive on dead and decaying plants (Seibold et al., 2018), as well as roosting bat and bird species (Radu, 2006).

Riparian regeneration

Many broadleaf species sprout vigorous shoots following herbivory – an adaption likely developed over millions of years of co-evolution alongside grazing herbivores (Del-Claro & Torezan-Silingardi, 2021). In our study, resprouting was documented in around half of all beaver-browsed trees. Similar effects have been observed in beaver-browsed willow and aspen in Scotland (Jones et al., 2009). Research from North America has shown that fresh, newly sprouted shoots from beaver-browsed trees are exploited by large herbivores (Baker et al., 2005; Hood & Bayley, 2009; Loeb & Garner, 2022). Excessive deer browsing is already a major inhibitor of woodland regeneration throughout Europe (Ramirez et al., 2018) and several authors have hypothesised about their potential interactions with Eurasian beavers (Jones et al., 2009; Stringer & Gaywood, 2016). Ultimately, if deer readily consume the regrowth from beaver-browsed trees (or browse/trample saplings stimulated by canopy gaps) then there could be cascading effects on key ecological processes that regulate riparian woodlands.

Ground vegetation cover

Ground vegetation plays an important role in the functioning of riparian woodland ecosystems (Broadmeadow and Nisbet, 2004). Our observation of an overall increase in ground cover of graminoids, bryophytes, ferns, shrubs, and herbs after 11-years is likely a result of increased light and soil moisture levels as a result of beaver browsing and damming. Other research in Scotland supports this hypothesis. For example, Law et al. (2017) observed that plants associated with higher light conditions had increased significantly in an enclosure ten years after the release of beavers. Herbs and graminoids specifically showed the greatest increases over time in our study. A substantial increase in the understorey of herbs can improve biodiversity of invertebrates (Ramberg et al., 2020). Furthermore, graminoids can trap sediment which helps to prevent erosion (Broadmeadow and Nisbet, 2004). However, the increase in ground vegetation may have potential implications for limiting seedling recruitment due to interspecific competition (Royo & Carson, 2014). Changes in ground vegetation cover elicited by prolonged beaver activity, whether from browsing or damming, may therefore have some cascading impacts on overall riparian woodland function. As well as changes in light and soil moisture regimes, ground vegetation can also be influenced by grazing deer. Deer grazing can decrease the cover of some species and even increase the cover of more graze-tolerant species (Tanentzap et al., 2009; Kirby et al., 2022). If beaver browsing (or damming) is inadvertently altering ground vegetation cover, this could influence resource availability for some deer species.

2.5. Conclusions

Assessing the long-term outcomes of beaver foraging is crucial for riparian woodland management yet is largely unstudied in Europe. Our findings highlight the two main factors that influence beaver foraging preferences as tree species and diameter. The importance of local availability of resources and their distance from shore was also emphasised. Overall, we illustrate that beaver browsing has strong spatial patterns that can be highly variable between beaver territories. After 11 years of selective beaver foraging, riparian woodland tree species composition showed no significant directional change, contrary to our initial hypotheses. Plots underwent a structural shift to larger, fewer trees but this was not directly correlated to beaver browsing intensity. The increase in deadwood levels and ground vegetation we observed has implications for the role of beavers in restoration projects where goals are to increase biodiversity and habitat heterogeneity. While individual plots or patches of riparian woodland may see quite drastic changes as a result of beaver browsing, these effects are seemingly not translated on a riparian woodland-level scale. These findings need to be considered within the context of riparian woodland management and mitigation of beaver effects as Eurasian beaver distribution continues to expand.

CHAPTER 3: TREE FELLING BY EURASIAN BEAVER PROMOTES REGENERATION IN RIPARIAN WOODLANDS WHILE INCREASING RESOURCE AVAILABILITY FOR DEER.

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3.0. Abstract

Interspecific interactions can influence ecosystem processes and are sensitive to species reintroductions. Our understanding of interactions between naturally co-occurring large herbivores, such as Eurasian beaver (*Castor fiber*) and long-established deer species, is limited, despite their potential implications for riparian woodland regeneration. Observations in Scotland indicate that deer readily exploit the regenerative secondary shoots that sprout from beaver-felled trees. This study, based in eastern Scotland, investigates the role of beaver herbivory in riparian woodland regeneration. We then explore three hypotheses about whether deer are attracted to this novel resource because it is either a) more readily available, b) nutritionally superior, or c) morphologically more appealing. We firstly quantified the secondary shoots available to browsing deer at different heights on felled and standing birch *(Betula* spp.*)* trees in twenty 25m^2 riparian woodland plots across five well-established beaver territories (occupancy ten years). Shoots from 156 birch and willow (*Salix* spp.) trees with contrasting levels of beaver and deer browsing were then analysed for nutritional content (nitrogen and carbon) and morphological characteristics (number of buds and lateral branches). We found that 62% of beaver-felled trees produced secondary shoots available to browsing deer. Compared to standing trees, resprouted beaver-felled trees had 18% more secondary shoots, that were significantly higher in nitrogen content (+13%), but similar in carbon content. These shoots also had a distinctive height distribution which could be more conspicuous to browsing deer. We conclude that beaver herbivory can promote riparian woodland regeneration and heterogeneity by creating a mosaic of mature and multi-stemmed coppiced trees. The addition of a novel, readily available and nutritious resource through beaver-browsing

could also enhance habitat quality for browsing deer, with the potential to affect deer distribution and feeding habits.

3.1. Introduction

Species reintroductions can play an important role in the mitigation of biodiversity loss (Seddon et al., 2007). Their main objective is to return extirpated species to their former range (IUCN/SSC, 2013). Although typically rooted in conservation, the importance of reintroductions is also highlighted in the field of restoration ecology where they can be used to reinstate key ecological processes that regulate ecosystem function (IUCN/SSC, 2013; Tanentzap & Smith, 2018). While it is broadly understood how predators influence large herbivorous prey, the outcomes of interspecific interactions between naturally co-occurring large herbivores and their ecosystem consequences are less studied. The importance of 'predator-prey' trophic interactions in restoration ecology are often overstressed at the expense of non-trophic interspecific interactions (Kéfi et al., 2012; Ellison, 2019), even though these can be just as crucial in the shaping of ecosystems (Fontaine et al., 2011; van der Zee et al., 2016). Indeed, changes in interspecific interactions within trophic levels are arguably a more realistic outcome of reintroductions in the more managed landscapes and densely populated countries of Europe where apex predators generally remain sparse. Wider understanding of such herbivore-herbivore interactions, and their ecosystem consequences is therefore a priority, especially when species co-occurrence has been altered through human interventions, e.g., one species has been reintroduced after a prolonged absence.

The Eurasian beaver (*Castor fiber*) is a herbivorous keystone species that has profound effects on riparian woodlands (Rosell et al., 2005). Following their near-extinction a century ago, beavers are now re-established across most of their former range through recent reintroductions and natural recolonisation (Halley et al., 2021). They are now living in highly populated, managed landscapes in countries such as Germany and the Netherlands (Wróbel, 2020). Beavers were officially reintroduced to Scotland in 2009 after an absence of over 400 years. Recent estimates have suggested that there are now 251 active beaver territories (around 954 individuals) located across Scotland's largest catchment (Campbell-Palmer et al., 2021). Beavers exert a substantial influence on their food resources which may have indirect consequences for other grazers. Using their sharp incisors, beavers fell tree stems of various sizes and species for food and dam/lodge construction materials. This unique type of browsing can promote tree regrowth in the form of secondary shoots that sprout from around the cut, akin to the process of coppicing. This behaviour indirectly influences the abundance of forage that is available for other large herbivores sharing riparian woodlands, the most common of these being species of deer (Cervidae).

Deer are well-known inhibitors of woodland regeneration (Ramirez et al., 2018). The main damage to woodlands is caused by excessive feeding on coppiced shoots, seedlings, and saplings, often before they can replace the loss of mature trees (Gill, 2000; Reimoser & Reimoser, 2010). In Scotland, around a third of native woodlands are rated as in “poor condition” due to herbivore impacts (NatureScot, 2016). Deer are identified as a major constraint in the success of Scotland’s native riparian woodland establishment (Burton et al., 2018; Ogilvy et al., 2022). Deer populations in Scotland have been steadily increasing over recent decades, particularly since the 1950s. The primary cause for this increase has been attributed to a significant expansion in forest cover, alongside a lack of large predators (Scottish Government, 2019). Although the exact number of wild deer in Scotland is largely unknown, recent estimates suggest that there are at least 360,000 red deer and 200,000 roe deer (Pepper et al., 2020). Roe deer are the most common ungulate species in terms of their distribution. They cover around 74% of the European continent and occupy a diverse variety of agricultural, woodland, and urban habitats (Linnell et al., 2020). They are also the most selective forager and adopt a selective ‘browser’ feeding strategy whereby they readily browse tree buds, shoots, and leaves (Ratcliffe & Mayle, 1992).

Many authors have alluded to the potential effects of interactions between beaver and established large woodland herbivores in Europe (Jones et al., 2009; Stringer & Gaywood, 2016; Ogilvy et al., 2022). However, research on beaver-deer interactions in a European context remains sparse. In North America, changes in woodland structure, composition, and regeneration processes due to beaver-deer interactions have been highlighted (Baker et al., 2005; Hood & Bayley, 2009; Johnston, 2017; Loeb & Garner, 2022). One study in Scotland recorded deer browsing on 68% of beaver-felled stumps that had produced secondary shoots (Iason et al., 2014), suggesting that this type of forage offers an attractive resource that would have been absent from un-coppiced woodlands prior to the beaver's reintroduction. However, exactly why deer seem to be attracted to the secondary shoots from beaver-felled trees is unclear.

One hypothesis is that the secondary shoots from beaver-felled trees are a readily available food source. Studies have shown that roe deer select foods that are more available, despite being of lower nutritional quality, simply because less energy is expended in searching for them (Palmer & Truscott, 2003; Borkowski & Ukalska, 2008). This observation has also been confirmed in moose (*Alces alces*) (Wam & Hjeljord, 2010). Research in Scotland reported high rates (77-86%) of resprouting in beaver-felled willow (*Salix* spp.) trees (Jones et al., 2009; Iason et al., 2014). The most vigorous resprouting following beaver browsing has been observed in birch (*Betula* spp.), willow, ash (*Fraxinus excelsior*) and rowan (*Sorbus aucuparia*). Poorer rates have been recorded in species less commonly selected by beaver, such as black alder (*Alnus glutinosa*) (Iason et al., 2014). Research by Jones et al. (2009) found that resprouting rates were up to 12 times higher from stumps cut by beaver than from standing trees. Beaver-browsing could therefore enhance the abundance of forage accessible to deer and provide a novel resource.

Another hypothesis is that secondary shoots are of higher quality, whether in terms of nutrition or palatability. Large herbivores have been shown capable of distinguishing differences in forage quality (P. Duncan et al., 1998; Ball et al., 2000). Research has demonstrated reductions in palatability after herbivore damage in birch (Wratten et al., 1984). Birch foliage is also reported to have lower nitrogen and higher phenolic concentrations for up to four years after leaf removal (Tuomi et al., 1990) implying that the nutritional value of regrowth from beaver-felled trees might be lower. In contrast, studies show that herbivore damage in trees can sometimes lead to an accelerated growth of any remaining parts to quickly offset the loss of biomass (Danell et al., 1985). A by-product of this accelerated, compensatory growth can be plant material of higher quality (Haukioja et al., 1990). During these rapid growth phases, some research has found that production of defence chemicals is low, but as growth slows, more resources are allocated to defence (Bryant et al., 1983). Two studies have investigated the chemistry of resprouted secondary shoots (following beaver felling), both from Fremont cottonwood trees (*Populus fremontii*) in the USA (Martinsen et al., 1998;

Durben et al., 2021). They found that the secondary shoots of beaver-felled trees were of higher nutritional quality when compared to those from standing trees. Despite key differences in tree (and beaver) species, we hypothesise that secondary shoots from beaver-felled trees will be of higher nutritional quality.

A third hypothesis proposes that the morphological characteristics of resprouted secondary shoots could play a role in their selection by deer. Researchers in Sweden followed the tracks of moose (*Alces alces*) in the snow and compared the nutritional content of the bites of forage that were taken to those in the immediate vicinity that the moose could have taken. The study concluded that plant selection by moose was related to plant morphology rather than nutritional aspects (Shipley et al., 1998). Roe and red deer (*Cervus elaphus*) have similarly been shown to base their foraging choices on structural aspects of plant morphology (A. Duncan et al., 1998; Renaud et al., 2003; Prendeville et al., 2015). Other physical features, such as budding on shoots, are thought to influence the likelihood of browsing by herbivores (Moore et al., 2000)

Currently there is little research to explicitly support any of these three hypotheses in Europe, as few published studies have investigated the relationship between Eurasian beaver and foraging choices of deer. If deer are regularly browsing the secondary shoots of beaver-cut stems, there could be significant long-term implications for the regeneration of riparian woodland and the distribution of roe deer grazing pressure more generally. At present, roe deer occupy 74% of Europe (Linnell et al., 2020) and beavers occupy every European country within their natural range except for Portugal and the Balkans (Halley et al., 2021; Pucci et al., 2021). As beaver populations continue to expand, interspecific interactions between beavers and deer in riparian woodlands will become increasingly commonplace. Understanding these interactions is essential to predict potential ecological effects on the wider landscape.

The overarching aim of this study was therefore to explore the mechanism behind beaver-deer interactions by firstly examining whether tree felling by beaver can promote riparian woodland regeneration before investigating the nutritional and morphological qualities of the regrowth from beaver-felled trees. We tested whether beaver-felling can promote woodland regeneration through the resprouting of secondary shoots in trees. We also hypothesised that resprouted secondary shoots of beaver-felled trees are a) more readily available, b) nutritionally superior, and/or c) morphologically more appealing when compared to deer-accessible browse at the base of trees not felled by beaver (hereafter ‘standing trees’).

3.2. Methods

3.2.1. Study Area

The study was carried out in two catchments of central eastern Scotland, where the stronghold of Britain’s beaver population occupies habitats ranging from narrow, shallow drainage ditches and ponds to large deep lochs and fast-flowing rivers (Campbell-Palmer et al., 2021a). The Tay catchment is the largest in Scotland and spans 4587km^2. Woodland covers around 16% of the catchment and contains a diverse variety of native species dominated by birches and commercial conifers. Arable/grassland dominates 32% of the low-lying, populated valleys (NRFA, 2022a). The smaller Forth catchment covers 1036km^2 of which woodland comprises 22%, with 48% arable/grassland lining the lower valleys (NRFA, 2022b). The four species of deer known to inhabit the study areas (in decreasing order of distribution area) are: roe, red, fallow (*Dama dama*), and sika (*Cervus nippon*) deer (BDS, 2016).

3.2.2. Survey and Sampling Sites

Beaver distribution maps from Campbell et al. (2012) and Campbell-Palmer et al. (2021a) were used to identify territories that had been active for around ten years. Eleven beaver territories were selected at random subject to landowner permission. Five of these territories were used as ‘survey sites’ to investigate whether tree felling by beavers promotes the growth of secondary shoots in riparian woodland. Two of these sites, plus an additional six territories were used as ‘sampling sites’ for sampling tree shoots for nutritional and morphological analyses (Figure 3.1). All territories provided access to riparian woodland dominated by birch and/or willow. They encompassed beaver-felled trees of all ages, ranging from one or more seasons old (for which enough time had passed to allow resprouting) through to freshly-felled trees (where insufficient time had passed for resprouting) reflecting the naturally heterogeneous pattern of resource use in an active beaver territory.

To account for the naturally high variation in the number of beaver-browsed trees within the territories, four 5x5m plots of varying beaver browsing intensity were established at each site. Each survey site included one control plot (no beaver browsing). Beaver browsing intensity (%) was quantified as the proportion of the total available tree stems in a plot that had been browsed by beaver. Beaver-browsed included those that were fully-felled (i.e., a stump), partially-felled (incompletely severed xylem with some remaining phloem connecting the lower stump and the upper tree stem) or gnawed (superficial bites of bark from the main stem). Every plot was located <10m from the water's edge to reflect the focal area of beaver activity. Downy birch (*Betula pubescens*) was the dominant tree species in all plots.

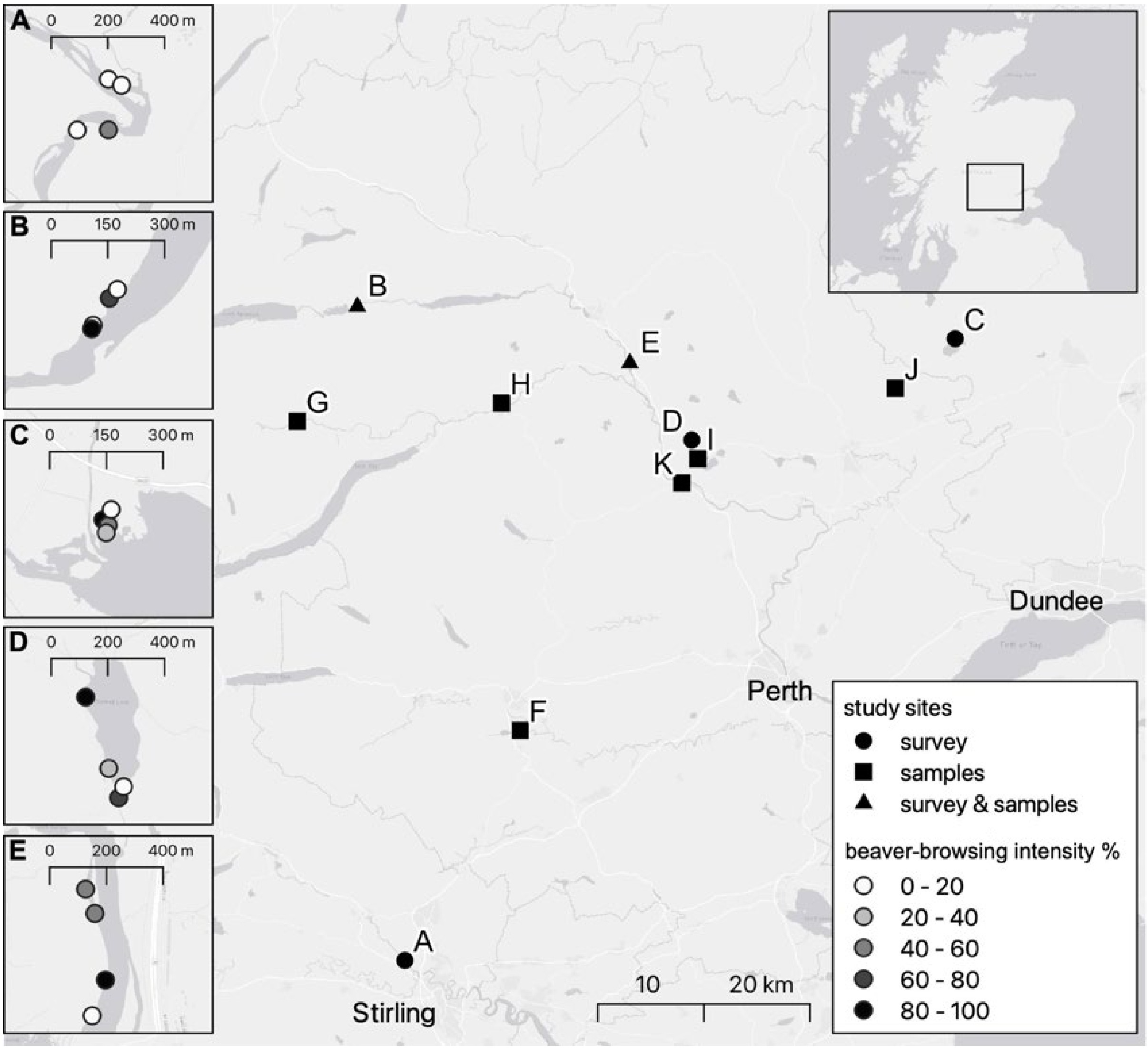

Figure 3.1. Map of survey (n=5) and sampling (n=8) sites across Tay and Forth catchments. Two survey sites were included as sampling sites (11 sites in total). Left insert panels display the plot distribution at each survey site and their beaver browsing intensity (darker dot colour indicates a higher proportion of beaver-browsed stems).

3.2.3. Forage availability

To assess the abundance of secondary shoots available to foraging deer in riparian woodlands, a series of plot-level and individual-tree-level measurements were taken. The twenty plots (15 with beaver browsing, 5 with no beaver browsing) over the five survey sites were visited over five days in early-September 2020. Only secondary shoots originating at a height of <150cm were studied as they comprise forage in the typical height range accessible to browsing roe deer (P. Duncan et al., 1998). The status of every tree was classified according to whether it was a) standing or felled by beaver and b) had secondary shoots originating <150cm above the ground.

In total, the twenty plots comprised 784 trees. A sub-sample of trees with secondary shoots originating <150cm were selected at random for further individual tree-level analyses. Within each plot, measurements were taken for up to five trees fully felled by beaver that had resprouted secondary shoots. This was repeated for up to five standing trees also displaying secondary shoots to act as a comparison (Figure 3.2). Since only those trees displaying secondary shoots were selected for further measurements, some plots contained fewer than five felled and/or standing trees. The individual-tree level data recorded were a) tree diameter (cm), recorded 20cm above ground level using a measuring tape, b) species identity and c) the total number of secondary shoots arising <150cm above the ground.

To investigate the structure of available deer forage, the secondary shoots were further stratified into three height categories (<50cm, 50-100cm, and 100-150cm). Since this depended on both where the secondary shoot originated and its height, an individual shoot could contribute to more than one height category. For example, if one secondary shoot resprouted 10cm from the base of a tree and measured 50cm tall, then it would contribute to the forage available in the <50cm and 50-100cm height band (Figure 3.3).

Figure 3.2. Example of birch (*Betula* spp.) tree a) standing and b) beaver-felled, both with secondary shoots located within deer-browsing height (<150cm).

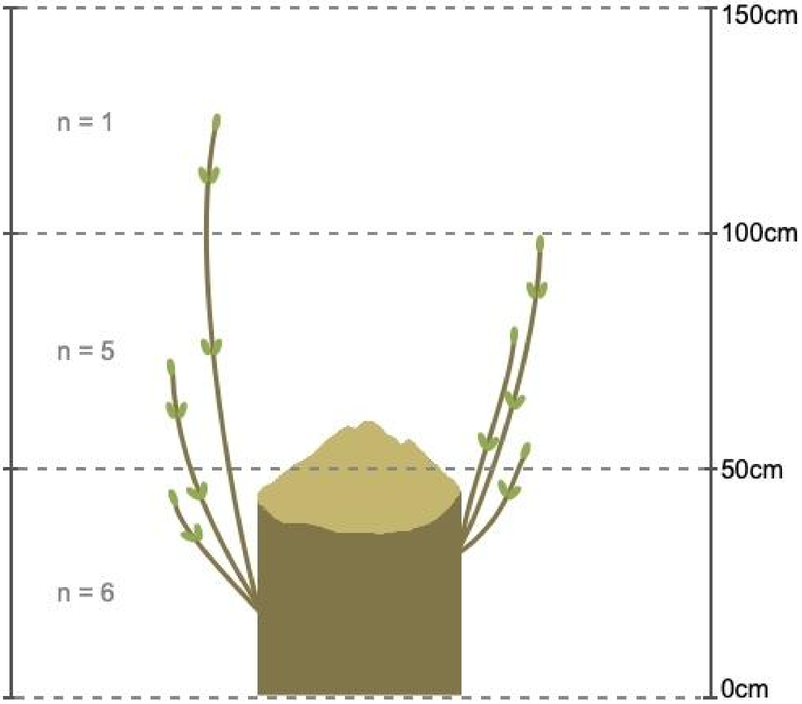

Figure 3.3. Diagram of the stump of a typical beaver-felled tree sprouting secondary shoots showing the three height-category classification system (<50cm, 50-100cm, 100-150cm) where ‘n=’ refers to the number of shoots present in each height band.

3.2.4. Forage quality and morphology

To assess the nutritional quality and morphological characteristics of forage available to deer, a total of 156 shoots (133 from birch and 23 from willow) growing within deer browsing height (<150cm) were collected. Sampling was at random from independent trees across eight beaver territories equivalent to a total area of approximately 0.5km^2 (see Appendix 3.1) and took place over eight days in mid-November 2020. Shoots were collected from trees subjected to a four-way combination of beaver felling and deer browsing treatments:

a. Deer-browsed secondary shoots from beaver-felled trees
b. Unbrowsed secondary shoots from beaver-felled trees
c. Deer-browsed secondary shoots from standing trees
d. Unbrowsed secondary shoots from standing trees (control).

As deer lack upper incisors, they create a tearing motion when browsing (Bang & Dahlstrom, 1972). Deer-browsed shoots were therefore characterised by the removal of the apical bud leaving a frayed, ragged edge (Figure 3.4). Sampled shoots from beaver-felled trees included any secondary shoots that had sprouted from trees characterised by a conical stump with visible beaver teeth marks. Secateurs were used to cut a 30cm length of apical shoot from an average of five trees of each treatment type at sites, dependent on availability. Samples were sealed in labelled bags and transported to the laboratory.

Figure 3.4. Example of a) deer-browsed shoot with characteristic removal of apical bud and frayed edge and b) example of unbrowsed secondary shoots from beaver-felled tree.

Morphological analyses

In the laboratory, shoot length (cm) was recorded using a measuring tape and diameter was measured 2cm from the shoot tip in millimetres using digital callipers. The buds present on shoots were counted with the aid of a 6x zoom magnifying glass under light. The total number of lateral branches on each shoot was also counted. Both the bud and lateral branch count were standardised by expressing the number of buds or branches per metre length of main shoot. These standardised values were used in all subsequent analyses.

Nutritional analyses

In the laboratory, the apical 5cm of each shoot was then cut and dried at 60°C for 48 hours. Each dried sample was then separately ground into a fine powder using a ‘Retsch’ ball mill (MM200 model). Approximately 3-5mg of each sample was then weighed into tin capsules (6x4mm size; ‘Elemental Microanalysis’). All weights were recorded to the nearest 0.01mg. Total nitrogen (N) and carbon (C) content (%) were then determined by dry combustion in a 'ThermoFisher Scientific' elemental analyser (FlashSmart model). C:N ratio, a measure of forage quality, was calculated. A lower C:N ratio generally indicates higher quality (van der Wal et al., 2000).

3.2.5. Apical bud vs shoot sampling

Deer-browsed shoots collected for nutritional and morphological analyses lacked their apical bud because it had been removed during browsing. A further small sub-analysis was therefore conducted to ascertain any possible differences in the C and N content of the apical bud and apical section of shoot that could influence the main data analyses. A total of 480 secondary shoots were collected across four of the sampling sites. Ten shoots (sub-replicates) were collected from each of twelve trees (replicates), each at four sites using standing birch trees that were unbrowsed by deer. Samples were collected in November 2021 and were of approximately 30cm in length. Each shoot and their tip were located <150cm above the ground. In the lab, the apical buds were separated from the shoots using tweezers. Ten sub-replicate apical buds collected from the shoots on a given tree were pooled into a single sample to meet the minimum dried weight of 3mg required for the C and N analyses. Ten apical 5cm shoot sections from each tree (with apical bud removed) were also similarly grouped for consistency resulting in an overall sample set of n=96 (apical bud; n=48, shoot minus apical bud, n=48). All samples were weighed to the nearest 0.01mg prior to drying and were then analysed for C and N content using the same methodology as the main sample set.

2.6. Statistical Analyses

Relationships between beaver felling and the availability, nutritional content and morphology of deer-accessible forage were investigated using linear mixed-effects models. All models included a random effect of site, except when analysing height-stratified secondary shoots, which included site and individual-tree as nested random effects. Response variables were transformed to normal distribution where required, and covariates were mean and centre-scaled. Potential interactive effects of explanatory variables were tested and removed from the model when non-significant. Models were selected for performance based on those with the lowest Akaike Information Criterion (AIC) scores. Residuals for all models were tested for normality and met model assumptions. Statistical analyses and graphs were produced using packages lme4, sjPlot and ggplot2 in R Studio version 1.4.1103.

The first model explored forage availability using the total number of secondary shoots per tree (log-transformed) as the response variable. The following predictors were included: beaver felling (standing/felled), tree species, tree diameter (cm), tree density of plot (n trees per ha), and beaver browsing intensity in plot (%). The height structure of secondary shoots was compared between beaver-felled and standing trees using the number of shoots per height category per tree (log-transformed) as the response. The same predictors were included, as well as height category (<50cm, 50-100, and 100-150cm). Post-hoc multiple comparisons were then carried out using Tukey's HSD test.

Nutritional value of sampled shoots was assessed using three linear mixed effects models with N and C content as well as C:N ratio as the response variables (all square root transformed). Site acted as the random effect. Beaver and deer browsing were included as separate factors each with two levels (± beaver, ± deer) to allow tests for interactions between the two browsing types. Tree species identity (birch/willow), shoot diameter (mm), number of buds (n per m) and lateral branches (n per m) were also included as predictors.

Morphological characteristics of shoots were examined using two linear mixed effects models with buds (n per m) and lateral branches (n per m) as response variables with site as the random effect. Both were square root transformed. Beaver and deer browsing were included again as two separate explanatory variables each with two levels. Other predictors included tree species identity (birch/willow) and shoot diameter (mm). The number of lateral branches could influence the number of buds and conversely, every bud has the potential to eventually become a branch. Therefore, when not acting as the response, the number of buds and lateral branches were included as explanatory variables to assess their relationships with each other. Finally, differences between the nutritional content of an apical bud vs an apical shoot minus bud were tested. Two linear mixed effects models were used to test whether the type of material (bud/shoot) influenced either the N or C content (%; square root transformed).

3.3. Results

3.3.1. Forage availability

In our 20 plots, an average of 62% (±7.8 *SE*, 14–100% range) of all beaver-felled trees resprouted secondary shoots that were accessible to deer (below a height of 150cm). An average of 49% (±8.4 *SE,* 0-100% range) of all standing trees had secondary shoots accessible to deer. Fifteen plots in total exhibited beaver felling activity and in three of these, every beaver-felled tree displayed growth of secondary shoots. There were no recorded instances, in the 15 plots where beaver felling activity was recorded, of no beaver-felled trees resprouting. When testing our first hypothesis, the model (Figure 3.5) revealed a strong association between beaver felling and the availability of secondary shoots which were 18% higher on felled trees than standing trees ($P<0.01$). Regardless of felling status, secondary shoots were more abundant on trees located in plots of higher tree density ($P<0.01$). Additionally, larger diameter trees were shown to support more secondary shoots ($P=0.03$).

Beaver browsing intensity (%) in a plot did not explain variation in the number of secondary shoots ($P=0.6$). Tree species identity was also investigated, and six species were recorded: willow (57%; n=81), birch (35%; n=50), alder (*Alnus glutinosa*) (3%; n=4) rowan (*Sorbus aucuparia*) (2%; n=3), ash (*Fraxinus excelsior*) (1%; n=2), and wild cherry (*Prunus avium*) (<1%; n=1). Willow and birch accounted for 92% of species recorded across the five beaver territories and were therefore the focus of the species analysis. The analysis showed that the number of secondary shoots were similar regardless of species with no significant difference between willow and birch ($P=0.9$).

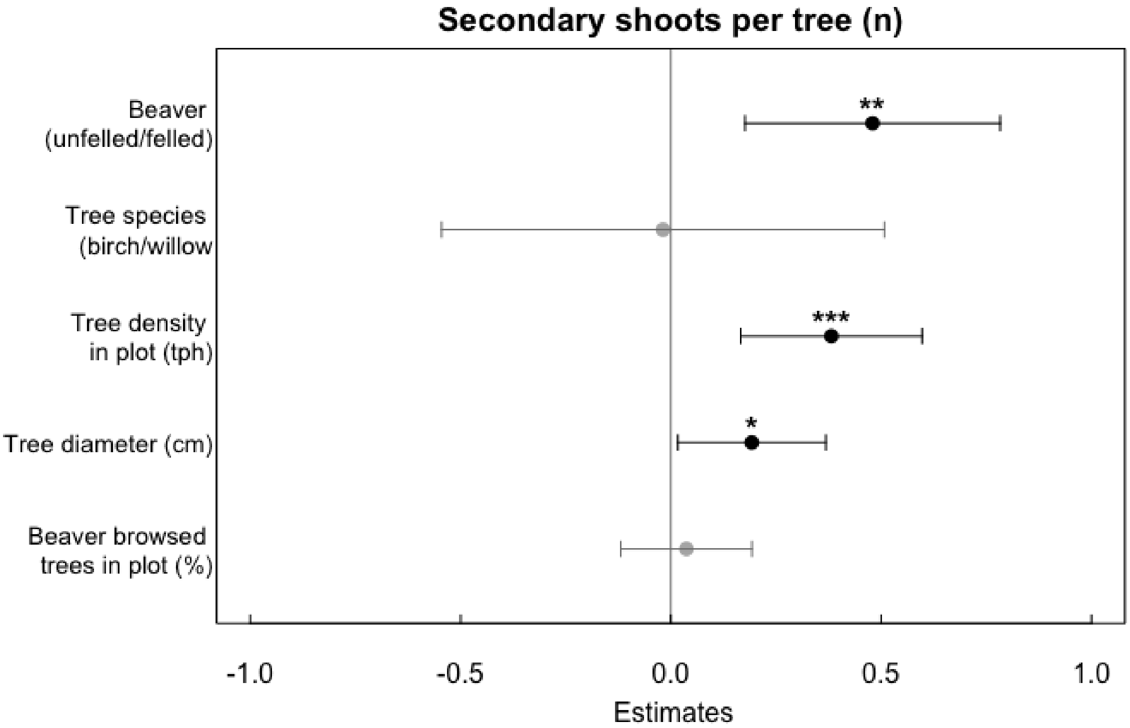

Figure 3.5. Forest plot output from a linear mixed model for response variable secondary shoots per tree (n). Predictors are coloured by significance (grey = not significant, black = significant). **P*=0.05; ***P*=0.01; ****P*<0.001.

The number of secondary shoots available to deer differed significantly amongst the three height categories (<50cm, 50-100cm, 100-150cm) (*P*=0.01) as well as between beaver-felled and standing trees (*P*<0.001) (see Appendix 3.2). These results were further reflected in a significant interaction between both height category and beaver felling in the model (*P*<0.001). Tukey post-hoc comparisons illustrated that beaver-felled trees had significantly more secondary shoots in two height categories: <50cm (*P*<0.001) and 100-150cm (*P*=0.02) compared to standing trees. In standing trees, the shoots were typically distributed relatively evenly across the three different height categories and thus could be said to be equally available to deer. In beaver-felled trees, the distribution of shoots showed more variation across height categories indicating a more heterogeneous organisation and were concentrated closer to the ground (Figure 3.6).

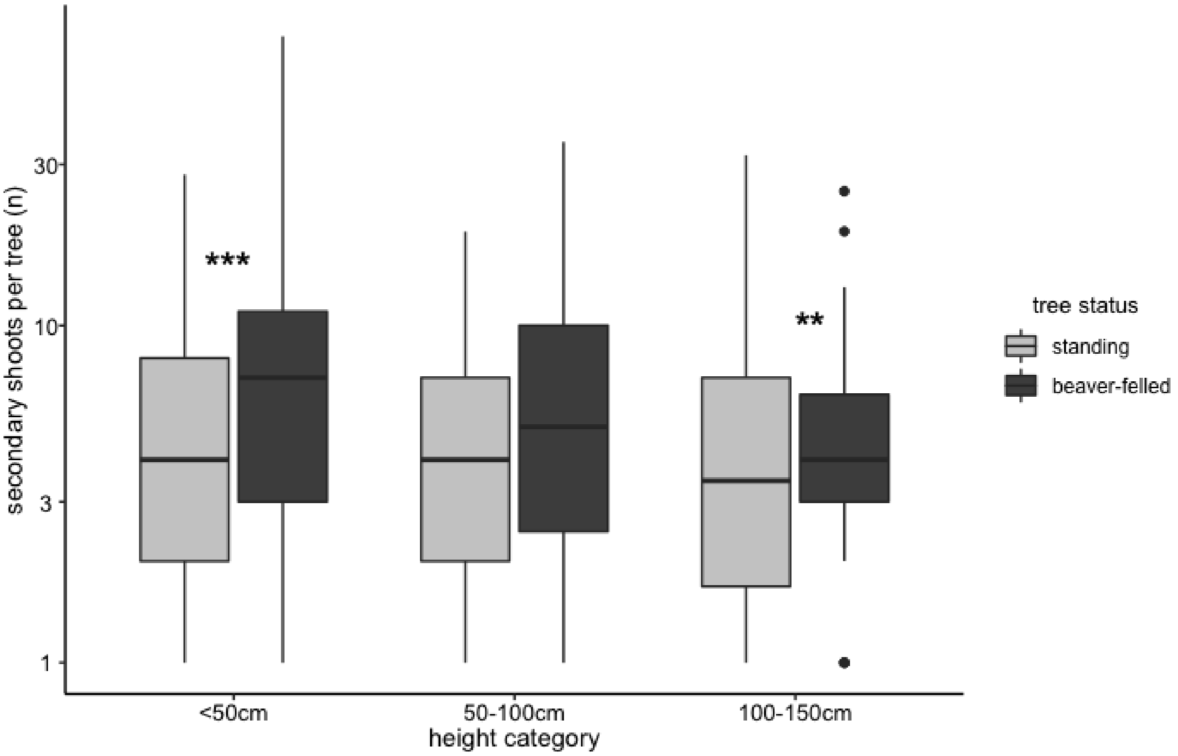

Figure 3.6. The height organisation of the number of secondary shoots (log scale) on trees (n=141) in three height categories <50cm, 50-100cm and 100-150cm in both standing and beaver-felled trees. Stars indicate significantly different mean numbers of shoots in height categories between beaver-felled and standing trees from a Tukey post-hoc groupwise comparison following the model summarised in Appendix 3.2 (**P*=0.05; ***P*=0.01; ****P*<0.001).

3.3.2. Forage quality

The total N content (%) of sampled shoots was significantly influenced by whether trees were felled by beaver (*P*<0.001) or browsed by deer (*P*=0.03; Figure 3.7a). The sampled secondary shoots from beaver-felled trees were 13% higher in N content than standing trees, implying that the former shoots were of higher dietary quality. By contrast, deer-browsed shoots demonstrated significantly lower N content (-8%) than unbrowsed shoots. There was no interaction between beaver felling and deer browsing. N content was also similar regardless of tree species (birch or willow) (*P*=0.6). The mean diameter of all sampled shoots was relatively small with little variation (2.3mm ±0.06 *SE*) and did not affect N content (*P*=0.4). The number of lateral branches on a sampled shoot also had no effect (*P*=0.7).

The relationship between C content (%) and the browsing of sampled shoots was less pronounced. The concentration of C had a marginal positive association with beaver felling although this effect was not significant (*P*=0.06; Figure 3.7b). No differences were observed between sampled shoots that were browsed and unbrowsed by deer (*P*=0.3). The concentration of C was, however, affected by tree species (*P*=0.03) with birch shoots more C-rich than willow. Sampled shoots with more lateral branches contained significantly less C (*P*<0.01). The concentration of C was not affected by any other morphological variables of sampled shoots such as the number of buds (*P*=0.3), or diameter (*P*=0.3).

The C:N ratio of sampled shoots showed a strong relationship with beaver felling (*P*<0.001; Figure 3.7c). Sampled shoots from beaver-felled trees had a 13% lower C:N ratio than unbrowsed trees, indicative of higher-quality forage. There were no significant differences in the C:N ratio of deer-browsed or unbrowsed sampled shoots (*P*=0.06), and there were no effects of any other variables in the model.

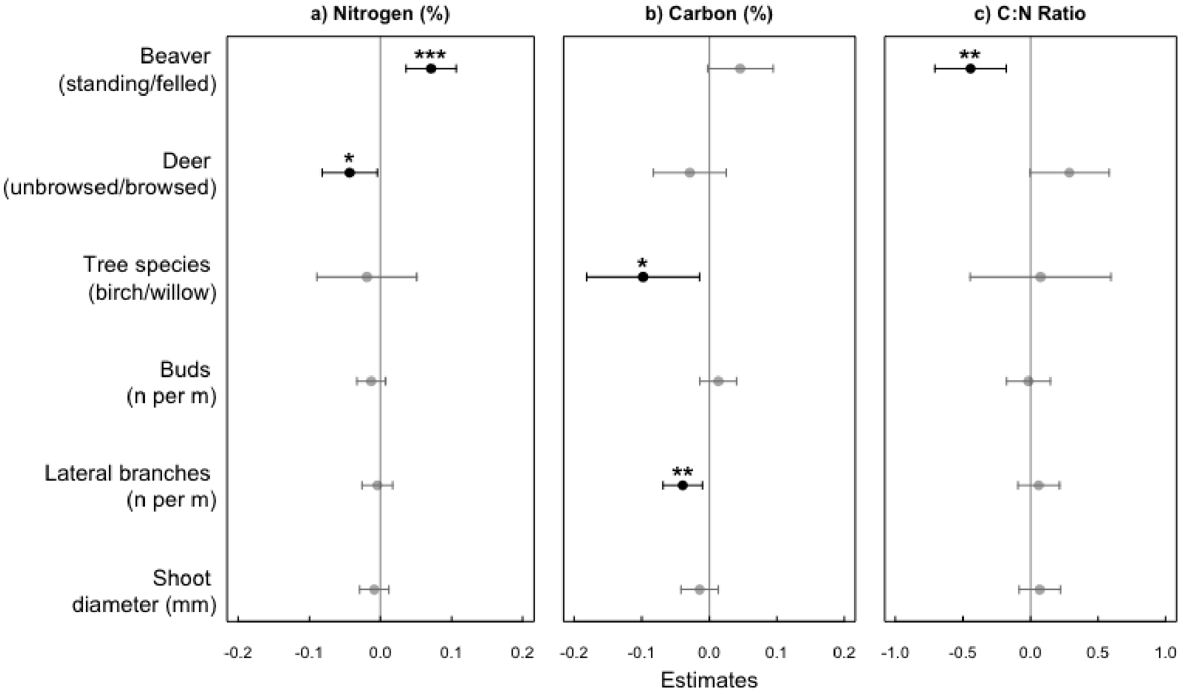

Figure 3.7. Forest plot outputs from linear mixed models for response variables a) nitrogen (N) (%), b) carbon (C) (%) and c) C:N ratio of sampled shoots. Predictors are coloured by significance (grey = not significant, black = significant). **P*=0.05; ***P*=0.01; ****P*<0.001.

3.3.3. Forage morphology

On average, there were 38 buds per metre (±1.2 *SE*, 14-97 bud range) of sampled shoots. The number of buds was significantly lower (-4%) in sampled shoots browsed by deer (*P*=0.02; Figure 3.8a), but beaver felling did not explain any variation in bud density (*P*=0.6). Buds were not affected by tree species (*P*=0.3) or diameter of the sampled shoot (*P*=0.5), but a strong, positive relationship between bud count and lateral branching was observed (*P*<0.001) (Figure 3.9).

There was an average of 6 lateral branches per metre (±0.4 *SE*, 0-29 branch range) on sampled shoots. Deer-browsed shoots were visibly more branched and had a significantly higher number (+27%) of lateral branches compared to unbrowsed shoots (*P*<0.001; Figure 3.8b). There were no effects of beaver felling on lateral branching (*P*=0.1). Tree species had a significant effect in the model (*P*=0.01) with birch trees having 27% more lateral branches than willow. No relationship between lateral branching and sampled shoot diameter was observed (*P*=0.2).

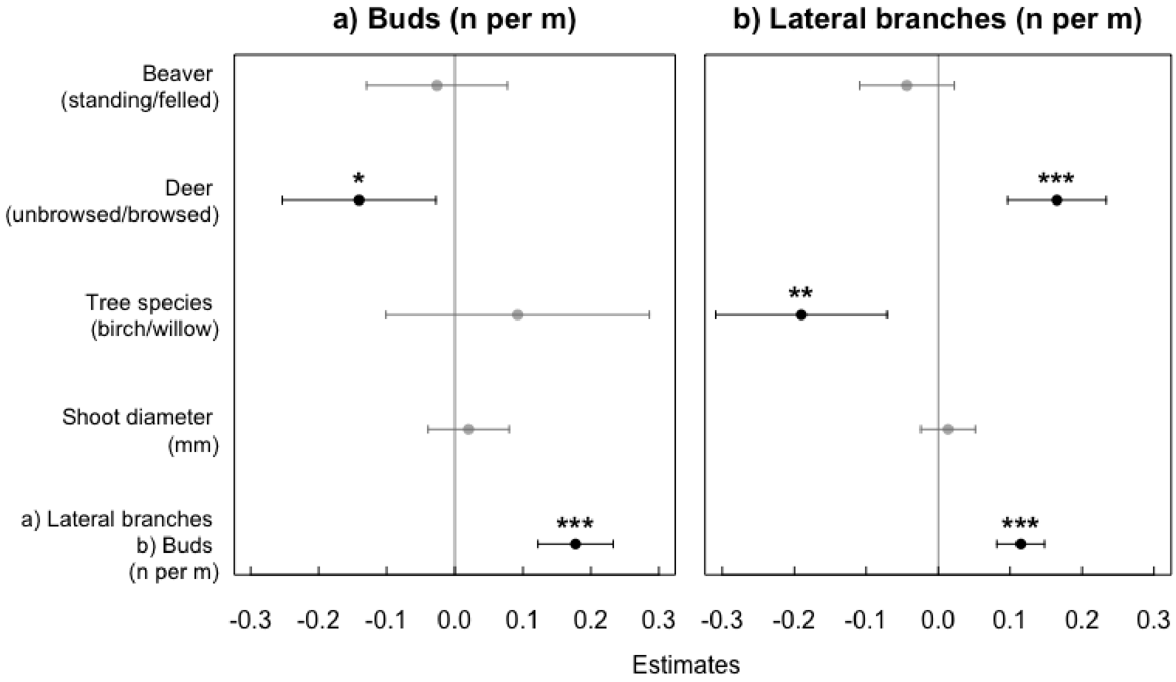

Figure 3.8. Forest plot outputs from linear mixed models for response variables a) buds (n per metre), and b) lateral branches (n per metre). Note that predictor 'lateral branches' is only included in plot A and 'buds' is only included as a predictor for plot B. Predictors are coloured by significance (grey = not significant, black = significant). **P*=0.05, ***P*=0.01, ****P*<0.001.

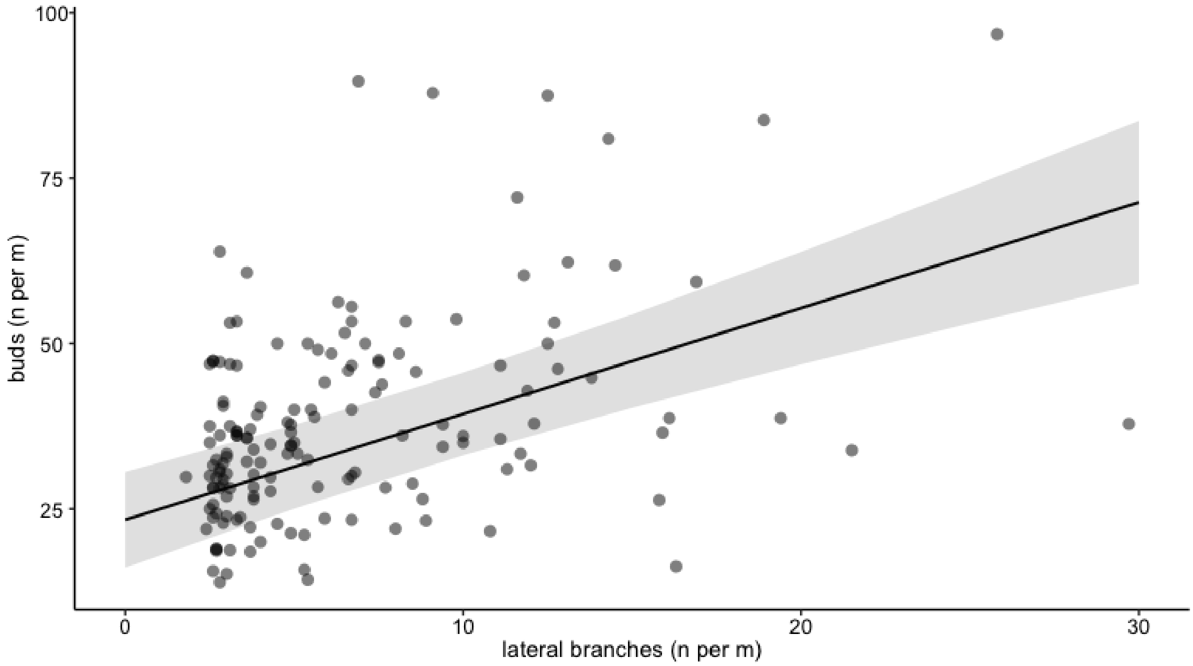

Figure 3.9. Relationship between the buds (n per metre) and lateral branches (n per metre) on sampled shoots subjected to a range of beaver and deer browsing treatments. Plotted points represent raw data values and the line represents overall model fit in Figure 3.8.

3.3.4. Apical bud vs apical shoot

When assessing for possible nutritional differences between the C and N content of the apical bud vs apical 5cm length of the apical shoot, N content was found to be significantly higher in apical buds (+39%) than apical shoots (*P*<0.001; Figure 10). There were also differences in the C content (*P*<0.001) and apical buds contained on average 13% more C than apical shoots (see Appendix 3.3).

Although buds contained higher N, the mean fresh weight of an individual apical bud was very small (1.7 ±0.1 mg *SE*) when compared to the mean fresh weight of an individual 5cm length of apical shoot (18 ±1 mg *SE*). Since mean bud weight typically accounted for a relatively small proportion of shoot weight (mean 8.5%), it was considered very unlikely that the apical bud removal by deer could alone account for the significantly lower N content observed in the deer-browsed sampled shoots.

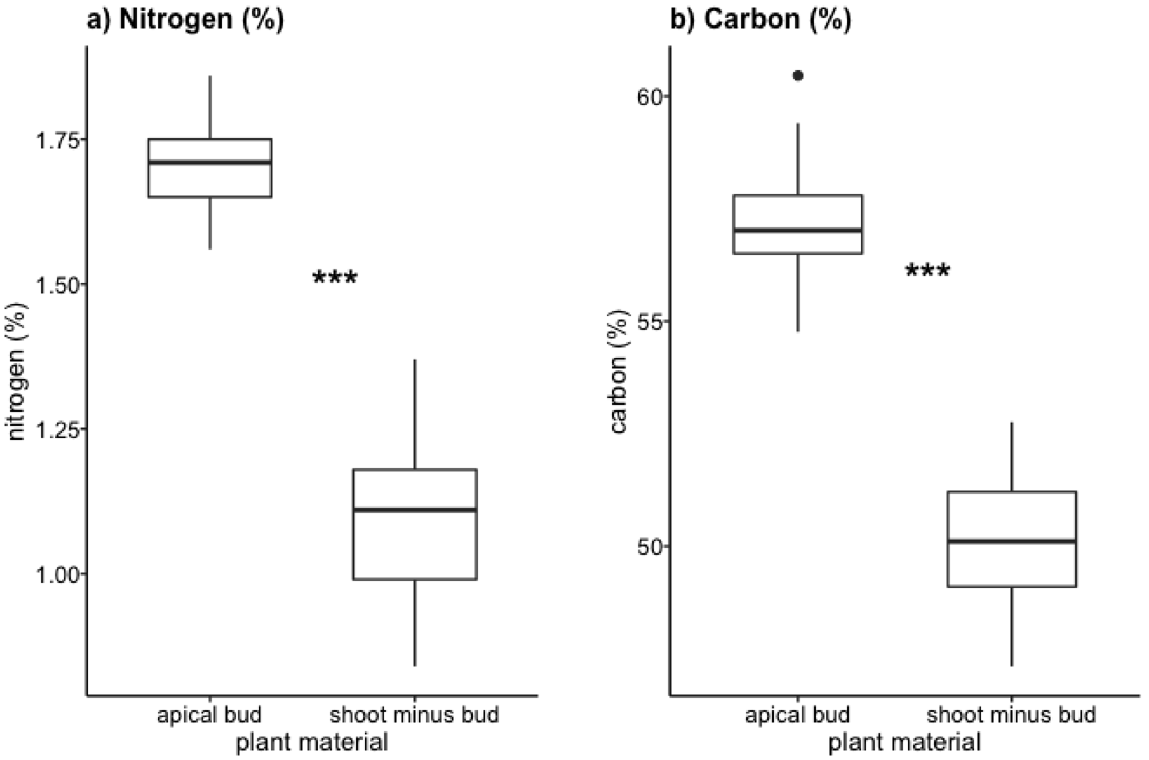

Figure 3.10. The nutritional concentration of a) nitrogen (%), and b) carbon (%) in plant material (apical bud vs shoot minus bud) collected from an additional subset of unbrowsed sampled shoots. Stars indicate *P*<0.001 (model output in Appendix 3.3).

3.4. Discussion

Beaver-felled trees supported more regrowth which was concentrated closer to the ground and therefore readily accessible to browsing deer. Secondary shoots from resprouted beaver-felled trees were also higher in quality and contained more N and C than those from standing trees. Shoots browsed by deer from all trees however, contained less N, were more branched, and had fewer buds relative to unbrowsed shoots. We discuss the reasons for this apparent inconsistency below. We also discuss how our findings help bridge a current knowledge gap in beaver-deer interactions and can act as the foundation of a wider understanding to inform adaptive species management.

3.4.1. Beaver felling: implications for woodland regeneration

The finding of a large proportion of beaver-felled trees (62%) with resprouted secondary shoots is consistent with previous research in Scotland where similar resprouting rates have been reported in a range of broadleaf species (Jones et al., 2009; Iason et al., 2014). Many broadleaved species will sprout vigorously following cuts or stress (Koop, 1987). This adaptation has likely developed over millions of years of co-evolution alongside the pressure of grazing herbivores (Del-Claro & Torezan-Silingardi, 2021). In our study, it was evident that mature birch and willow trees had been transformed into stumps with a multi-stemmed architecture of young resprouted secondary shoots. A similar effect is achieved through coppicing by people which is one of the earliest known forms of woodland management (Buckley, 2020). Coppicing creates structural heterogeneity which is linked to high biodiversity and conservation value (Kirby et al., 2017). Our results highlight the importance of beavers in a self-regulating woodland regeneration system.

3.4.2. Forage availability

Our results indicate that beaver herbivory significantly increases the available forage to browsing deer in riparian woodlands, which confirms our first hypothesis. Habitat use by deer is strongly determined by the availability of food (Palmer & Truscott, 2003; Borowski et al., 2021). By providing a novel resource of forage that would have otherwise been absent prior to the beaver's reintroduction, tree-felling by beaver may indirectly exert an influence on the distribution of deer. The length of time required to search for food also plays an important role in deer foraging (Nudds, 1980). The spatial arrangement of an increased abundance of secondary shoots concentrated around the base of a beaver-felled tree may help reduce forage search time for deer and increase efficiency. It is known that roe deer can track changes in resource availability by relying on memory rather than perception (Ranc et al., 2021). We hypothesise that well-established beaver territories may therefore face higher browsing pressures from deer than newly-established territories.

As the majority of beaver activity is concentrated within 10m of the water's edge (Haarberg & Rosell, 2006; Janiszewski et al., 2012; Wazna et al., 2018) we anticipate this zone as the interface of beaver-deer interactions. Obstacles in woodlands (such as large logs) have been shown to prevent deer from accessing saplings which influences their foraging decisions (van Ginkel et al., 2021). Fallen logs from surrounding beaver-felled trees, as well as flooding from localised beaver damming may pose barriers to deer access to some resprouted secondary shoots. Although localised deer densities are difficult to accurately ascertain (Smart et al., 2004), roe deer are known to tolerate wading through wetter foraging grounds to selectively access higher quality browse (Barančeková, 2004). In contrast, a recent study in Denmark demonstrated that roe and red deer actively avoided areas of high beaver activity (Svanholm Pejstrup et al., 2023). However, research in Scotland reported that 68% of beaver-browsed trees located within 30m of the water's edge were browsed by deer (Iason et al., 2014). Furthermore, all deer-browsed shoots in our study were sampled within 10m of the water's edge, indicating that deer do readily utilise this food resource, despite potential barriers from localised habitat modifications by beaver.

3.4.3. Forage quality

Our hypothesis that secondary shoots from resprouted beaver-felled trees were significantly more nutritious than those from standing trees was confirmed. High N concentrations are known to occur in young, fast-growing tissues to support rapid protein synthesis during bursts of growth (Mattson, 1980). Previous research has illustrated that herbivory can induce nutritional changes of C and N in woody plants (Bryant et al., 1983). As N is an essential dietary nutrient and limiting element for herbivores (Mattson, 1980), deer are likely to prefer shoots with elevated N concentrations. Secondary metabolites that serve as plant defence chemicals also play a role in forage palatability for deer (Budny et al., 2021). Resprouted secondary shoots following North American beaver felling in Fremont cottonwood trees had 14-20% higher N (but the same C) when compared to standing trees (Martinsen et al., 1998; Durben et al., 2021). The findings of both studies were consistent with our own findings despite differences in tree (and beaver) species.

In contrast, we found that deer-browsed shoots were lower in N than unbrowsed shoots. From our study design, it is impossible to ascertain whether deer are preferentially selecting shoots lower in N, or that shoots become lower in N as a result of deer browsing. Deer-browsed shoots were characterised by the removal of the N-rich apical bud. However, it was concluded that apical bud removal alone could not account for the lower N levels due to the low proportion of weight contributed by buds to an intact shoot. Furthermore, the number of buds on shoots also did not account for any variation of N in our model. Nonetheless, the apical bud plays an important role in shoot growth through hormone regulation whilst acting as the main meristem (Muller & Leyser, 2011). Therefore, potential consequences for shoot growth arising from apical bud removal by deer on the secondary shoots from beaver-felled trees should not be underestimated.

Most of the literature implies that roe deer actively select the most nutritious forage (P. Duncan et al., 1998; Mancinelli et al., 2015) which suggests that the lower N content we observed in browsed shoots is a physiological response to deer browsing. However, the nutritional status of shoots would need to be assessed before and after deer browsing to explicitly determine cause and effect. Trees have been shown to respond to unidentified elicitors in the saliva of roe deer, resulting in changes in phytohormone levels that regulate physiology and development, as well as secondary metabolites that act as defence chemicals (Keefover-Ring et al., 2016; Ohse et al., 2017; Barrere et al., 2022). Similar effects have also been observed with moose saliva (Bergman, 2002). Other factors, such as beaver saliva could pose a similar elicitor effect on trees during felling, ultimately influencing the chemistry of secondary shoots.

3.4.4. Forage morphology

Plant morphology can play a role in ungulate foraging selection (Shipley et al., 1998; Prendeville et al., 2015). For example, cafeteria-style experiments with red deer showed a preference for browsing on taller Sitka spruce saplings (*Picea sitchensis*) (A. Duncan et al., 1998). A similar experiment tested red deer foraging preferences for different forms of oak saplings (*Quercus pedunculata*) (Drexhage & Colin, 2003; Renaud et al., 2003). They offered saplings that were structurally ‘normal’ (control), ‘bushy-topped’ (top-heavy without apical dominance) and ‘five-shoot’ (a multi-stemmed coppice-like form). Their results showed that red deer had a significant preference for browsing on the coppice-like structure of oaks over the others. In our study, individual shoots from resprouted beaver-felled trees did not differ morphologically in their number of buds or branches when compared to standing trees. However, collectively, the shoots from resprouted beaver-felled trees were significantly higher in density and had a distinct height distribution arising from fixed points on the stump. This arrangement is likely to make them more conspicuous to browsing deer and influence their attractiveness.

Secondary shoots that sprout following cuts or stress are capable of forming large trees (Koop, 1987) and are therefore arguably of higher ecological importance than lateral branches. From our study, it cannot be distinguished whether deer selected branchier shoots with fewer buds, or that shoots produced more branches and fewer buds in response to deer browsing. Research comparing fenced and non-fenced plots of young oak (*Quercus petraea*) noted that trees browsed by large herbivores were significantly more branched (Drexhage & Colin, 2003; Churski et al., 2022). An increase in lateral branching has even been proposed as a defence mechanism that acts as a “cage” around larger trees to physically prevent herbivores from accessing vulnerable leader stems (Churski et al., 2022). As well as lateral branching, herbivore browsing has also been suggested to stimulate changes in morphology in birch trees, inducing compensatory growth of dormant buds to produce long-shoots with more leaves than unbrowsed shoots (Danell et al., 1985; Herder et al., 2009). This implies that a change in shoot morphology in our study may have occurred *after* deer browsing, potentially as a compensatory growth strategy, rather than our findings depicting an initial preference for branchier shoots.

3.5. Conclusions

Tree felling by beaver creates a heterogeneous habitat mosaic of mature trees and juvenile resprout growth which results in an indirect interspecific interaction with deer in riparian woodlands through a change in resource availability. Although it is unclear if the secondary shoot growth can completely replace the trees felled by beaver, our study confirms that beaver-felling promotes habitat complexity through the growth of multi-stemmed architecture of secondary shoots. We present evidence that deer are likely to be attracted to the secondary shoots from beaver-felled trees by confirming three (non-mutually exclusive) hypotheses. Our finding that secondary shoots from beaver-felled trees were a) more abundant, b) nitrogen-enriched and c) distinctly distributed when compared to standing trees suggests that deer will be attracted to this readily available, nutritious, and conspicuous resource. This change in resource availability is likely to have significant implications for deer distributions and ongoing riparian woodland management that merits longer term study where beaver and deer interact.

CHAPTER 4: SIMULATED BEAVER-DEER INTERACTIONS AND THEIR EFFECTS ON AN EXPERIMENTAL RIPARIAN WOODLAND.

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4.0. Abstract

Riparian woodlands are high conservation value habitats but can be dramatically affected by large browsing herbivores. The Eurasian beaver (*Castor fiber*) is an ecosystem engineer that is expanding across Scotland following a long absence, into riparian woodlands already being structurally affected by deer. Beaver-deer interactions are understudied in Europe, despite economic and conservation implications. Here we show, based on tracking the growth of experimental willow stands, how deer browsing affects beaver-coppiced trees. Grey willow (*Salix cinerea)* saplings, common in beaver diets, were planted to mimic 96 resprouted beaver-felled trees in paired exclosures located along a soil moisture gradient in Scotland. Saplings were left to develop for two growing seasons to simulate an abandoned beaver territory. Winter browsing by roe deer (*Capreolus capreolus*) was simulated by clipping shoot tips at two intensities (intermediate and heavy). Traits indicative of tree resource allocation, growth, and structure (specific leaf area, height, diameter, leafy growing tips) were measured over the year, before and after clipping, and compared with that of unclipped control trees in a Before-After Control-Impact experimental design. We found that clipping elicited changes in resource allocation, tree growth and structure, but responses varied with clipping intensity. Relative to controls, intermediate clipping resulted in trees with 13% fewer leafy growing tips, while heavy clipping promoted a 5% increase in height. The vertical distribution of leafy growing tips in clipped trees differed from controls with 28-32% fewer growing tips located in the height range most accessible to roe deer (50-100cm). Soil moisture was found to exert a strong, positive influence on tree resource allocation as well as maximum height and diameter. Our findings show that tree response to heavy clipping was consistent with compensatory growth to recover biomass, leading to 'spindly' trees. Intermediate clipping may divert willow resource allocation to defence over time, most likely to deter future deer herbivory. We hypothesise deer browsing of resprouted beaver-felled trees can suppress tree growth, but effects will depend on deer density. Changes in soil moisture

associated with beaver damming may also play an important role in regulating beaver-deer interactions and tree responses.

4.1. Introduction

Riparian woodlands provide invaluable ecosystem services and play an integral role in the transfer of energy between terrestrial and freshwater ecosystems. They can provide structural diversity, which in turn allows them to act as a stronghold for biodiversity (Przepióra & Ciach, 2022), whilst serving as effective wildlife corridors (Corbacho et al., 2003). Experimental riparian woodland removal has emphasised their role in regulating nutrient dynamics, sediment, and bank stabilisation (Larson et al., 2018). They can buffer the aquatic environment from effects of agricultural diffuse pollution (Turunen et al., 2019). Planting of riparian woodland is also a feasible mitigation option for easing climate change effects by regulating rising water temperatures through increased shading (Turunen et al., 2021). Allochthonous inputs of leaf litter from riparian woodlands are also drivers of basal energy flow in most small stream food webs (Effert-Fanta et al., 2022; Erdozain et al., 2021). In Europe, most freshwater habitats were historically bordered by riparian woodlands (Brown et al., 2018). However more recently, temperate riparian woodlands are considered threatened habitats (Janssen et al., 2016). In Scotland, surveys have found that over 50% of riparian vegetation is in poor condition with no woody vegetation lining banks and shores (Ogilvy et al., 2022).

Following near-extinction due to prolonged hunting pressures, the Eurasian beaver (*Castor fiber*) has now recently recolonised riparian woodlands across much of its former European range through reintroduction projects and natural dispersal (Wróbel, 2020; Halley et al., 2021). Beaver dam building can raise water levels and help transform degraded riparian woodland into a mosaic of complex wetlands by boosting biodiversity and habitat heterogeneity (Willby et al., 2018; Law et al., 2019). Beavers are also widely known for their ability to influence the structure of riparian woodlands through the cutting and felling of trees. Beaver browsing can elicit regenerative responses in trees whereby multiple shoots sprout from beaver-felled stumps as a natural form of coppicing (Iason et al., 2014; Jones et al., 2009). These unique damming and tree-felling abilities have led to beavers being labelled as ‘ecosystem engineers' (Jones et al., 1994) and placed them at the forefront of stream restoration projects (Pollock et al., 2014; Brown et al., 2018). However, beavers are also being returned (often after long absences) to riparian woodlands in parts of Europe that are already profoundly altered by native large herbivores.

Around 90% of Europe is occupied by at least one species of wild ungulate (Linnell et al., 2020). In Scotland, deer (Cervidae) browsing impacts are considered a major threat to native woodland regeneration (Burton et al., 2018; Ogilvy et al., 2022). Deer can strongly influence vegetation dynamics (Gill, 1992b; Hester et al., 2010) and their populations are managed throughout Europe as a result (Reimoser & Putman, 2011). While deer browsing is a natural component of many woodland ecosystems, excessive levels of browsing can negatively impact ecological function (Ramirez et al., 2018). Negative effects of deer browsing can be observed at a local-scale (Joys et al., 2004) but also at a landscape-level (Petersson et al., 2019). Deer browsing of coppiced shoots, seedlings and saplings inhibits woodland regeneration (Gill, 2000; Tanentzap et al., 2009) raising concerns for riparian woodlands of conservation value. Even at relatively low deer densities (e.g., 4-6 deer km^{-2}), damage can be substantial and is thought to be influenced by additional factors such as climate and landscape characteristics (Tanentzap et al., 2009; Jarnemo et al., 2014; Spake et al., 2020). Deer are thought to shift their diets seasonally and generally increase the number of woody plants in their winter diet (Spitzer et al., 2020). Willow (*Salix* spp.) can form a substantial component of roe deer diets in winter (Czernik et al., 2013; Krasnov et al., 2015) when there are fewer alternative herbaceous plants.

Plant functional traits can be effective indicators when predicting woodland responses to herbivore grazing (Díaz et al., 2016). Specific leaf area (SLA hereafter) is the ratio of one-sided leaf area to leaf dry mass (mm^2mg^{-1}) and acts as a general indicator of plant resource allocation and relative growth (Ianovici et al., 2015; Díaz et al., 2016). In response to deer browsing, fast-growing species (such as willow) can allocate resources into carbon acquisition to offset loss in biomass (Palmer & Truscott, 2003). Other tree species invest more resources into defence in response to browsing, relying on phenolic compounds to reduce palatability or physical defences such as thorns or thickened leaves to deter grazers (Coley, 1983; Milewski et al., 1991; Shelton, 2000; Iason, 2005). As a result, fast-growing species tend to have higher SLA and are often more palatable to herbivores, whilst defence strategists must invest less in growth and consequently often have a lower SLA (Abdala-Roberts et al., 2018; Cornelissen et al., 2003). Deer browsing is generally thought to influence plant growth, structure, and resource allocation. However, the precise effects on individual trees and the dynamics of woodlands are highly context-dependent (Hester et al., 2010). Effects can differ with trees species and age, as well as browsing timing and intensity. Numerous abiotic conditions also play a role (Gill, 1992b). Therefore, the impacts of deer browsing on trees are difficult to generalise. Understanding the drivers of this variability is crucial to predict the responses of riparian ecosystems to ongoing environmental changes.

All native European broadleaved tree species are capable of coppicing or suckering in response to herbivore browsing (Koop, 1987). Research in Knapdale Forest, Scotland, has documented resprouting in up to 58% of beaver-browsed trees in woodland plots. However, this research also highlighted that 68% of the resprouted trees were subsequently browsed by deer (Iason et al., 2014). If regrowth from beaver-felled trees is subsequently browsed by deer, impeding further growth, there could be a simplification in the structure of the woodland, and potentially deterioration or even loss of the habitat. Despite the implications for riparian woodland management and conservation, the potential woodland impacts of beaver-deer interactions is unstudied in a European context. In North America, potential changes in forest structure and regeneration processes due to beaver-deer interactions have been highlighted, where intense herbivory by large herbivores can disrupt natural beaver-willow mutualisms and might even exclude beavers at higher herbivore densities (Baker et al., 2005; Hood & Bayley, 2009; Baker et al., 2012; Loeb et al., 2022). Those findings now require application to a European context where the pre-existing effects of excessive deer browsing, well recognised as being detrimental, could potentially be exacerbated by the addition of returning beavers.

In this study, a novel experimental approach was used to assess the impacts of deer browsing on beaver-influenced riparian woodlands. In Perthshire, Scotland, experimental willow stands were established in deer-proof enclosures to mimic a riparian woodland formed from resprouted beaver-felled tree stumps over a distance from the water's edge within which beaver would normally feed. Trees were then manipulated by clipping in winter to simulate deer browsing before being re-measured after one growing season. Our study aimed to determine the effects of intermediate and heavy clipping intensity on the following characteristics of trees: a) SLA, b) height, c) diameter, as well as d) abundance and density of leafy growing tips. As soil moisture can play an important role in tree growth in response to herbivory (Bilyeu et al., 2008; Johnston et al., 2007), the interaction of these responses to clipping with soil moisture were also determined. We hypothesised that simulated winter deer browsing would result in trees of a higher SLA, height, and diameter - consistent with documented growth responses to browsing. A reduction in the abundance and density of leafy growing tips, as well as an overall effect of soil moisture, were also expected.

4.2. Methods

4.2.1. Study site

The study site is located on a 520-ha privately-owned estate in Perthshire, Scotland (56° 38' 57.3"N, 03° 16' 59.9"W). Land use on the estate is predominantly organic agriculture with grazing livestock including sheep and cattle, as well as ecotourism. Woodland habitat is scattered and comprises plantations, conifers, and native hardwoods. The experiment was established on a 3-ha patch of sloping semi-improved neutral grassland in the west of the estate, bordered by a spring-fed burn (depth 0.1-1m). Eurasian beavers have been present on the estate since 2002 and have bred annually since 2005. During this study, three-four established beaver families were present, each consisting of a minimum of a breeding pair and two sub-adults and/or kits. Roe deer and small herbivores such as brown hare (*Lepus europaeus*), rabbit (*Oryctolagus cuniculus*) and bank vole (*Myodes glareolus*) are also present.

4.2.2. Experimental design

We employed a Before-After-Control-Impact (BACI) design (Stewart-Oaten et al., 1986) to evaluate clipping treatment effects whilst considering the natural variation in tree growth between growing seasons. In April 2019, three paired 10m x 10m exclosures (each 100 m^2) were established along a perpendicular transect from the edge of a stream. Paired exclosures (labelled A-F (Figure 4.1)) were located at 0-10m, 30-40m and 50-60m from the stream. A total of 576 grey willow (*Salix cinerea*) saplings were sourced from a local nursery and planted in a specific formation to mimic a resprouted tree previously felled by beaver. The planting formation (herein referred to as 'clusters') consisted of one taller sapling (50cm in height) surrounded by four-five shorter saplings (20-30cm in height). The taller sapling represented the felled tree stump and the surrounding shorter saplings represented secondary shoots that had resprouted in response to the felling (Figure 4.2).

Sixteen clusters of saplings were planted at 2m spacing inside every exclosure, totalling 96 simulated resprouted beaver-felled 'trees.' Each individual sapling was labelled with a unique numbered waterproof tag detailing its exclosure, cluster, and an individual sapling identification number to allow reliable repeated measurements. Saplings were protected from small rodents with one-two stacked 20cm tall 'Tubex vole-guard(s)' and support was provided with a 1m-tall bamboo cane during the first 6 months of sapling growth. Large herbivores were excluded from each exclosure using a double row of short fencing (90cm tall) which consisted of an inner standard stock fence with a rabbit-netting underlayer, as well as an outer row of single line-wire. Saplings were untouched for two full growing seasons to mimic an abandoned beaver territory before the survey period commenced in August 2020.

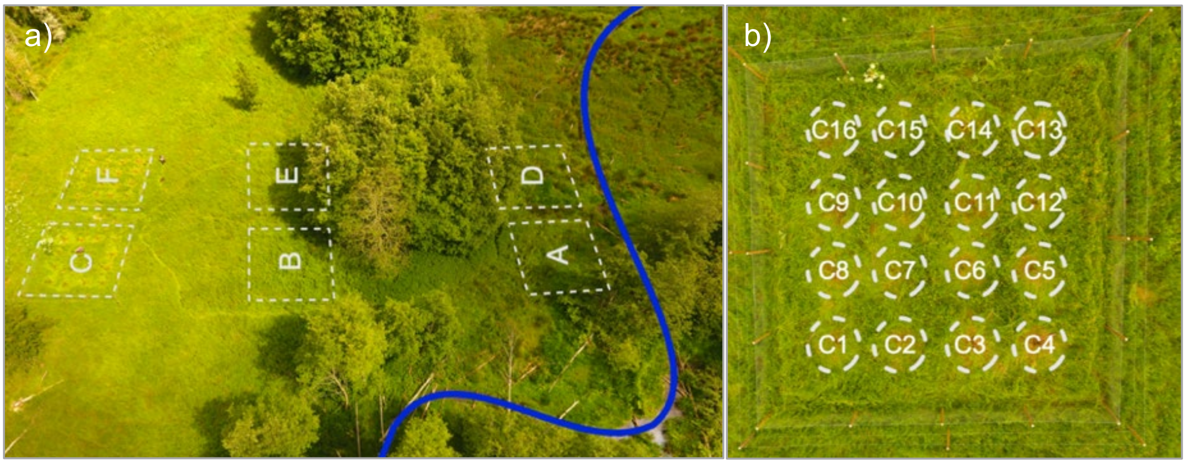

Figure 4.1. Aerial photos of a) the six outlined 10 x 10 m exclosures labelled A-F (the blue line indicates the stream) and b) and within-exclosure 'cluster' organisation labelled 1-16.

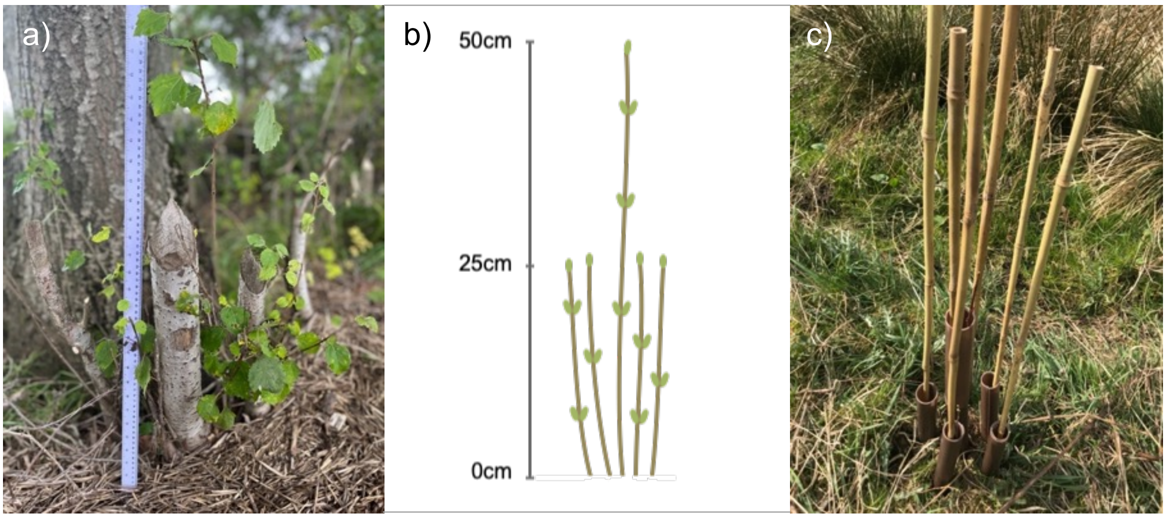

Figure 4.2. Photo of a) resprouted beaver-felled tree stump (Populus spp.) and diagram representation of b) of a planted tree cluster in our study (one taller sapling surrounded by four-five shorter saplings). Photo of c) planted tree cluster in April 2020 with vole guards and bamboo cane supports.

4.2.3. Field surveys

Trees were monitored between August 2020 and August 2021 (one growing season). Exclosures were becoming dominated by coarse grasses (*Dactylis glomerata*, *Arrhenatherum elatius* and *Holcus lanatus*) and ruderal species (*Urtica dioica* and *Rumex obtusifolius*), so a $1m^2$ radius around each tree cluster was cleared by trampling prior to the growing season to facilitate surveyor access. At the start of the monitoring period, a total of 336 saplings remained (overall initial survival rate of 58%) with all but one planted cluster containing surviving trees (see Appendix 4.1 for summary statistics). Diameter of every tree was measured to the nearest 1mm at ~5cm from the ground using callipers. Height (cm) of each tree was measured initially using a tape measure in 2020 and subsequently with a 3m survey-staff in 2021. At each cluster, three soil moisture readings were taken using a soil moisture probe (Delta T-Devices, HH150 model) and the mean (%) was calculated.

At the start of the monitoring period, the number of growing tips were counted per tree. Growing tips were classified as points of leafy growth on branches (a pair of leaves that could form a branch or shoot) (Figure 4.3a). Over the course of the experiment, the foliage of trees became too abundant/dense to then reliably determine the number of growing tips per tree. At the end of the experiment, growing tips were therefore alternatively counted on a cluster-basis.

A grid constructed with 2m length bamboo canes was used to categorise growing tips into four height bands (cm): <50, 50-100, 100-150, and >150 (Figure 4.3b). Density of growing tips (n per cm) was calculated by dividing the total number of growing tips per tree cluster by the summed total of tree height per cluster.

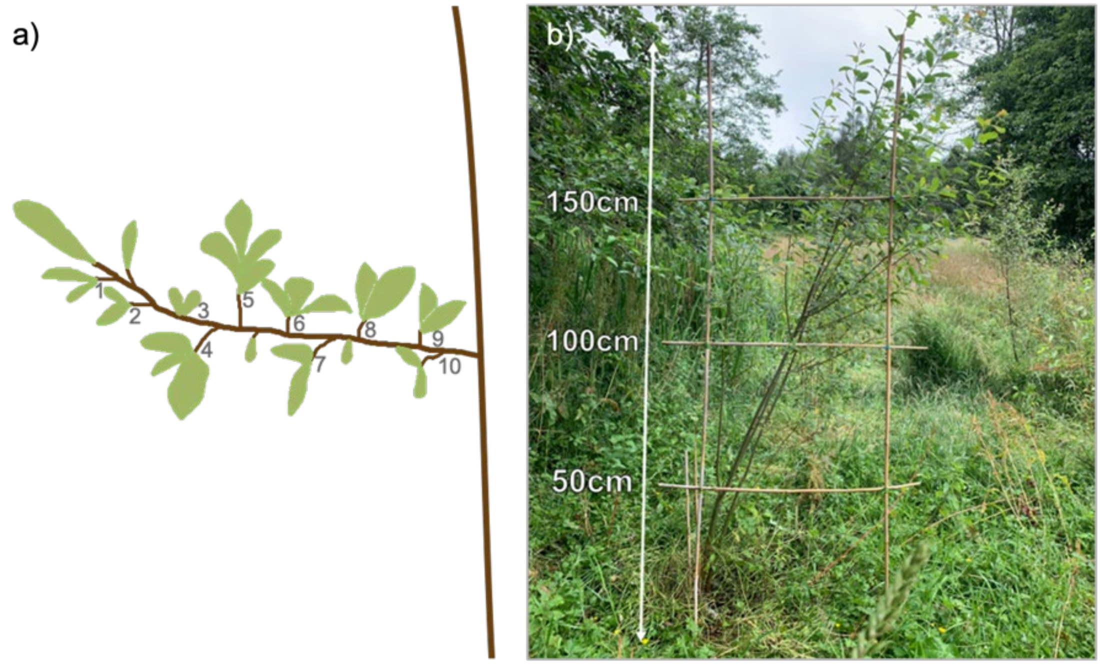

Figure 4.3. Diagram of a) typical willow branch and example of leafy growing tip counting where numbers represent each counted leafy growing tip, and photo of b) bamboo cane 'grid' used to count and categorise leafy growing tips into four height bands: <50cm, 50-100cm, 100-150cm and >150cm.

4.2.4. Simulated browsing

Winter deer browsing was simulated through the manual process of clipping trees in early March 2021 (halfway through the monitoring period). Simulated deer browsing (herein 'clipping') was carried out on a cluster basis. The total number of growing tips located <150cm from the ground was counted per cluster before calculating how many growing tips to clip. Clipping treatments consisted of the following three levels: a) no tips clipped (control), b) 33% of tips clipped (intermediate), and c) 66% of tips clipped (heavy). These clipping intensities were chosen to reflect a spectrum of the maximum browsing intensity (68%) that was reported on resprouted beaver-felled trees in Knapdale Forest (Iason et al., 2015). Leafy growing tips were clipped in a tearing motion using the blunt side of standard scissors. This motion aimed to mimic the hard upper mouth plate of roe deer and the frayed edge characteristic of roe deer-browsed shoots (Bang & Dahlstrom, 1972). Growing tips were clipped randomly but only within the height accessible to browsing roe deer (0-150cm). Clipping treatments were dispersed throughout each exclosure with the following conditions: (i) no two same treatments were applied in adjacent clusters; (ii) only one treatment type in each row was replicated, and (iii) all three treatments were represented in every row (see Appendix 4.2).

4.2.5. Specific leaf area (SLA)

To measure SLA, five leaves (sub-replicates) were taken from the tallest tree in each cluster (replicates) at the start (n=474 leaves), and end (n=472 leaves) of the monitoring period. Leaves were stored in paper bags to absorb any moisture and aid preservation. Each leaf was individually photographed within 48 hours of picking, and its total surface area (mm^2) was measured using ‘LeafByte’ (v1.3.0) software. The leaves were oven-dried at 60°C for 48 hours and their dry mass (mg) was measured to three decimal places. SLA (mm^2mg^{-1}) was calculated as [leaf area (mm^2)/leaf mass (mg)] and mean SLA was determined for each tree cluster.

4.2.6. Statistical analyses

Statistical analyses and graphs were produced using packages lme4, car, rescale, and ggplot2 in R Studio (v1.4.1103). Response variables were transformed to meet model assumptions of normal distribution where specified. Models were selected for performance based on those with the lowest Akaike Information Criterion (AIC) scores.

Explanatory variables

Soil moisture was converted to a scale to minimise the effects of high temporal variation in rainfall. Mean soil moisture (%) at the start and end of the monitoring period were scaled separately using the ‘rescale’ function in R Studio so that each set of values ranged from one (driest) to ten (wettest). Clipping was included in all models as a three-level factor (control, intermediate and heavy). Potential collinearity among explanatory variables was assessed using variance inflation factors (VIF), and a Pearson correlation test. Tree diameter and height were collinear ($P<0.001$) and were therefore never included in the same model.

BACI approach

Linear mixed models were used to investigate the following five response variables: mean SLA (mm^2mg^{-1}; square root transformed), mean tree height (cm; square root transformed), mean diameter (cm; log transformed), total leafy growing tips (n; square root transformed) and density of growing tips (n; square root transformed). Explanatory variables included were year (2020 or 2021), clipping intensity (control, intermediate, heavy) and soil moisture (scale 1-10). In line with the BACI approach, we fitted 'year' × 'clipping' as an interaction term in each model to test if clipping resulted in a change in tree responses that differed from controls (unclipped trees) over the growing season. 'Tree cluster' (A1, A2 etc.) was included as a random effect to account for repeated observations between years.

Relative between-season change

The maximum tree height (cm) and maximum diameter (cm) for each tree cluster was determined and their relative between-season change was calculated (%). To assess the effects of soil moisture on tree growth, relative change in maximum tree height and diameter (%; both square root transformed) were fitted in linear mixed models with soil moisture (scale 1-10) as the explanatory variable. Soil moisture data in 2020 and 2021 were averaged before scaled from one (driest) to ten (wettest). The effects of clipping could not be tested on relative change in maximum tree height or diameter as clipping was carried out at a tree cluster-level rather than individual-tree level. Therefore, it could not be guaranteed that a specific tallest or thickest stem was clipped precisely at intermediate or heavy intensity. 'Exclosure' (A, B, C etc.) was included as a random factor to account for repeated measurements within sampling locations.

Vertical growing tip distribution

The vertical leafy growing tip distribution of trees in 2021 was investigated by fitting the total number of leafy growing tips (n) per cluster located in the each of the four following height categories as response variables: <50cm, 50-100cm, 100-150cm, and >150cm (all square root transformed) in linear mixed models. Clipping (control, intermediate, heavy) and soil moisture (year 2021; scale 1-10) were fitted as explanatory variables. 'Exclosure' was fitted as a random factor.

4.3. Results

4.3.1. Tree resource allocation, growth, and structure

Regardless of clipping, trees showed significant variation in their growth between the start and end of the experiment (Figure 4.4). During this time, there was a significant decline in mean SLA (*P*<0.001) and increases in mean tree height and diameter, as well as total growing tips (*P*<0.001). The BACI models (Figure 4.5) demonstrated that at the beginning of the experiment, there was pre-existing, significant variation in mean SLA of the trees. By chance, the mean SLA of trees that were subsequently used as controls was around 5% lower than trees that were later clipped at intermediate intensity (*P*=0.05). No initial significant variation was observed in mean tree height and diameter, total growing tips, or growing tip density prior to clipping (*P*>0.2).

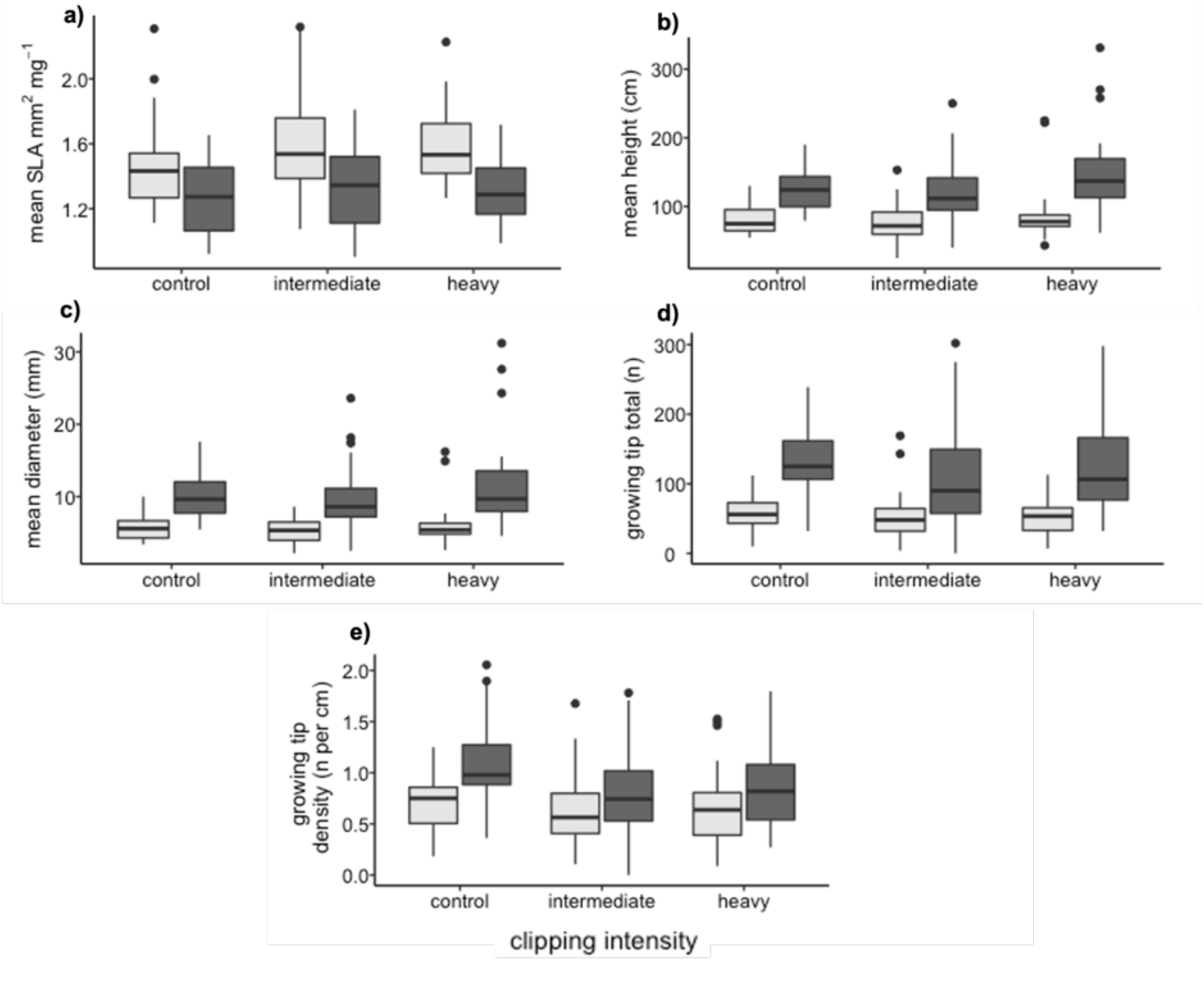

Figure 4.4. Boxplots showing variation between three clipping levels (control, intermediate, heavy) and years (2020, 2021) in mean a) specific leaf area (SLA, mm^{2}mg^{1}), b) tree height (cm) and c) diameter (mm), as well as d) total growing tips (n) and e) density of growing tips (n per cm) per cluster. Colours indicate year; white = 2020, and grey = 2021.

At the end of the experiment, intermediate clipping resulted in trees with significantly fewer leafy growing tips (-13%) compared to unclipped trees (*P*=0.05). Heavily-clipped trees had slightly fewer growing tips (-4%) compared to unclipped trees, however this effect was not significant (*P*=0.7). Heavily-clipped trees were significantly taller (+5%) than unclipped trees (*P*=0.03), but intermediate clipping had no relationship with tree height (*P*=0.8). Mean SLA demonstrated a trend toward a marginal, negative association with intermediate clipping; however, this effect was non-significant (*P*=0.08). Heavy clipping had no significant effect on mean SLA (*P*=0.6). There was also no effect on diameter (*P*>0.1). Compared to controls, growing tip density (n) was lowest in trees clipped at intermediate intensity (-20%; *P*=0.1), and heavily-clipped trees to a lesser extent (-7%; *P*=0.6), however these effects were not significant. Soil moisture had a significant, positive effect on mean SLA (*P*<0.001), but no other tree response variables in the BACI models (*P*>0.3). Soil moisture had a significant, positive effect on relative change in maximum tree height (*P*<0.001; Figure 4.6a) and diameter (*P*=0.01; Figure 4.6b).

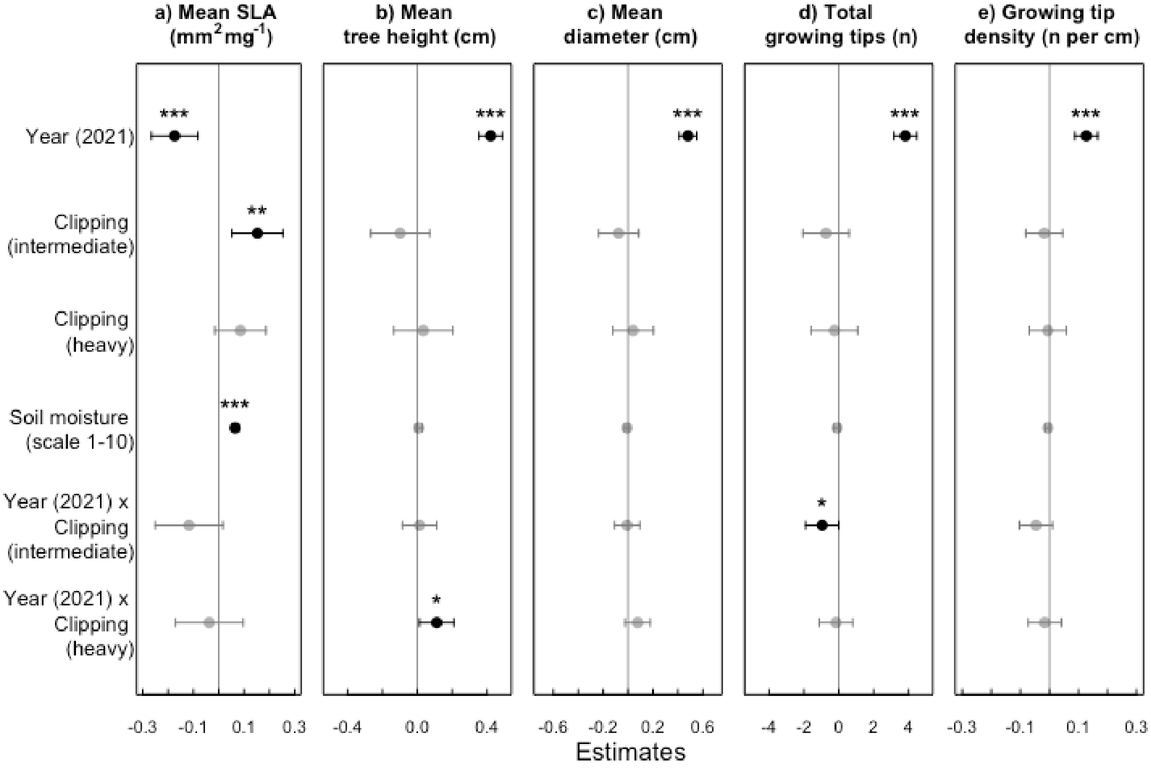

Figure 4.5. Forest plot outputs from linear mixed models. Response variables are mean a) specific leaf area (SLA) (mm^{2}mg^1), b) tree height (cm), c) diameter (cm) as well as d) total growing tips (n) and e) density of growing tips (n per cm). Predictors are coloured by significance (grey = not significant, black = significant). **P*=0.05.

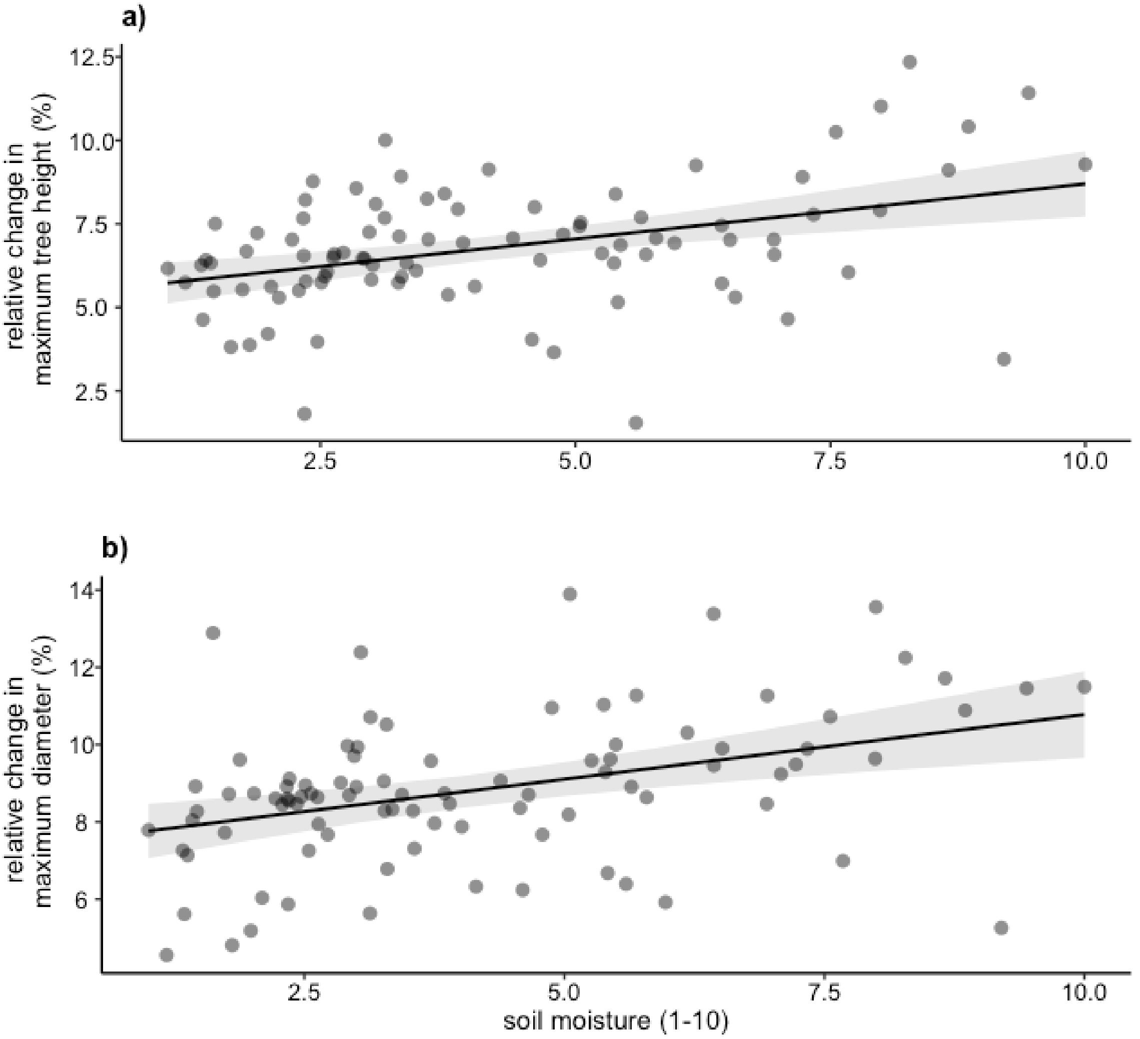

Figure 4.6. The relationship between the between-season relative change in a) maximum tree height (%), and b) maximum diameter (%) and soil moisture (scaled 1-10). Plotted points represent raw data values and line represents overall model fit (summarised in Appendix 4.3).

4.3.2. Leafy growing tip distribution

Regardless of clipping, most of the leafy growing tips were located within 50-100cm of tree height (40 ±2.2% SE), Figure 4.7). However, trees clipped at intermediate intensity had significantly fewer growing tips (-32%) within this area (*P*<0.01), but no other height bands (*P*>0.2, Figure 4.8) when compared to unclipped trees. Similarly, heavily-clipped trees had a significantly lower abundance of growing tips (-26%) only within 50-100cm (*P*=0.01, Figure 4.8b). This contrast is further evident when visually comparing the vertical distribution of total leafy growing tips in clipped trees with unclipped trees (Figure 4.8). The side profile of leafy growing tip distribution of intermediate is visually distinct from that of unclipped trees, whereas heavy-clipped and unclipped trees are closely matched. Higher soil moisture conditions resulted in fewer growing tips located above 150cm in height (*P*<0.001), but it had no effect on the abundance of growing tips located in any other height bands (*P*>0.07).

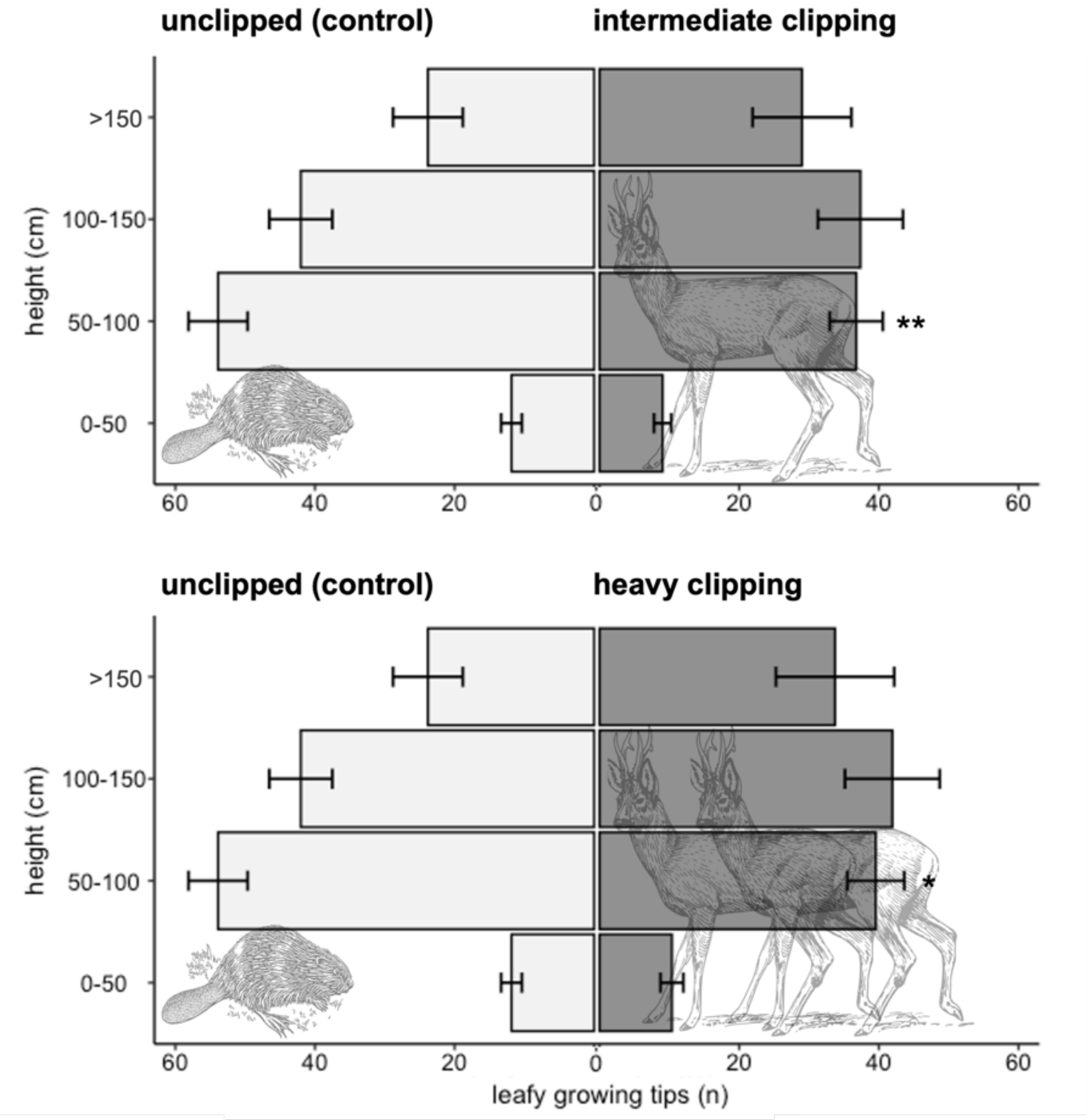

Figure 4.7. Distribution of mean total growing tips (%) in four height bands (<50cm, 50-100cm, 100-150cm, >150cm) on trees with no clipping vs a) intermediate, and b) heavy clipping (with standard error bars). Images of beaver and roe deer are approximately scaled to height. Stars indicate significantly different values between when compared to unclipped (control) trees. *P=0.05; **P=0.005.

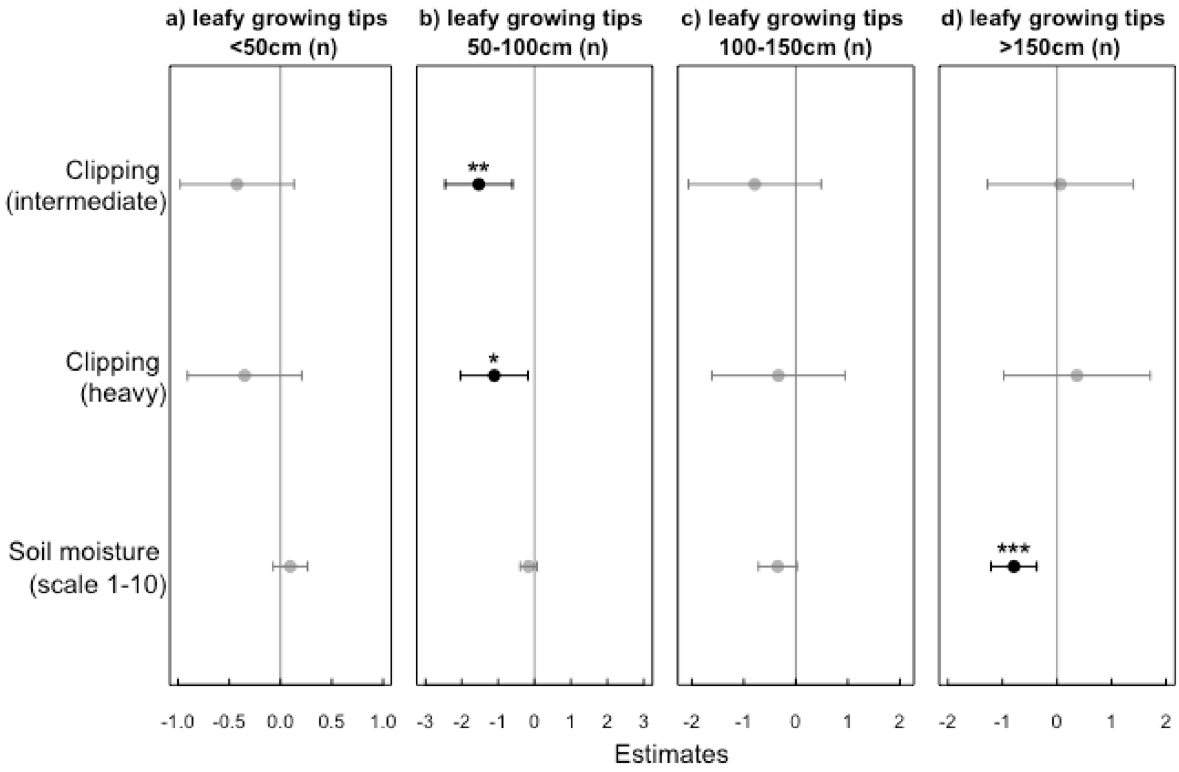

Figure 4.8. Forest plot outputs from linear mixed models. Response variables are leafy growing tips within a height of a) <50cm, b) 50-100cm, c) 100-150cm and d) >150cm. Predictors are coloured by significance (grey = not significant, black = significant). *P=0.05; **P=0.005; ***P=0.005.

4.4. Discussion

Understanding interactions between herbivores and how they shape woodland development is of crucial importance to forestry and conservation management. This is especially relevant in regions with limited riparian woodland extent and where both beaver and deer numbers are increasing. This study is the first to describe the changes in resource allocation, growth and structure of trees influenced by beaver-deer interactions in a European context. Over one growing season, we found that trees clipped at intermediate intensity had a significant overall reduction (-13%) in the abundance of leafy growing tips, compared to unclipped trees. Heavy-clipped trees were significantly taller (+5%), with no increase in mean diameter. When compared to unclipped trees, both intermediate- and heavy-intensity clipping differed in their vertical distribution of leafy growing tips and had significantly fewer growing tips (-28% and -32% respectively) within the height of 50-100cm. Mean SLA, as well as relative change in maximum tree height and diameter, were significantly influenced by soil moisture.

4.3.1. Specific Leaf Area

At the start of the experiment, all recorded SLA values of simulated resprouted beaver-felled trees were within the normal range for grey willow (Gervais-Bergeron et al., 2021). The initial variation in mean SLA is likely a result of unmeasured confounding environmental factors, such as soil nutrients and light levels (Gong & Gao, 2019). All mean SLA values of simulated resprouted beaver-felled trees declined over one growing season regardless of clipping, which is consistent with other research on willow and can be attributed to age or proliferation of leafing (Dušek & Květ, 2006). As higher SLA values generally correlate with increased leaf palatability (Cornelissen et al., 2003), our results imply that newly resprouted beaver-felled trees may be more susceptible to deer herbivory than older regrowth.

Contrary to our initial hypotheses, there was no significant effect of intermediate or heavy clipping on mean SLA. Previous studies on a variety of woody species indicate that browsing typically results in plants with a higher SLA (Lind et al., 2012; Keefover-Ring et al., 2016; Hedwall et al., 2018), whereas our data suggested the direction of an opposite trend in grey willow. To date, there are no studies that specifically assess how deer browsing influences the SLA of willow. Research on simulated roe deer browsing on oak saplings (*Quercus robur*) demonstrated no change in SLA six months after clipping, which was similar to our findings. However, when measuring the same oak trees two years later after repeated clipping, SLA was significantly higher (Barrere et al., 2022). A limitation of short-term studies is that they may not fully account for the complexity of long-term ecological interactions. The study period of one growing season in our experiment may not have captured all the changes that could occur in response to deer browsing.

Unlike our study, Barrere et al. (2022) applied samples of roe deer saliva during their clipping treatments. Herbivore saliva has been shown to elicit unique chemical responses in browsed trees (Ohse et al., 2017) and using a combination of both beaver and deer saliva in studies of future beaver-deer interactions may be informative. Our findings of a very weak association of intermediate clipping and mean

SLA may allude to the direction of a delayed, longer-term effect. It further implies that intermediate browsing of resprouted beaver-felled trees could elicit an initial shift in resource allocation from rapid growth into defence over the following growing seasons, possibly to deter further herbivory. In contrast, heavily-browsed resprouted trees may adopt the compensatory growth strategy (Crawley, 1984) and prioritise rapid growth to offset the greater loss of biomass. This pattern may become more evident after further growing seasons, and with ongoing deer browsing.

4.3.2. Tree height and diameter

Our finding of significantly taller trees with heavy (but not intermediate) clipping further reinforces the idea that there are two contrasting resource allocation strategies in trees subjected to differing browsing intensities. The observation of an increase in height observed with heavy clipping is consistent with the compensatory growth hypothesis (Crawley, 1984) and may have woodland-level effects. For example, studies have highlighted that high deer densities in woodlands can lead to tree canopies that are 1-5m taller (Eichhorn et al., 2017; Reed et al., 2022). Instead of overcompensating in height growth, other research has shown browsed willow trees were able to match the height of unbrowsed trees in the following growing season (Guillet & Bergström, 2006). However, this response was highly dependent on the time of clipping (summer vs winter) and age of trees (new vs old plantation). Compensatory responses were strongest in old plantations that were clipped in the summer. Compared to young trees, mature trees have more resources that can be quickly reallocated to regrowth to recover from browsing. The responses of younger trees observed in our study may not fully reflect the responses of older trees that have ample resources due to better established below-ground structure.

Studies in North America have shown that high intensity ungulate browsing can suppress compensatory growth in simulated beaver-cut willow and produce short, shrub-like plants (Baker, 2003; Hood & Bayley, 2009). These contrasting findings illustrate that although an increase in height growth with heavy clipping was observed in our study, this response is not generalisable and is likely dependent on specific biotic and abiotic factors.

Furthermore, the increase in tree height that was observed with heavy clipping was unmatched by a greater increase in diameter, despite our observations of height-diameter collinearity. This finding is consistent with research on winter browsing by moose (*Alces alces*) which found increased growth in height, but reduced growth in diameter, in browsed birch shoots (*Betula pendula*) (Herder et al., 2009). A rapid increase in plant height would be beneficial to allow the most vulnerable top leader shoot to grow beyond the reach of subsequent deer browsing (Crawley, 1984). However, if this growth does not correspond with diameter, then browsing may produce taller, but thinner trees. This ‘spindly’ profile could be less stable and more susceptible to damage by wind or snow and other climactic factors.

4.3.3. Leaf abundance and vertical distribution

The observation of reduced abundance of leafy growing tips following clipping confirms our initial hypotheses. Other research has similarly shown that winter browsing of willow by elk (*Cervus canadensis*) produces trees with a lower number of leaves (Peinetti et al., 2001). Baker et al. (2005) simulated beaver-cutting on willow trees in North America and subjected them to repeated heavy elk browsing for three years. The leaf biomass of their elk-browsed simulated beaver-cut willow was around ten times lower than controls. This implies the effects observed in our study may still be evident after future growing seasons, although grazing is also unlikely to be a one-off event and effects seen after one season may be reinforced by successive seasons of browsing. However, our methodology differed from Baker et al. (2005) in that they analysed effects of natural elk browsing rather than simulated clipping. During foraging, herbivores are known to deposit nutrients through their dung and urine into the soil (Haynes & Williams, 1993) which can ultimately influence tree growth. Although our study lacked herbivore nutrient import, we were able to remove biomass in a controlled and quantified manner that would be unachievable through natural browsing.

Although simulated browsing in our study removed leafy material from trees <150cm in height, clipped trees had significantly fewer leafy growing tips located specifically within 50-100cm after one growing season, but in no other height bands. In our study, clipped trees had the opportunity to compensate for the removal of leafy growing tips during the following growing season. The lack of growing tips on clipped trees specifically within 50-100cm observed after the growing season may hint at an indirect strategy that helps trees avoid extensive future roe deer herbivory. Roe deer prefer to forage around their shoulder height for ease (~75cm) (Nichols et al., 2015). Roe deer browsing has been shown to alter the biomass distribution in exclosure experiments on young oak trees where browsed trees had a higher proportion of biomass located belowground (Drexhage & Colin, 2003). The reduction of leafy growing tips located within 50-100cm in our study was not accompanied by greater amounts in any of the other height bands. It is unclear whether trees may have alternatively diverted their biomass into their root system, although this might provide greater stability to the heavily-browsed trees that become spindlier. Nonetheless, if winter deer browsing results in resprouted beaver-felled trees with consistently fewer leafy growing tips, there could be cascading ecological implications for insect pollinators (McDermott et al., 2021) or bird species (Gill & Fuller, 2007) that rely on understorey foliage.

Our findings showed that trees clipped at intermediate intensity had a lower (-20%) growing tip density. However, contrary to our hypothesis, this effect was non-significant. Although not entirely consistent, the literature generally implies that repeated browsing of the top leader stem in some tree species can suppress growth and result in bushier trees (i.e., higher leaf density), whereas browsing of the lateral branches can result in compensatory growth and spindlier trees (Kupferschmid, 2007). The leafy growing tips in our study were clipped at random, but always below 150cm. Therefore, it was possible that the leader stem was clipped in some but not others, especially in trees that were already taller than 150cm. Pépin et al., (2006) noted that the top leader stem of some willow seedlings could be browsed by deer once and still result in compensatory growth. The regrowth from beaver-felled stumps initially consists of several unbranched shoots. If changes in tree structure in response to browsing are dependent on whether the top leader stem is browsed, then we hypothesise that deer browsing of secondary shoots from beaver-felled trees will generally result in suppressed growth.

4.3.4. Soil moisture

The strong, positive correlation between soil moisture and mean SLA was indicative of trees directing their resource allocation into rapid leaf growth in wetter soils. Although soil moisture had no relationship with mean tree height or diameter in the

BACI models, there was a significant, positive effect on maximum tree height and diameter. This indicates that higher soil moisture conditions allowed the dominant stem in each cluster to grow faster, an effect which may have been masked by the height of the shorter stems included in the averaged height and diameter values. While trees growing near standing water will naturally be subject to greater water logging influence, beaver dam construction can result in localised increases in soil moisture (Law et al., 2017). Soil moisture has been shown to decrease with distance from beaver ponds (Donkor & Fryxell, 2000). This damming effect may be over and above the basic topographic one and may alter seasonal soil moisture regimes, keeping them higher in summer. Studies have shown that wetter soils can allow willow trees to grow tall quickly enough to potentially escape the browsing height of elk (Bilyeu et al., 2008). In our study, there was no significant interaction between soil moisture and clipping on any of the tree growth responses. However, the significant effect of soil moisture on SLA and maximum tree height/diameter strongly highlights the potential importance of this abiotic variable in the dynamics of beaver-deer interactions.

It has been recognised that prolonged high soil moisture conditions (i.e., flooding) may not always result in healthy trees and can impede the survival of willow (Pezeshki et al., 1998). However, increased soil moisture through beaver damming also may be able to negate some of the effects of deer browsing. We found that trees growing in wetter soils had significantly higher SLA. Beaver damming may therefore have a similar result and shift the tree's resource allocation towards rapid growth. Inevitably, this would allow trees to grow quicker, placing their top leader stem out of reach of browsing deer. As soil moisture generally tends to decrease with distance from the shore, we can hypothesise that woodland further from the water's edge might see the most prominent structural changes from deer browsing.

4.5. Conclusions

The potential impacts of beaver-deer interactions are virtually unstudied in Europe yet are of crucial significance for riparian woodland conservation and management. We demonstrate that after one growing season, beaver-deer interactions can systemically alter the resource allocation, growth, and structure of riparian trees. The intensity of browsing is most likely to result in contrasting responses in trees. Intermediate browsing may eventually result in better-defended trees that are less palatable to herbivores, whereas heavy browsing may produce rapid-growing ‘spindly’ trees. From our findings, we hypothesise that deer browsing of resprouted beaver-felled trees is likely to suppress tree growth. However, individual–tree-level responses are likely highly-specific and dependent on the key characteristics of plants (age and species), deer browsing (intensity and frequency) and their local environment (soil moisture levels). Beaver damming and its effect on soil waterlogging may also regulate the dynamics of beaver-deer interactions and future research should therefore not be based on browsing alone.

CHAPTER 5: GENERAL DISCUSSION

Freshwater ecosystems have been described as some of the most sensitive ecosystems to global change (Feld et al., 2018). Planting and restoring riparian woodlands can mitigate some of the effects of global change on freshwaters, whilst providing numerous ecosystem services (Woodward et al., 2010). Reintroductions are also being increasingly utilised as nature-based solutions in the field of restoration ecology to restore lost ecological processes that produce resilient, biodiverse, self-regulating ecosystems (Tanentzap & Smith, 2018). However, the reintroduction (or removal) of one species can completely reshape the structure and functioning of ecosystems, with potentially significant knock-on effects (Ripple & Beschta, 2012). These knock-on effects may subsequently conflict with other restoration policies, such as those aiming to protect or enhance riparian woodlands.

Many reintroductions in restoration ecology focus on restoring top-down trophic interactions (Kéfi et al., 2012). Few studies focus on the interspecific interactions between herbivores (such as beaver and deer). As a result, herbivore interspecific interactions are rarely considered or included in policies or woodland targets, despite their potential role in shaping ecosystem function. Furthermore, it is uncommon for riparian woodlands to be specifically included in targets and they often fall between the cracks into a category of either wetland or woodland (Ogilvy et al., 2022). Arguably, neither of these designations fully encompasses the vast ecological benefits and services that arise from their unique ecotonal position.

This thesis comprises the first research in a European context to explore beaver and deer interactions in riparian woodlands in detail. The hypotheses explored are rooted in preliminary field studies, literature reviews and key modelling studies from North America. The findings of studying the combined effects of beaver and deer browsing, in a habitat of high conservation value, provide new insights into woodland resilience in the face of evolving global change.

5.1. Thesis summary

The introductory chapter of this thesis highlighted how beaver and deer populations are expanding and that they can each independently present significant influences on riparian woodlands through browsing. A pertinent research gap was identified in beaver-deer interactions in European riparian woodlands, with implications that span beaver, deer, and riparian woodland management.

In Chapter 2, we investigated beaver tree foraging preferences and long-term impacts (11 years) of beaver browsing in riparian woodlands. As beavers are highly selective foragers known as 'ecosystem engineers' and 'keystone species' (key drivers of landscape change) (Jones et al., 1994), we expected to see pronounced changes in woodland structure and composition over 11 years. The main finding from this study was that changes may be relatively more subtle than anticipated. Although beaver browsing can have significant impacts on trees at a patch scale, the woodland-level effects of browsing are less obvious over time. Other key findings that can inform beaver management are that beavers were highly selective for tree species (e.g., hazel) and smaller diameters (<10cm) and predominantly forage within 10m of the shore. While tree felling by beavers can be a very graphic localised influence, dam building, subsequent inundation and death of trees is likely a more wholesale and drastic influence.

Figure 5.1. Surveying woodland transects inundated due to localised beaver damming in Knapdale Forest, Scotland (K Wilson, November 2019).

In Chapter 3, we then investigated how tree felling by beaver influences woodland regeneration, before determining the drivers behind their interaction with deer. We found that beaver felling actively promotes the growth of secondary shoots, but we were unable to ascertain if tree felling by beaver fully replaces mature trees. Furthermore, we discovered that tree felling by beaver provided deer with a nitrogen-enriched, abundant, novel forage that would otherwise be absent in un-coppiced woodlands without beavers.

Chapter 4 then delved into the mechanistic aspects of beaver-deer interactions. We planted an experimental riparian willow woodland to assess how deer browsing on simulated beaver-felled trees affected their resource allocation, structure, and growth. We found that after one growing season, simulated deer browsing (clipping) had significant impacts on growth and structure, which varied with clipping intensity and soil moisture. Intermediate clipping resulted in trees with significantly fewer leafy growing tips and a weak association with higher SLA, implying a future shift in resource allocation towards defence (Figure 5.2). Heavy clipping produced significantly taller trees, consistent with compensatory growth to recover biomass, potentially leading to ‘spindly’ trees.

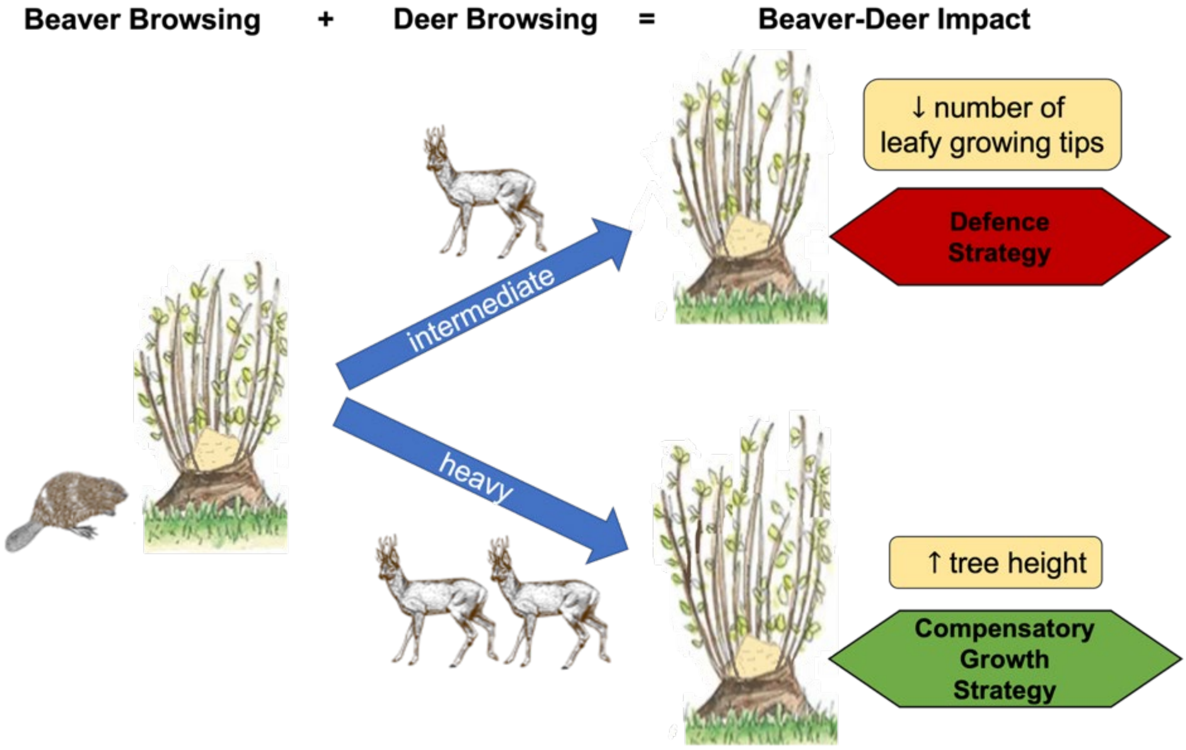

Figure 5.2. Diagram summarising the main findings arising from beaver-deer browsing interactions in Chapter 4.

This final discussion chapter now focuses on a review of our approaches in the context of future research needs, before using the main findings of our research to hypothesise predicted outcomes and propose guidance for managing deer and riparian woodlands in the presence of beavers. The significance of these findings is also placed into the wider context of conservation policy, habitat restoration and species reintroduction.

5.2. Experimental methodology & future research

A wide range of techniques were used to establish relationships between beaver and deer in riparian woodlands in this thesis. In Chapter 2, the primary consideration was to ensure that our data collection methods were compatible with the previous study by Iason et al. (2014) in the same study area to allow a valid assessment of change. Although this provided the baseline for a set group of variables to record, our scope to deviate from the original methods was limited. The visual analyses of ground vegetation cover could be viewed as subjective, and research has shown high levels of decadal environmental variation in ground vegetation cover (Kirby et al., 2022). A full census of ground vegetation species diversity (richness and coverage of each species) would be more reliable and provide more detailed information on key shifts in species-richness or functional traits over time. Although the monitoring period of 11 years is seemingly the longest study on Eurasian beaver foraging to date, it is still a remarkably short period of time when compared to the beaver's extirpation. North American studies have demonstrated important long-term impacts of prolonged selective browsing by beaver, such as shifts in woodland composition (Johnston & Naiman, 1990) and woodland structure (Peinetti et al., 2009). Resurveying Knapdale Forest transects after a further 30 or 40 years will provide key insights on Eurasian beaver territory persistence and whether selective browsing alters woodland composition and structure over the longer term.

In Chapter 3, the palatability of secondary shoots from beaver-felled trees for deer was investigated by measuring levels of nitrogen (N) and carbon (C). Although N and C are effective indicators of nutritional content, there are an array of components that contribute to the palatability of forage (Bryant et al., 1983). Leaf removal often induces the production of defence metabolites rendering foliage less palatable (Tuomi et al., 1990). Comparing defence metabolites (such as phenolic acids, tannins and flavanols) in unbrowsed and deer-browsed material will provide further insight to the physiological factors behind beaver-deer interactions. Furthermore, plant species respond to herbivory in different ways (Bryant et al., 1983). Our research mainly focused on birch and willow due to their local availability, but other woody species should also be investigated to gauge a wide range of potential plant responses to beaver-deer interactions. Although we found that herbivory responses are highly context-dependent, understanding the drivers of this variability in a variety of contexts is critical to predict riparian ecosystems responses to ongoing global change.

Exclosure experiments are crucial in understanding herbivore interactions (Hester et al., 2000). Our experimental woodland study (Chapter 4) was initially designed to include natural deer browsing in the paired exclosures as opposed to simulating deer browsing via clipping. Half of the fenced exclosures were opened to deer browsing but remained closed to beaver browsing by removing the outer layer of line wire. Exclosures were monitored over winter using camera traps, but no deer entered to browse on the willow (but readily grazed *around* them (Figure 5.3)). This selective fencing method was not effective, possibly due to shortcomings in the exclosure design where the exclosure area was too small for deer to easily jump in/out (Pepper, 1999) or due to the ready availability of forage externally. In place of natural browsing, the experiment was adapted to simulate deer effects by clipping. The input of deer nutrients (urine and dung) or ungulate salivary components can have significant impacts on riparian woodlands (Ohse et al., 2017; Riesch et al., 2022). Nonetheless, the clipping methodology was beneficial as it allowed precise control over the browsing intensities, which we could not have achieved using wild animals.

Figure 5.3. Camera trap image from exclosure experiments in Chapter 4 at Bamff Estate, Perthshire. Roe deer on right hand side (K Wilson, February 2021).

There are ample means of manipulating the experimental design of Chapter 4 to answer key interspecific herbivore browsing questions. Given the opportunity to repeat the study without a restricted timeframe, we would simulate beaver felling on mature willow trees and then monitor the process of resprouting (i.e., timing, rate). Mature trees are potentially more resilient to browsing than young trees due to an increased reserve of resources that can be quickly diverted to recovery. This alternative design could firstly provide insight into woodland regeneration in beaver territories. The impacts of simulated and natural deer browsing could then be compared between exclosures to investigate the role of confounding biotic factors such as deer nutrient inputs and saliva. Additionally, deer and beaver entry could also be permitted into selected exclosures to assess hypotheses of competitive exclusion and woodland responses under a double browsing pressure. Plans are in place to continue this experiment in 2023 and make assessments on the effects of repeated browsing over further growing seasons. In general, although our research focuses on the herbivory aspects of beaver-deer interactions, we found evidence that soil moisture may also play an important role in the dynamic. The effects of beaver dam building should therefore be incorporated into future beaver-deer studies.

Figure 5.4. Aerial view of two of six exclosures established to investigate beaver-deer interactions in Chapter 4 at Bamff Estate, Perthshire (A Law, April 2019).

5.3. Outcomes & wider implications

5.3.1. Beaver management

Mammalian herbivory plays a pivotal role in shaping ecosystems, however it can also be a major source of human-wildlife conflict (Reimoser & Putman, 2011). Human wildlife conflict is a global social issue that can threaten human livelihoods and influence the outcome of animal reintroduction and conservation projects (Madden, 2004). In 2022, the human population surpassed eight billion and is expected to reach 9.7 billion in 2050 (United Nations, 2022). Humans are therefore likely to come into increasing contact with wildlife populations and conflict may become a more common occurrence. Understanding the foraging preferences of key herbivore species, especially when they have been absent for centuries, can allow us to manage their impacts and mitigate any conflicts that may arise more effectively.

Beaver management has polarized landowners and conservationists for decades in Scotland (Coz & Young, 2020), Europe (Wróbel & Krysztofiak-Kaniewska, 2020) and North America (Yarmey & Hood, 2020). Like deer, beaver management issues typically concern the farming and forestry industries (Wróbel & Krysztofiak-Kaniewska, 2020). For example, 60% of all beaver management problems in Scotland in 2018-2019 were recorded on agricultural land (Campbell-Palmer et al., 2021a). Whilst beaver damming appears to result in the highest number of human-beaver conflicts, tree-felling also plays a significant part (Janiszewski & Hermanowska, 2019). The foraging preferences of beavers are generally well studied (Haarberg & Rosell, 2006; Janiszewski et al., 2017; Wazna et al., 2018); however, Chapter 2 of this thesis comprises the first study to monitor the impacts of Eurasian beaver foraging over a prolonged period (11 years). Our findings demonstrated that beaver browsing had no significant changes in woodland composition over this period. Although beavers may still have drastic patch-scale impacts during their initial arrival into a territory, it may come as a relief to some landowners to know that the structure and composition of the riparian woodland will not be significantly altered by beaver browsing over these time scales.

In Chapter 2, we also demonstrated clear beaver foraging patterns in a sample size comprising around 600 trees. Recent research in the Czech Republic studied beaver foraging preferences in around 22,000 trees (Mikulka et al., 2022). Despite dramatically different sample sizes and environments, the foraging preferences of beavers were almost identical in terms of preferred species, diameter, and distance from the water. These findings confirm that beaver foraging is highly predictable which is potentially valuable information when trying to mitigate human-beaver conflicts.

Current beaver management and mitigation solutions involve a combination of culling, translocation, and practical mitigation techniques. Many European countries such as Norway, Sweden and Finland have a seasonal, fixed hunting period for beaver (Parker & Rosell, 2001). The Scottish Government's decision to issue licences to cull beavers, a species protected under EU law, has however proved controversial. Translocations are generally the offered alternative and involve rehoming 'problem beavers' to less-populated areas. Other non-lethal practical mitigation techniques involve wrapping trees with mesh wire or layering them in deterrent paint (Campbell-Palmer et al., 2016; Westbrook & England, 2022). Fences and human paths are also effective in preventing riparian vegetation damage (Nolte et al., 2003; Loeb et al., 2014). Installing flow levelling devices ('beaver deceivers') into dams are an effective technique for reducing inundation of roads and pathways (Taylor & Singleton, 2003). However, these solutions are quick-fixes and are often only applied after an initial problem has been identified, by which point it is often too late for preventative methods.

Figure 5.5. An example of human-beaver conflict: beavers begin felling a large (~40cm diameter) poplar tree (*Populus* spp.) in the direction of a busy road in Perthshire (K Wilson, October 2022).

The root of the human-beaver conflict problem in Scotland (and likely elsewhere in Europe) lies within the current poor state of riparian woodlands and their contracted distribution (Brown et al., 2018). With fewer, and poorer quality riparian woodlands, beavers may have little option but to venture into agricultural or populated areas in search of food. This scenario of poor-quality habitat, coupled with an increasing human population, is synonymous with most human-wildlife conflicts around the world. For example, degraded forest habitats in India have driven large herbivores such as nilgai (*Boselaphus tragocamelus*), and Asian elephant (*Elephas maximus*) to raid crops, affecting local livelihoods (Tahoor et al., 2021). Planting high quality riparian woodlands along water courses on a national scale - most likely to happen for reasons of stream or floodplain restoration, diffuse pollution reduction, or climate mitigation - may also therefore offer a long-term, preventative solution to human-beaver conflicts. Knowing that beaver foraging follows highly predictable patterns can help us tailor where best to enhance riparian woodlands to prevent human-beaver conflict before problems occur.

Figure 5.6. A thin strip (<10m) of degraded riparian vegetation separates the river Isla (left) and a cider apple tree (*Malus* spp.) plantation (right) in Perthshire (K Wilson, October 2020).

5.3.2. Deer management

Understanding the spatial ecology of large herbivores throughout the world is crucial due to their ability to influence vegetation, wildfires, and ultimately climate (Owen-Smith, 2014; Ramsay et al., 2022). Many large herbivores have undergone declines in recent decades; however, deer populations are increasing (Ripple et al., 2015). Their distribution is strongly dictated by the availability of food (Palmer & Truscott, 2003; Borkowski & Ukalska, 2008). We observed that beaver-inhabited riparian woodlands had a higher cover of herbs (Chapter 2) and abundance of nutritious secondary shoots (Chapter 3). Therefore, we infer that tree felling by beaver may ultimately influence deer distribution by attracting them into riparian woodlands. Potential shifts in deer distribution could have important consequences for their management as well as vegetation dynamics.

Deer can contribute to extensive commercial crop damage (Putman & Moore, 1998). In 2018, around 40% of the total European Union area comprised agricultural land (Eurostat, 2018). Meanwhile, Eurasian beaver populations are expanding rapidly into populated, managed, low-relief areas in western and central Europe (Wróbel, 2020). If tree felling by beaver promotes an abundant, nutritional, and novel source of deer forage located within the riparian woodlands that border arable farmland, then a diversionary feeding effect may be created for deer. As well as lessening deer browsing impacts on crops, this effect could also reduce deer impacts on managed commercial forestry stands located close to riparian woodlands. Diversionary feeding of ungulates has shown to be an effective, but costly, mitigation method (Kubasiewicz et al., 2016). Our findings suggest that beavers could naturally provide this ‘service’ for free. Furthermore, deer reproductive and survival rates, as well as increased weight/condition, are associated with an increase in forage availability (Milner et al., 2014). Tree felling by beavers may therefore support an increase in the productivity of deer populations living in and around beaver-inhabited riparian woodlands. However, it is unlikely that tree felling by beaver would have a significant positive impact on overall deer population numbers.

Another scenario is that deer may eventually outcompete beavers. Hood and Bayley (2008a) implied that in restricted-quality habitats in Canada, beaver and ungulates could forage to the point of competitive exclusion. They showed that heavy deer browsing suppressed the growth of trees preferred by beavers which led to beavers having to adapt their foraging strategy. It was found that competitive beaver-deer exclusion could be ‘buffered’ and both species could thrive - but only in high quality, diverse riparian woodlands. In terms of competitive exclusion, deer utilise a specific niche of the total woodland resource that is typically not browsed by beavers i.e., saplings. Deer forage on young saplings and twigs of several millimetres in diameter (Gill, 1992a), whereas beavers typically browse stem diameters of >3cm (Haarberg & Rosell, 2006). By stimulating tree suckering, beaver felling has the potential to increase the resource of the stem size preferred by deer therefore leading to an increase in beaver-deer interactions. If deer repeatedly hinder the development of saplings into mature trees through intensive browsing, there may be a reduced resource for beavers in the future. The scenario would be particularly applicable in degraded (or newly-established) riparian woodlands that lack trees of diverse species, ages, and sizes. However, in mature, diverse, and resilient riparian woodlands, it is expected that beavers and deer will generally occupy two distinct browsing niches.

If beavers are forced out of riparian woodlands by deer, they may enter more human-dominated landscapes, which could lead to more human-beaver conflict. It could be argued that this is a likely scenario in Europe in future years because riparian woodlands are currently severely restricted in their quality and extent (Brown et al., 2018). A recent study in Denmark investigated how beavers influence space use by deer but found that roe and red deer avoided areas of high beaver activity (Svanholm Pejstrup et al., 2023). Ultimately, these findings were attributed to anthropogenic disturbance, which was thought to supersede the influence of beaver activity on space use by deer.

Furthermore, a process-orientated model developed by Baker et al. (2012) in the USA demonstrated that there is a specific ecological threshold of ungulate density that beaver can tolerate before being excluded via food limitation. Their threshold value (<20 elk km^2) is not applicable to a European context due to fundamental differences in species and environment. Nonetheless, there is likely to be a particular threshold of deer density that maintains a functional beaver-deer dynamic in Scotland, although this is likely to be highly site-specific. Deer populations are still rising throughout Europe despite continuous culling efforts (Linnell et al., 2020; Carpio et al., 2021). Therefore, resting the solution to the beaver-deer interaction problem on deer culling alone may be unrealistic. Targeted effort and funding should alternatively be invested into protecting, planting, and enhancing riparian woodlands to reduce the potential risk of beaver-deer competitive exclusion.

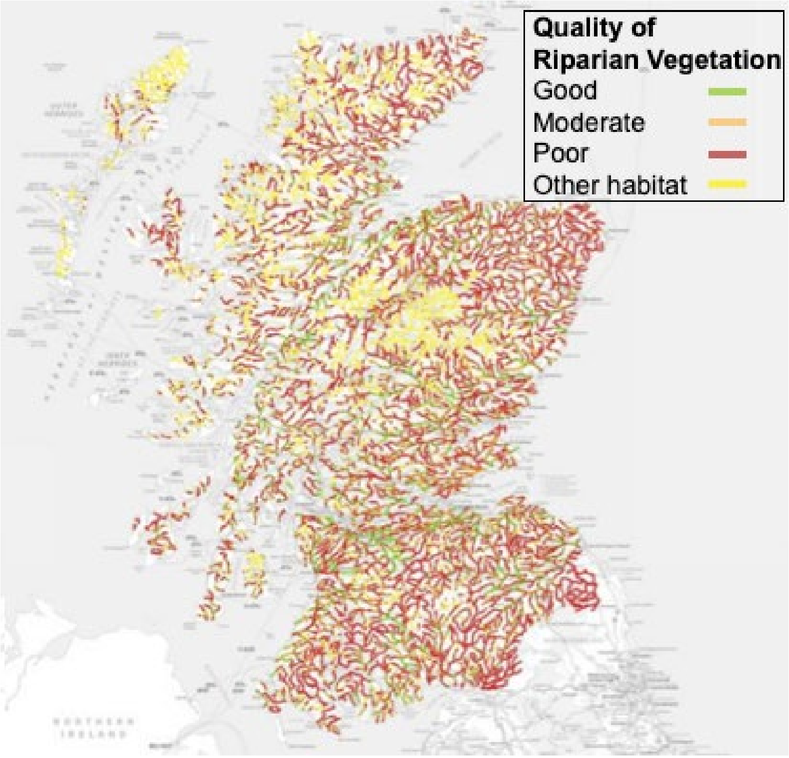

Figure 5.7. Riparian vegetation quality in Scotland based on Morphological Impact Assessment System surveys in 2015-16. Red indicates ‘poor quality’ riparian vegetation. Adapted from Ogilvy et al. (2022).

5.3.3. Riparian woodland management

Woodland expansion and restoration is a global aim. For example, the ‘Bonn Challenge’ is a campaign that aims to regenerate 350 million ha of deforested and degraded landscapes across the world by 2030. Scotland has pledged to support this challenge and has outlined ambitious woodland creation goals (Scottish Government, 2019). Scotland’s Forestry Strategy (2019-2029) aims to restore native woodland by working with private woodland owners and deer management plans. However, the detailed 50-page strategy fails to mention riparian woodlands. In scientific literature and policy, riparian woodlands tend to be categorised as either woodlands or wetlands, arguably neither of which accurately represents this unique habitat. Beavers are also not mentioned in Scotland’s Forestry Strategy despite their ability to shape riparian woodlands. Although it is unclear if the regrowth that is stimulated can completely replace the trees felled by beaver, our research confirms that beaver-felling promotes multi-stemmed architecture. Provided that deer do not suppress this regrowth through browsing, tree felling by beaver may thus contribute to wider riparian woodland expansion and restoration goals. However, it should be noted that beavers can only revive degraded riparian woodlands in places where there are at least some trees to transform.

Rewilding and restoration

The use of beaver reintroductions in restoration ecology has been described as ‘a cost-effective means of repairing degraded riparian areas’ (Ripple et al., 2022). In recent years, ‘rewilding’ has been a frequently used term in conservation around the world. Rewilding encompasses many definitions but broadly describes the process of returning degraded landscapes back to their former unmanaged ‘wild’ state (Jørgensen, 2015). There are multiple branches of rewilding, not all of which include translocations or reintroductions (Hayward et al., 2019). For example, ‘Pleistocene rewilding’ typically involves restoring lost historic ecological processes via translocations (Donlan et al., 2006), but ‘passive rewilding’ alternatively comprises abandoning rural land to natural succession (Navarro and Pereira, 2012).

Rewilding is a highly polarizing concept. While the ideology of the term is generally favoured by conservation bodies, the concept has resulted in an active discourse with the people who inhabit the rural landscapes that are to be rewilded (Martin et al., 2021). For example, rewilding has been compared to the second wave of the Highland Clearances in Scotland (Martin et al., 2021). The term ’rewilding’ has since been labelled a buzzword in the scientific community with some authors suggesting that simply referring to ’ecological restoration’ avoids confusion and eases controversy (Hayward et al., 2019). Realistically, very few people are likely to live specifically within riparian woodlands due to flooding risks. Riparian woodlands could therefore act as ideal model ecosystems in practical restoration ecology projects without any concerns of displacing human livelihoods at the expense of conservation. We propose that if beavers are to be utilised in restoring riparian habitats in Europe (or North America), then the site-specific browsing impacts of other large herbivores should be studied beforehand.

Resilience to climate change

Riparian woodland restoration has been frequently described as a key strategy in mitigating effects of climate change on freshwater ecosystems (Rivaes et al., 2014; Jackson et al., 2018). Freshwaters are particularly vulnerable to climate change because water temperature and availability are both highly climate-dependent (Woodward et al., 2010). Riparian woodland planting has been shown to regulate river water temperatures (Justice et al., 2017) and contribute to carbon sequestration (Dybala et al., 2018). Beaver translocation has also been proposed as an effective solution specifically for climate change mitigation (Hood & Bayley, 2008b; Dittbrenner et al., 2018; Westbrook et al., 2020). Ungulate browsing, against a backdrop of climate change, is likely to exacerbate structural changes in riparian woodlands. For example, in the presence of red deer, Scots pine (*Pinus sylvestris*) growth responded more strongly to climate warming than in the absence of deer (Vuorinen et al., 2020). Given that forest structure has direct impacts on functional diversity (Thom et al., 2021), ungulate herbivory may ultimately influence riparian woodland resilience to climate change. Planting and enhancing high-quality, heterogeneous riparian woodlands through balanced interspecific interactions may therefore also help to increase riparian woodland resilience to climate change.

The beaver-deer dynamic in an area of reintroductions

Our findings surrounding beaver-deer interactions raise important questions for the reintroduction of other woodland species that have been absent for centuries. To date, the Eurasian beaver is still the only approved mammal reintroduction to Britain. Throughout Europe, bison (*Bisus bonasus*), are being reintroduced to restore lost trophic interactions and fill a wide range of foraging niches to promote biodiverse ecosystems (Vasile, 2018; Lord et al., 2020). Various horse and cattle breeds are also being introduced as surrogates for the extinct tarpan (*Equus ferus*) and aurochs (*Bos primigenius*) (Cromsigt et al., 2018). Next on the reintroduction wish list for Scotland are lynx and wolf. The ecological and social feasibility of both lynx and wolf reintroductions have been widely debated (Nilsen et al., 2007; Hetherington et al., 2008; Johnson & Greenwood, 2020; Gwynn & Symeonakis, 2022). Realistically, if the reintroduction of beaver (a 20kg herbivore) took two decades of debate due to social implications and public perceptions, then the reintroduction of wolf (a 40kg carnivore) is unlikely to occur any time soon.

Nonetheless, the reintroduction of the wolf (and lynx to a lesser extent) would likely shape beaver-deer interactions in Scotland. As a key predator of both beaver and deer (Meriggi et al., 2011; Gable et al., 2018a), the addition of a widespread wolf population in Scotland could potentially exert control over the beaver-deer dynamic through regulating population sizes. Conversely, the reintroduction of wolves to Yellowstone National Park, USA, in the 1990s ultimately benefitted beavers (Ripple & Beschta, 2004). The resident elk population adapted behaviourally to reduce wolf predation by spending less time foraging in fixed or open locations. The pronounced change in elk distribution ultimately resulted in a resurgence of willow which provided an ample source of forage for the beaver population (Ripple & Beschta, 2012). Although the outcome of wolf reintroduction on beaver-deer interactions in a Scottish context can only be speculated, it has the potential to shape riparian woodlands and the ecosystem services they provide. It also highlights that we need a robust understanding of existing interspecific interactions between herbivores before other species are reintroduced for habitat restoration purposes.

Monitoring browser impacts in riparian woodlands

As beaver distribution is expanding, and deer populations are steadily rising, beaver-deer interactions in riparian woodlands are likely to become more commonplace. Therefore, the ongoing impacts of beaver-deer interactions should be monitored in woodland assessments. For example, the Woodland Herbivore Impact Assessment is a method used in Scotland to assess and monitor the impact of large herbivores (deer, cattle, sheep, pigs etc.) on woodland habitats (Armstrong & Holl, 2015). Adapting pre-existing national, standardised woodland survey methods to include beaver-deer impacts will readily inform how woodlands are being impacted over time. Specifically, incorporating simple quantitative measurements of deer browsing on the secondary shoots that resprout from beaver-felled trees could be a beneficial addition.

The extent to which beaver browse on the resprouted secondary shoots from beaver-felled trees is largely unknown. Some studies have recorded low levels of beaver browsing on secondary shoots, but do not report specific rates (Jones et al., 2009; Iason et al., 2014). Others suggest an avoidance due to high levels of defence chemicals (Durben et al., 2021). The resprouted secondary shoots can be considered the basis of a tree’s ability to re-establish and indeed to become a utilisable food source to beaver in the future. If there is no recruitment of saplings into the riparian woodland territory (e.g., due to high deer activity) then beavers may be compelled into eating the regrowth. This would essentially elicit a double browsing pressure on the resprouted secondary shoots from beaver-felled trees. Acquiring national, long-term data on the combined interactive beaver-deer browsing effects as part of standardised woodland herbivore monitoring could be critical for predicting the future of riparian woodlands.

5.4. Conclusion

Despite their crucial significance for riparian woodland conservation and management, beaver-deer interactions are virtually unstudied in Europe – until now. As beaver and deer continue to expand into intensely-modified, populated landscapes, their interactions in riparian woodlands, and the consequences of these will become increasingly commonplace. Restoring lost interspecific interactions between large herbivores can be considered as a key aim in restoration projects. However, we demonstrate that this ideology is not straightforward in practise, especially when one species (deer) has undergone pronounced expansion during the other's prolonged absence (beaver). Deer are predominantly managed for their detrimental impact on vegetation dynamics; however, we argue that their management should also focus on balancing their interspecific interactions with beaver in riparian woodlands. Overall, our findings raise important questions for human-wildlife conflict, restoration ecology, climate change and the reintroduction of other woodland mammals. The answers do not lie within current mitigation and quick-fix management methods. Moving forward, implementing nationwide riparian planting and enhancement, as well as integrating monitoring of ongoing beaver-deer impacts within woodland herbivore impact assessments, should be considered a preventative priority in Scotland's (and Europe's) future beaver, deer, and riparian woodland management policies and targets. These changes will also have wider benefits for freshwaters and help to restore ecosystems that are resilient in the face of ongoing global change.

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Appendices

Appendix 2.1. Knapdale Forest survey plot details.

Transect	Distance from water	Established	Grid Reference	N stems in May 2010	N stems in May 2021	Beaver activity
Lily Loch	0-4m	2010	NR7880388441	76	54	Y
Lily Loch	6-10m	2010	NR7880988430	65	51	Y
Linne	0-4m	2009	NR8002891433	16	16	Y
Linne	6-10m	2009	NR8003191439	5	5	N
Linne	16-20m	2009	NR8003791451	4	2	N
Linne	26-30m	2009	NR8004391459	24	15	N
Buic	0-4m	2010	NR7882988860	16	29	Y
Buic	6-10m	2010	NR7882288861	27	23	Y
Buic	16-20m	2010	NR7881788862	51	33	N
Creagmhor	0-4m	2009	NR8049291072	31	26	Y
Creagmhor	6-10m	2009	NR8049391073	10	8	N
Creagmhor	16-20m	2009	NR8050191064	42	38	Y
Creagmhor	26-30m	2009	NR8051091058	33	24	N
Coille-Bharr	0-4m	2009	NR7785189397	26	33	Y
Coille-Bharr[a]	6-10m	2009	NR7784689391	1	0	NA
Coille-Bharr	16-20m	2009	NR7784389387	47	21	Y
Coille-Bharr	26-30m	2009	NR7782389384	56	36	Y
Barnluasgan	0-4m	2018	NR7924191293	NA	12	Y
Barnluasgan	6-10m	2018	NR7923491297	NA	9	Y
Barnluasgan	16-20m	2018	NR7922891300	NA	44	Y
Faery Isles	0-4m	2018	NR7752289567	NA	56	Y
Faery Isles	6-10m	2018	NR7751689571	NA	35	Y
Loch Mckay	0-4m	2018	NR7991388568	NA	13	Y
Loch Mckay	6-10m	2018	NR7991888566	NA	5	Y
Loch Mckay	16-20m	2018	NR7992588566	NA	8	Y
Losgunn	0-4m	2018	NR7905289725	NA	17	Y
Losgunn	6-10m	2018	NR7905689710	NA	25	Y
Losgunn	16-20m	2018	NR7905489710	NA	21	N
Losgunn	26-30m	2018	NR7905489707	NA	5	N
Laraiche[b]	0-4m	2018	NR7859085961	NA	33	N
Laraiche[b]	6-10m	2018	NR7858685956	NA	10	N
Laraiche[b]	16-20m	2018	NR7858085949	NA	19	N
Laraiche[b]	26-30m	2018	NR7857485943	NA	10	N

[a] *removed from analyses due to no trees being present*

[b] *removed from analyses due to lack of beaver territory*

Appendix 2.2. Parameter estimates from model investigating tree selection by beaver.

Generalised Linear Mixed Model (GLMM) with binomial error distribution and a logit link investigating the effects of tree species, tree diameter (cm), duration of territory occupancy (short vs long) and distance from the shore (0-4m, 6-10m, 16-20m, 26-30m) using the browsing status (browsed/unbrowsed) of trees as the response variable. Transect was used as random effect. Tree species codes are in Table 2.1.

Predictors	*Estimate*	*SE*	*Z Value*	*P Value*
(intercept)	-2.11	0.71	-	-
Species (Betpub)	0.48	0.39	1.23	0.22
Species (Corave)	1.49	0.58	2.57	**0.01**
Species (Picsit)	0.5	0.81	0.61	0.5
Species (Salix)	2.76	0.65	4.24	**<0.001**
Species (Sorauc)	2.11	0.81	2.60	**0.009**
Diameter (cm)	0.1	0.03	3.39	**<0.001**
Duration of occupancy (long)	<0.01	0.81	<0.01	0.99
Distance (6-10m)	-0.51	0.26	-1.96	**0.05**
Distance (16-20m)	-2.14	0.44	-4.82	**<0.001**
Distance (26-30m)	-2.22	0.64	-3.45	**<0.001**

Appendix 2.3. Parameter estimates from models investigating changes in woodland structure over time.

a) Linear mixed model investigating the effect of relative change in mean plot diameter (%), distance from shore (0-4m, 6-10m, 16-20m, 26-30m) and beaver browsing intensity (%) on relative change in tree stem density (%). Predictors were centred and scaled. Transect was used as a random effect.

Predictors	*Estimate*	*SE*	*T Value*	*P Value*
(intercept)	-10.2	13.8	-	-
Relative change in tree diameter (%)	-30.9	8.87	-3.5	**0.01**
Distance from shore (6-10m)	-2.2	15.3	-0.1	0.9
Distance from shore (16-20m)	9.9	25.8	0.4	0.7
Distance from shore (26-30m)	0.18	23.3	0.008	0.99
Beaver browsing intensity (%)	3.1	7.7	0.4	0.7

b) Linear mixed model investigating the effect of relative change in tree stem density (%), distance from shore (0-4m, 6-10m, 16-20m, 26-30m) and beaver browsing intensity (%) on relative change in mean plot diameter (%). Predictors were centred and scaled. Transect was used as a random effect.

Predictors	*Estimate*	*SE*	*T Value*	*P Value*
(intercept)	4.44	6.68	-	-
Relative change in tree density (%)	-12.4	3.97	-3.14	**0.01**
Distance from shore (6-10m)	10.2	8.22	1.24	0.25
Distance from shore (16-20m)	30.6	11.4	2.66	**0.03**
Distance from shore (26-30m)	20.7	11.7	1.76	0.1
Beaver browsing intensity (%)	5.9	3.57	1.67	0.1

Appendix 2.4. Parameter estimates from models investigating change in ground vegetation cover over time.

Five linear mixed models investigating the effect of year (2010 and 2021) and distance from water (0-4m, 6-10m, 16-20m, 26-30m) on ground cover (%) of a) graminoids, b) bryophytes, c) ferns, d) shrubs, and e) herbs. Both shrubs and herbs response variables were square root transformed. Transect was used as a random effect.

Response	Predictors	*Estimate*	*SE*	T value	*P Value*
a) Graminoids	(intercept)	46.36	11.8	-	-
(% ground cover)	Year [2021]	19.09	10.21	1.87	0.07
	Distance from water [6-10m]	1.6	10.01	0.16	0.87
	Distance from water [16-20m]	-14.45	12.18	-1.19	0.24
	Distance from water [26-30m]	-21.79	14.21	-1.53	0.14
b) Bryophytes	(intercept)	54.9	10.6	-	-
(% ground cover)	Year [2021]	0.17	8.52	0.02	0.98
	Distance from water [6-10m]	7.75	8.76	0.88	0.38
	Distance from water [16-20m]	19.03	9.49	2.00	**0.05**
	Distance from water [26-30m]	20.12	12.28	1.6	0.11
c) Ferns	(intercept)	2.04	0.64	-	-
(% ground cover)	Year [2021]	0.98	0.65	1.55	0.15
	Distance from water [6-10m]	0.37	0.84	0.44	0.66
	Distance from water [16-20m]	1.47	0.85	1.72	0.11
	Distance from water [26-30m]	0.69	0.94	0.73	0.47
d) Shrubs	(intercept)	22.8	10.4	-	-
(% ground cover)	Year [2021]	5.5	10.7	0.51	0.64
	Distance from water [6-10m]	12.55	13.0	0.96	0.36
	Distance from water [16-20m]	-9.68	12.0	-0.81	0.45
	Distance from water [26-30m]	-13.21	20.22	-0.65	0.53
e) Herbs	(intercept)	1.64	0.41	-	-
(% ground cover)	Year [2021]	3.06	0.41	7.44	**<0.0001**
	Distance from water [6-10m]	-0.67	0.53	-1.28	0.22
	Distance from water [16-20m]	0.33	0.5	0.67	0.51
	Distance from water [26-30m]	0.44	0.6	0.73	0.47

Appendix 3.1. Study site characteristics and sampling totals.

Site characteristics and collected shoot samples from four deer and beaver felling treatments: BD = deer-browsed shoots from beaver-browsed trees, BND = non-deer-browsed shoots from beaver-browsed trees, NBD = deer-browsed shoots from non-beaver-browsed trees, and NBND = shoots with no beaver/deer browsing (control). Samples collected were birch (*Betula* spp.) unless denoted by brackets which refer to willow (*Salix* spp.).

Site number	Name of freshwater	Freshwater type	Location	Number of samples collected BD	BND	NBD	NBND	(total)
1	Dunalastair reservoir	loch	56° 42' 07.3"N, 04° 06' 18.0"W	5	5	5	5	**20**
2	River Lyon	river	56° 35' 59.6"N, 04° 15' 33.7"W	5	0	5	5	**15**
3	River Tay	wetland	56° 37' 25.8"N, 03° 52' 17.4"W	5	3(7)	5	6(5)	**31**
4	River Tummel	river	56° 39' 32.8"N, 03° 40' 31.6"W	7	5	5	5	**22**
5	River Earn	loch	56° 20' 55.1"N, 03° 49' 42.4"W	5	5	5	6	**21**
6	Loch of Craiglush	river	56° 34' 59.5"N, 03° 33' 45.6"W	2	5	5	5	**17**
7	River Braan	river	56° 33' 40.6"N, 03° 35' 38.0"W	0	(6)	0	(5)	**11**
8	Bamff ponds	wetland	56° 38' 49.8"N, 03° 16' 04.1"W	0	8	5	6	**19**
			total	**29**	**44**	**35**	**48**	**156**

Appendix 3.2. Parameter estimates from model investigating the height structure of secondary shoots on trees.

Linear mixed model investigating the effect of height category and tree felling on shoots available (n; log transformed) in each height band. Predictors were centred and scaled. Site and individual tree were used as nested random effects.

Predictors	*Estimate*	*SE*	*T Value*	*P Value*
(intercept)	0.77	0.16	-	-
Height category (50-100cm)	0.39	0.15	2.56	**0.01**
Height category (100-150cm)	0.59	0.15	3.89	**<0.001**
Beaver felling (felled)	0.91	0.16	5.51	**<0.001**
Height (50–100 cm) x Beaver felling (felled)	-0.52	0.22	-2.35	**0.01**
Height (100–150 cm) x Beaver felling (felled)	-1.43	0.22	-6.42	**<0.001**

Appendix 3.3. Parameter estimates from model investigating the nutritional content of plant material (bud vs shoot).

Two linear mixed models investigating the effect of plant material (shoot/bud) on a) nitrogen content (%) and b) carbon content (%). Both response variables (n) were square root transformed. Site was used as a random effect.

Response	Predictors	*Estimate*	*SE*	*T Value*	*P Value*
a) Nitrogen (%)	(intercept)	1.32	0.01	-	-
	Plant material (shoot)	-0.26	0.01	-24.7	**<0.001**
b) Carbon (%)	(intercept)	7.58	0.02	-	-
	Plant material (shoot)	-0.49	0.02	-28.9	**<0.001**

Appendix 4.1. Experimental woodland summary statistics at start vs end of monitoring period.

a) Chapter 4 summary statistics for the experimental woodland in August 2020 prior to monitoring period. Total number of *Salix cinerea* per exclosure, their mean diameter (cm), mean height (cm), mean growing tips per cluster (n) and mean soil moisture (%) ± standard error (range).

Exclosure	Total tree stems (n)	Mean tree height (cm)	Mean diameter (mm)	Mean growing tips per cluster (n)	Mean soil moisture (%)
A	49	81 ± 6.4 (25-222)	5.6 ± 0.5 (1.8-14.9)	42.2 ± 6.3 (10-85)	76.4 ± 2.5 (57.7-100)
B	54	81 ± 8.6 (18-235)	5.8 ± 0.6 (1-15.2)	58.0 ± 4.1 (33-88)	46.7 ± 1.6 (23.1-47.9)
C	66	75 ± 4.3 (22-170)	5 ± 0.4 (1.5-14.4)	59.2 ± 7.3 (13-112)	31.5 ± 3.7 (23.9-84.6)
D	48	101 ± 8.5 (22-240)	6.8 ± 0.6 (1.6-18.5)	70.9 ± 13.4 (4-169)	55.1 ± 2.7 (34.9-72.2)
E	56	69 ± 6.8 (18-225)	4.9 ± 0.5 (1.1-14.2)	48.9 ± 6.9 (6-133)	52.5 ± 2.6 (37.5-76.4)
F	63	73 ± 3.9 (28-165)	4.9 ± 0.3 (1.8-12.2)	46.5 ± 5.4 (16-95)	25.5 ± 1.1 (18.8-32.9)

b) Summary statistics for the experimental woodland in August 2021 at the end of the monitoring period. Total number of *Salix cinerea* per exclosure, their mean diameter (cm), mean height (cm), mean growing tips per cluster (n) and mean soil moisture (%) ± standard error (range).

Exclosure	Total tree stems (n)	Mean tree height (cm)	Mean diameter (mm)	Mean growing tips per cluster(n)	Mean soil moisture (%)
A	46	146 ± 9.6 (42-270)	11.4 ± 1 (3.2-32)	122.8 ± 17.7 (32-252)	41.4 ± 2.8 (24.6-60.3)
B	46	137 ± 13 (29-295)	10.6 ± 1.2 (2.1-26.7)	153.2 ± 14.5 (83-225)	21.4 ± 1.1 (15.7-33.2)
C	59	115 ± 6.4 (26-226)	9 ± 0.7 (2.5-26.2)	94.6 ± 9.9 (41-167)	13 ± 0.6 (8.8-17)
D	46	160 ± 11.3 (39-345)	12.6 ± 1.3 (2.4-35.5)	159 ± 25.5 (29-302)	33.4 ± 3 (20.2-61.2)
E	44	111 ± 11.5 (20-290)	8.4 ± 1 (1.1-24.3	95 ± 19.1 (7-294)	26.3 ± 2.8 (7.4-41.6)
F	59	101 ± 4.6 (33-189)	7.5 ± 0.4 (2.8-16.4	83.8 ± 8.5 (55-126	13.5 ± 0.6 (8.7-18.7)

Appendix 4.2. List of clipping treatments used in study design.

The simulated browsing treatment application per cluster of *Salix cinerea* trees with A) no leafy growing tips clipped (control), B) one third of leafy growing tips clipped and C) two thirds of leafy growing tips clipped. ‘N/A’ indicates there were no surviving trees in the cluster to record.

Cluster ID	Clipping treatment
A1	B
A2	A
A3	C
A4	B
A5	A
A6	B
A7	C
A8	A
A9	C
A10	B
A11	A
A12	C
A13	B
A14	C
A15	A
A16	B
B1	A
B2	B
B3	C
B4	A
B5	C
B6	B
B7	A
B8	B
B9	C
B10	B
B11	C
B12	A
B13	B
B14	A
B15	C
B16	A

Cluster ID	Clipping treatment
C1	C
C2	A
C3	C
C4	B
C5	C
C6	A
C7	B
C8	A
C9	C
C10	A
C11	C
C12	B
C13	B
C14	C
C15	B
C16	A
D1	C
D2	A
D3	B
D4	C
D5	A
D6	C
D7	B
D8	*N/A*
D9	B
D10	C
D11	A
D12	C
D13	A
D14	B
D15	A
D16	C

Cluster ID	Clipping treatment
E1	B
E2	A
E3	B
E4	C
E5	A
E6	C
E7	B
E8	A
E9	C
E10	B
E11	A
E12	C
E13	A
E14	B
E15	A
E16	B
F1	A
F2	B
F3	A
F4	C
F5	A
F6	B
F7	C
F8	B
F9	A
F10	B
F11	A
F12	C
F13	A
F14	B
F15	A
F16	C

Appendix 4.3. Parameter estimates from models investigating the effect of soil moisture on maximum tree height and diameter.

Two linear mixed models investigating the effect of soil moisture (scale 1-10) on *maximum* a) tree height (cm) and b) diameter (mm) per tree cluster. Both response variables were square root transformed. 'Exclosure' was used as a random effect.

Response	Predictors	*Estimate*	*SE*	*T Value*	*P Value*
a) Maximum tree height (cm)	(intercept)	5.4	0.38	-	-
	Soil moisture	0.33	0.08	4.1	**<0.001**
b) Maximum diameter (cm)	(intercept)	7.4	0.43	-	-
	Soil moisture	0.33	0.09	3.7	**0.01**

Appendix 4.4. Plots from supplementary models investigating the effects of clipping on the relative change in tree growth, structure, and resource allocation.

Plots from additional linear mixed models for relative change (%) between 2020 and 2021 in mean a) specific leaf area (SLA) (%), b) total leafy growing tips (n), c) tree height (cm), and d) tree diameter (cm). Predictors are coloured by significance (grey = not significant, black = significant). **P*=0.05. Response variables were square root transformed. 'Exclosure' was used as a random effect.