



Tree felling by beaver promotes regeneration in riparian woodlands whilst increasing resource availability for deer

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ABSTRACT

Interactions between species influence ecosystem functions and are sensitive to reintroductions. Our understanding of interactions between naturally co-occurring large herbivores, such as Eurasian beaver (*Castor fiber*) that are now re-establishing throughout their range, and well-established native ungulates, is limited, despite the potential implications for riparian woodlands. Observations in Scotland indicate that roe deer (*Capreolus capreolus*) readily exploit the regenerative secondary shoots produced after tree felling by beaver. Our study, based in eastern Scotland, investigates the role of beaver herbivory in riparian woodland regeneration and asks whether deer are attracted to this novel resource because it is either a) more readily available, b) nutritionally superior, or c) morphologically more appealing than accessible browse on unfelled (standing) trees. We firstly quantified the secondary shoots available to browsing deer at different heights on felled and standing birch (*Betula* spp.) trees in twenty riparian woodland plots across five well-established beaver territories (occupancy ten years). Shoots from birch and willow (*Salix* spp.) trees with contrasting levels and combinations 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, regenerating beaver-felled trees had 18% more secondary shoots. These shoots were significantly higher in nitrogen content (+13%), but similar in carbon content and concentrated closer to the ground. Our results show 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 common, readily available, and nutritious resource through beaver browsing could, however, also enhance habitat quality for browsing deer, with the potential to affect deer distribution and feeding habits.

1. Introduction

Species reintroductions can play an important role in the mitigation of biodiversity loss. Their main objective is to return extirpated species to their former range (IUCN/SSC, 2013). Although typically rooted in species 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 and Smith, 2018). It is broadly understood how predators influence their large herbivorous prey, and that this interaction can have cascading effects. However, interspecific interactions between naturally co-occurring large herbivores and their ecosystem consequences are less well studied (Ellison, 2019, Kéfi et al.,

2012) even though these non-trophic interactions can prove just as crucial in shaping 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 often remain sparse. Populations of herbivore species are expanding and diversifying, and therefore increasingly likely to interact, whether directly or indirectly. Wider understanding of such herbivore-herbivore interactions, and their ecosystem consequences is therefore important, especially when (i) one species has been reintroduced after a prolonged absence, and when these interactions (ii) occur in fragmented/degraded landscapes, and (iii) may conflict with other land management objectives.

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The Eurasian beaver (*Castor fiber*) is a herbivorous keystone species that has profound effects on wetland ecosystems and 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 supported by legal protection (Halley et al., 2021). They now occupy highly populated, managed landscapes across Europe (Wróbel, 2020). Beavers fell tree stems of various sizes and species for food and dam/lodge construction materials. This unique form of browsing can promote tree regrowth in the form of secondary shoots that sprout from around the cut base, akin to the process of traditional coppicing (Savill, 2004). Tree felling by beavers may therefore indirectly influence the abundance of forage available for other large herbivores that share riparian woodlands, particularly deer (Cervidae).

Throughout Europe, deer populations have been steadily increasing over recent decades, particularly since the 1950s, in parallel with a significant expansion in forest cover (Carpio et al., 2021). While some degree of mammalian herbivory contributes to the natural dynamics of woodland ecosystems, unnaturally high levels can threaten woodland health and expansion (Ramirez et al., 2018; Spake et al., 2020). Deer are identified as a major constraint in the re-establishment of Scotland's native riparian woodland (Burton et al., 2018; Ogilvy et al., 2022). Surveys conducted on Scotland's native woodlands between 2010 and 2015 documented herbivore browsing (primarily by deer) in approximately 60% of native woodland transects (Forest Research, 2020).

Changes in woodland structure, composition, and regeneration processes arising from beaver-deer interactions have been documented in North America (Baker et al., 2005; Hood and Bayley, 2009; Johnston, 2017; Loeb and Garner, 2022). In Europe, researchers have alluded to similar effects due to interactions between beaver and large woodland herbivores (Jones et al., 2009; Stringer and Gaywood, 2016; Ogilvy et al., 2022). However, despite the large and growing geographical area in which beaver-deer interactions may occur, studies of their direct and indirect effects remain sparse. Of the available studies, one based in Scotland using riparian woodland monitoring plots (Iason et al., 2014) documented deer browsing on 68% of beaver-felled stumps that had produced secondary shoots, suggesting that beaver-deer interactions could be relatively commonplace. It also implies that this type of forage, which may have been largely absent at this scale from un-coppiced woodlands prior to the beaver's reintroduction, could potentially offer an attractive resource for deer. In contrast, one study in Denmark found that deer avoid areas of high beaver activity (Pejstrup et al., 2023). The limited (and conflicting) understanding of this interaction further highlights a notable knowledge gap.

Despite potentially important implications for riparian woodland regeneration, no studies have investigated the drivers behind beaver-deer interactions – and exactly why deer utilise the secondary shoots from beaver-felled trees therefore remains unclear. One hypothesis is that deer utilise these shoots simply because this resource is disproportionately abundant. Roe deer (*Capreolus capreolus*) select foods that are more available, despite being of lower nutritional quality, because search energy is lower (Palmer and Truscott, 2003; Borkowski and Ukalska, 2008). In Scotland, high rates (77–86%) of resprouting have been documented in birch (*Betula* spp.) and willow (*Salix* spp.) trees following beaver browsing (Jones et al., 2009; Iason et al., 2014) providing anecdotal evidence that beaver-browsing could inadvertently enhance the forage accessible to deer (Jones et al., 2009). However, the latter research was conducted within a single semi-natural beaver enclosure and further, multi-site experiments are required to test effects at a broader scale. Whether an increased availability in forage can drive deer to select this resource is therefore uncertain.

An alternative hypothesis, given that large herbivores can distinguish differences in forage quality (P. Duncan et al., 1998; Ball et al., 2000), is that secondary shoots are of higher quality, whether in terms of nutrition or palatability. Studies show that browsing of trees can stimulate growth of any remaining plant tissue to offset the loss of biomass

(Danell et al., 1985). A by-product of this accelerated, compensatory growth can be plant material of higher browse quality (Haukioja et al., 1990). During these rapid growth phases, investment in chemical defence is low, but this shifts as growth slows (Bryant et al., 1983). On the other hand, research has documented reduced palatability in birch recovering from herbivory (Tuomi et al., 1990; Wratten et al., 1984). Studies investigating the chemistry of resprouted secondary shoots (following beaver felling) of Fremont cottonwoods (*Populus fremontii*) (Martinsen et al., 1998; Durben et al., 2021) found that these were nutritionally superior to shoots from standing trees.

A final hypothesis is that the morphological characteristics of resprouted secondary shoots influence their selection by deer. Researchers in Sweden tracked moose (*Alces alces*) and compared the nutritional content of the bites of forage that were taken to those in the immediate vicinity that could have been taken. They concluded that moose selected plants based on morphology rather than nutritional aspects (Shiple et al., 1998). Roe and red deer (*Cervus elaphus*) have similarly been shown to base their foraging choices on structural aspects of plant morphology, such as height, shape, and structure (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 no research in Europe that has evaluated these three hypotheses. Although studies have anecdotally reported evidence of indirect beaver-deer interactions in European riparian woodlands (Jones et al., 2009; Pejstrup et al., 2023), this is the first to investigate the mechanistic drivers underlying the relationship between Eurasian beaver and foraging choices of deer. We firstly examine whether tree felling by beaver promotes riparian woodland regeneration through the resprouting of secondary shoots. Next, we investigate the comparative nutritional and morphological qualities of regrowth from beaver-felled trees. We assess whether resprouted secondary shoots of beaver-felled trees may be utilised by deer because they are either a) more readily available, b) nutritionally superior, and/or c) morphologically more appealing than other deer-accessible browse on standing trees. As beaver populations expand further, interactions with deer in riparian woodlands will become increasingly commonplace. Understanding the drivers behind such interactions is essential to predict potential ecological effects on the wider landscape and inform adaptive woodland management.

2. Methods

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, streams, and ponds to large lochs (lakes) and rivers (Campbell-Palmer et al., 2021). Beavers were officially reintroduced to western Scotland in 2009 (with unofficial releases in the east of the country dating back to the early 2000s) after an absence of over 400 years. The latest estimates suggest there are 251 active beaver territories (range of 602–1381 individuals) in the east located across the Tay and Forth catchments (Campbell-Palmer et al., 2021).

The Tay catchment is the largest in Scotland and spans 4587 km². Woodlands cover around 16% and contain a diverse variety of native tree species dominated by birches and commercial conifers. Arable/grassland accounts for 32% and is concentrated in low-lying and more populous valleys (NRFA, 2022a). The smaller Forth catchment covers 1036 km² of which woodland comprises 22%, with 48% arable/grassland (NRFA, 2022b).

The four species of deer known to inhabit the study areas (in decreasing order of range) are: roe, red, fallow (*Dama dama*), and sika (*Cervus nippon*) (BDS, 2016). Roe deer will use a variety of agricultural, woodland, and urban habitats, but are the most likely deer species to

occupy lowland riparian zones based on their ecology (Linnell et al., 2020; Ratcliffe and Mayle, 1992). They are also the most selective forager and will readily browse newly sprouted tree shoots (Ratcliffe and Mayle, 1992). Our direct observations supported by distribution mapping (NBN Trust, 2024) confirmed that roe deer were the dominant deer species foraging in the study area. Although the number of wild roe deer in Scotland is not accurately known, and notoriously difficult to determine at a localised scale (Smart et al., 2004), latest estimates suggest that there are at least 200,000 in the country (Pepper et al., 2020).

2.2. Survey and Sampling Sites

Beaver distribution maps from Campbell et al. (2012) and Campbell-Palmer et al. (2021) were used to identify territories active for at least ten years. Eleven beaver territories were selected at random, subject to landowner permission. Of these, five territories were used as 'survey sites' to investigate how tree felling by beavers affects production of secondary shoots in riparian woodland. Two of these sites, plus an additional six territories (Fig. 1) were used as 'sampling sites' for collecting secondary shoots for nutritional and morphological analysis. All territories provided access to riparian woodland dominated by birch and/or willow. Territories encompassed felling of differing ages, ranging from one or more seasons old (which accommodates resprouting)

through to freshly-felled trees (with insufficient time for evidence of resprouting) reflecting the naturally heterogeneous pattern of resource use in an active beaver territory.

To account for the naturally high fine-scale spatial variation in the number of beaver-browsed trees within the territories, four 5×5m plots covering a gradient of beaver browsing intensity were established at each site. Each survey site included one control plot (no beaver browsing). All plots (including control plots) were located <10 m from the water's edge to reflect the focus of beaver felling activity. 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 trees included those that were fully-felled (i.e., a stump), partially-felled (incompletely severed xylem with some remaining phloem connecting the basal stump and the upper tree stem) or gnawed (superficial bites of bark from the main stem). Downy birch (*Betula pubescens*) was the dominant tree species in all plots. Trees that had fallen due to other natural disturbances were infrequently observed at the scale of our 5×5m plots.

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-

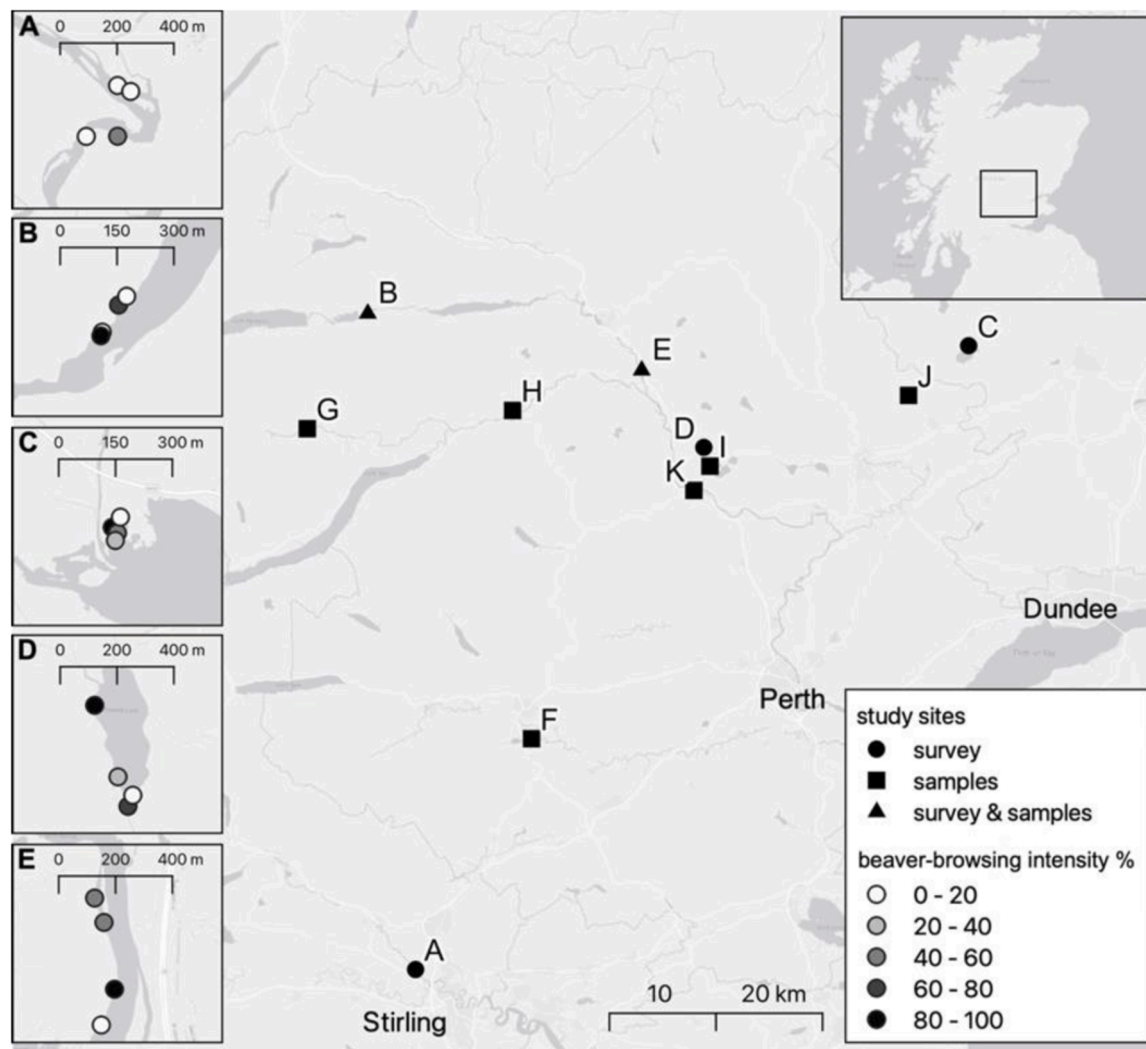


Fig. 1. Map of survey (n=5) and sampling (n=8) sites across Tay and Forth catchments. Two survey sites were included as sampling sites (giving 11 sites in total). Left insert panels display the plot distribution at each survey site and their beaver browsing intensity (darker colour indicates a higher proportion of beaver-browsed stems).

level measurements were taken. The twenty plots (15 with beaver browsing, 5 with no beaver browsing) at the five survey sites were visited over five days in early-September 2020. Only secondary shoots originating at a height of <150 cm were considered as they comprise forage in the typical height range accessible to browsing roe deer (P. Duncan et al., 1998). The status of every tree (i.e., woody stem >1 cm diameter) was classified according to whether it was a) standing or felled by beaver and b) had secondary shoots originating <150 cm above the ground.

In total, the twenty plots contained 784 trees. A sub-sample of trees ($n = 141$) with secondary shoots originating <150 cm were selected at random for further individual tree-level analyses. Within each plot, measurements were taken for up to five trees that were fully felled by beaver and had resprouted secondary shoots ($n = 66$). Mature, standing trees can also provide viable forage located <150 cm by sprouting basal or non-basal secondary shoots directly from the main stem in response to various environmental stressors (Del Tredici, 2001). Measurements were therefore repeated for up to five standing trees also displaying secondary shoots to act as a comparison ($n = 75$) (Fig. 2). Since only those trees displaying secondary shoots were selected for further measurements, some plots unavoidably contained fewer than five felled and/or standing trees. The individual-tree level data recorded were a) tree diameter (cm) measured 20 cm above ground level using a tape, b) species identity and c) the total number of secondary shoots arising <150 cm above the ground.

To further investigate the abundance of forage available to deer, secondary shoots were then categorised into three height categories (<50 cm, 50–100 cm, and 100–150 cm). 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 10 cm from the base of a tree and was 50 cm tall, then it would contribute to the forage available in the <50 cm and 50–100 cm height band (Fig. 3).

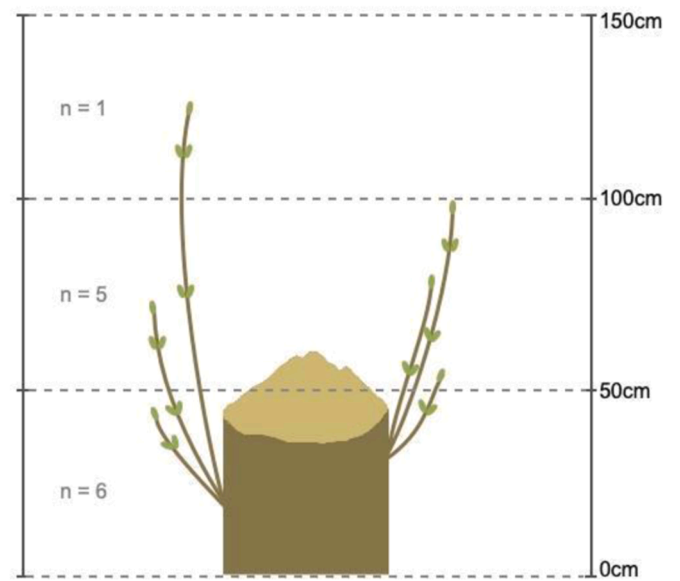


Fig. 3. Diagram of the stump of a typical beaver-felled tree sprouting secondary shoots showing the three height-category classification system (<50 cm, 50–100 cm, 100–150 cm) used to determine the abundance of forage available at each height. ‘N=’ refers to the number of shoots present in each height band as an example.

2.4. Forage quality and morphology

To assess the nutritional quality and morphological characteristics of forage available to deer, 156 shoots (133 from birch and 23 from willow) growing within deer browsing height (<150 cm) were collected during winter. Deer typically alter their diets seasonally by consuming more woody plants during winter months (Spitzer et al., 2020) when fewer



Fig. 2. Examples of birch (*Betula pubescens*) a) standing and b) beaver-felled, both with secondary shoots located within deer-browsing height (<150 cm).

herbaceous plants are available (Czernik et al., 2013; Krasnov et al., 2015). Independent trees were sampled randomly from across eight beaver territories, equivalent to a total area of approximately 0.5 km² (see Appendix A) during mid-November 2020 after leaf fall. Shoots were collected from trees subjected to a four-way combination of beaver felling and deer browsing:

- 1) Deer-browsed secondary shoots from beaver-felled trees
- 2) Unbrowsed secondary shoots from beaver-felled trees
- 3) Deer-browsed secondary shoots from standing trees
- 4) Unbrowsed secondary shoots from standing trees (control).

As deer lack upper incisors, they create a tearing motion when browsing (Bang and Dahlstrom, 1972). Deer-browsed shoots were therefore easily characterised by the removal of the apical bud leaving a frayed, ragged edge (Fig. 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. Secondary shoots showing signs of browsing by beaver were excluded, although these were rarely encountered. Apical shoots (30 cm lengths) were collected from an average of five independent trees from each of the four browsing combinations (unbrowsed/browsed by beaver/deer) at each of the 8 sites, dependent on availability. Samples were sealed in labelled bags and transported to the laboratory.

2.4.1. Morphological analyses

In the laboratory, exact shoot length (cm) was recorded using a measuring tape and diameter was measured 2 cm from the shoot tip in millimetres using digital callipers. The buds present on shoots were counted alongside the number of lateral branches per shoot. Bud and lateral branch counts were standardised by expressing them per metre length of main shoot. These standardised values were used in all subsequent analyses.

2.4.2. Nutritional analyses

In the laboratory, the apical 5 cm of each shoot was 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 3–5 mg of each sample was then weighed into tin capsules (6×4mm size; 'Elemental Microanalysis'). All weights were recorded to the nearest 0.01 mg. Total nitrogen (N) and carbon (C) content (%) were 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).

Deer-browsed shoots lacked their apical bud because it had been removed during browsing. A further sub-analysis was therefore conducted to compare the nutritional content of the apical bud and apical section of shoot. A total of 480 additional 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 30 cm in length. Each shoot and their tip were located <150 cm above the ground.

In the laboratory, 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 3 mg required for the C and N analyses. Ten apical 5 cm 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 0.01 mg prior to drying and were then analysed for C and N content using the same methodology as the main sample set.

2.5. Statistical Analyses

Relationships between beaver felling and the availability, nutritional content and morphology of deer-accessible forage were assessed using



Fig. 4. Examples of a) deer-browsed shoot with characteristic removal of apical bud and frayed edge and b) unbrowsed secondary shoots from beaver-felled tree.

linear mixed-effects models. Statistical analyses and plots were produced using packages lme4 (Bates et al., 2014), sjPlot (Lüdtke, 2023) and ggplot2 (Wickham, 2016) in R Studio version 1.4.1103. All linear mixed-effects models included site identity as a random effect, except when analysing height-stratified secondary shoots, which included site and individual-tree as nested random effects. Response variables were normalised if required, and covariates were mean and centre-scaled.

Correlations between predictor variables (e.g., number of buds vs number of branches on secondary shoots) were then assessed in a correlation matrix and checked for variance inflation (VIF). However, there was no indication of variance inflation as all VIF scores were <4. Furthermore, residuals from all models were tested for normality and met model assumptions, and the best-fitting models were selected on the basis of Akaike Information Criterion (AIC) scores. Potential ecologically meaningful interactive effects (e.g., between tree species and diameter resulting from selective foraging by beavers) of explanatory variables were also tested. Where interactions were not-significant and increased the AIC score, they were removed from the model.

2.5.1. Forage availability

Forage availability was modelled using the total number of secondary shoots per tree (log-transformed) as the response. 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 (%).

In a separate model, the height distribution 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 as the forage availability model were included, as well as height category of secondary shoots (<50 cm, 50–100, and 100–150 cm). An analysis of variance (ANOVA) was then applied to this model in order to carry out post-hoc multiple comparisons (Tukey's HSD test) to assess potential differences in forage abundance across the different height categories.

2.5.2. Forage quality

Nutritional quality of sampled shoots was modelled using C and N content or C:N ratio as the response (all square root transformed). Beaver and deer browsing effects on the secondary shoots were included as separate factors each with two levels (beaver unfelled/felled, deer unbrowsed/browsed) to allow tests for interactions between the browsing types of the two species. 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. Separate models were used to test whether the type of material (apical bud vs apical shoot minus bud) influenced either the N or C content (%; square root transformed).

2.5.3. Forage morphology

Morphological characteristics of shoots were modelled using buds (n per m) and lateral branches (n per m) as response variables (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). Since the number of lateral branches could both influence the number of buds or be a product of it, the number of buds and lateral branches were included as explanatory variables to assess their relationships with each other.

3. Results

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 150 cm). On average, 49% (± 8.4 SE, 0–100% range) of standing trees per plot had secondary shoots accessible to deer.

Fifteen plots in total exhibited beaver felling activity. All of these contained at least some felled trees bearing secondary shoots and in three plots every beaver-felled tree displayed growth of secondary shoots. When testing our first hypothesis, the model (Fig. 5) revealed a strong association between beaver felling and the availability of secondary shoots, which were 18% more numerous on felled trees than standing trees ($P < 0.01$). Regardless of felling status, secondary shoots were more abundant on trees in plots of higher tree density ($P < 0.01$). Additionally, larger diameter trees supported more secondary shoots ($P = 0.03$).

Beaver browsing intensity (%) did not explain variation in the number of secondary shoots ($P = 0.6$) (Fig. 5). Of the six tree species recorded across the five beaver territories, willow and birch accounted for 92% and were therefore the focus of the analysis. The model showed that the number of secondary shoots was independent of the identity of these species ($P = 0.9$).

The number of secondary shoots available to deer differed significantly amongst the three height categories (<50 cm, 50–100 cm, 100–150 cm) ($P = 0.01$) as well as between beaver-felled and standing trees ($P < 0.001$) (see Appendix B). 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: <50 cm ($P < 0.001$) and 100–150 cm ($P = 0.02$) compared to standing trees. In standing trees, the shoots were typically distributed relatively evenly across the three different height categories (Fig. 6).

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 ($P = 0.03$; Fig. 7a). Secondary shoots from beaver-felled trees had a 13% higher N content than those on standing trees. 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 similar regardless of tree species (birch or willow) ($P = 0.6$). The mean diameter of all sampled shoots was relatively small with little variation (2.3 mm ± 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. Carbon content had a marginal positive association with beaver felling ($P = 0.06$; Fig. 7b). No differences were observed between sampled shoots whether browsed or not by deer ($P = 0.3$). Carbon content was, however, affected by tree species ($P = 0.03$) with birch shoots more C-rich than willow. Shoots with more lateral branches contained significantly less C ($P < 0.01$). The concentration of C was unaffected by the number of buds ($P = 0.3$) or shoot diameter ($P = 0.3$).

The C:N ratio of sampled shoots showed a strong relationship with beaver felling ($P < 0.001$; Fig. 7c). Sampled shoots from beaver-felled trees had a 13% lower C:N ratio than unbrowsed trees, indicative of higher-quality forage. There was a marginal positive effect of deer browsing on the C:N ratio ($P = 0.06$), but no effects of any other variables in the model.

When assessing nutritional differences between the C and N content of the apical bud vs the secondary shoot minus its apical bud, N content was found to be significantly higher in buds (+39%) than shoots without buds ($P < 0.001$; Fig. 8). There were also differences in the C content ($P < 0.001$) with buds containing on average 13% more C than shoots (see Appendix C). 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 5 cm length of apical shoot (18 ± 1 mg SE). Since mean bud weight typically accounted for a relatively small proportion of intact shoot weight (mean 8.5%), apical bud removal by deer cannot alone account for the significantly

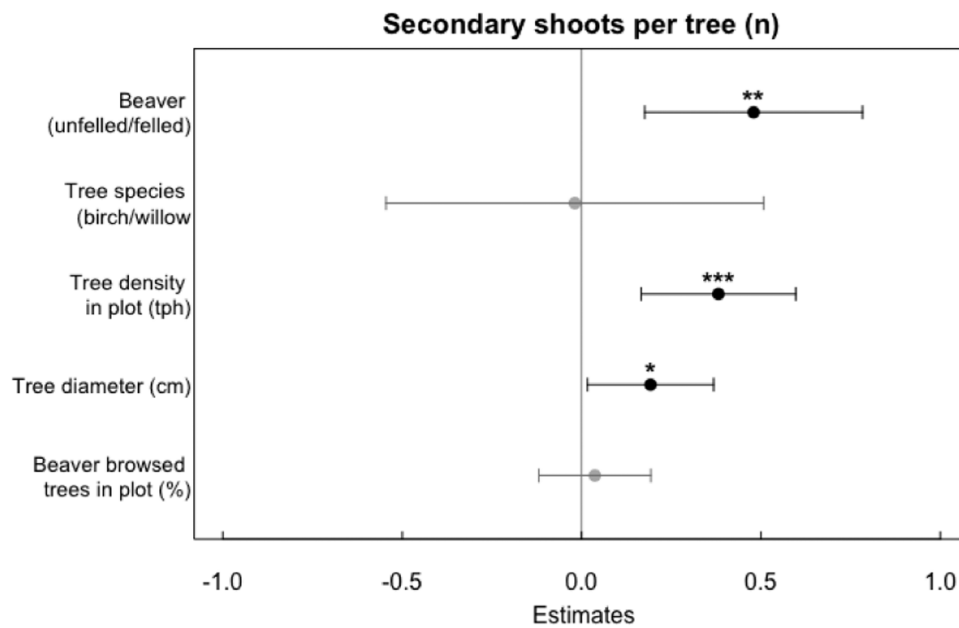


Fig. 5. Forest plot output from a linear mixed model for response variable secondary shoots per tree (n). For factors the first level named in brackets is the reference level. Predictors are coloured by significance (grey = not significant, black = significant). * $P=0.05$; ** $P=0.01$; *** $P<0.001$.

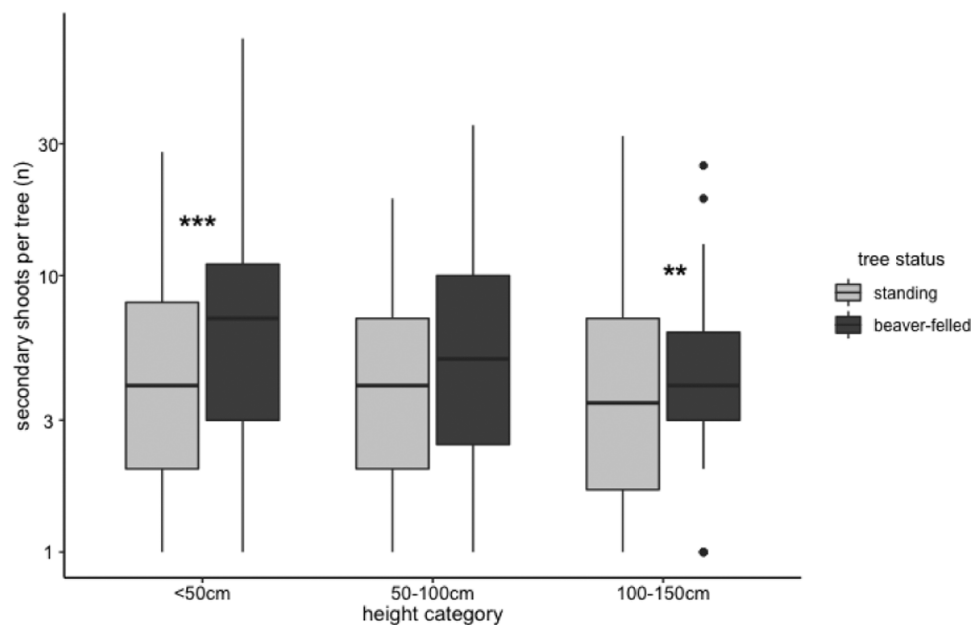


Fig. 6. The vertical height distribution of secondary shoots (log scale) on trees ($n=141$) in three height categories <50 cm, 50–100 cm and 100–150 cm on standing and beaver-felled trees. Stars indicate significantly different mean numbers of shoots between beaver-felled and standing trees from a Tukey HSD post-hoc groupwise comparison following the model summarised in Appendix 3 (** $P<0.01$; *** $P<0.001$).

lower N content we observed in the deer-browsed sampled shoots.

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 secondary shoots browsed by deer ($P=0.02$; Fig. 9a), but beaver felling status 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 ($P<0.001$) (Fig. 10).

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 ($P<0.001$; Fig. 9b). Lateral branching was unaffected by beaver felling ($P=0.1$). Tree species had a significant effect in the model ($P=0.01$) with birch trees having 27% more lateral branches than willow. There was no relationship between lateral branching and shoot diameter ($P=0.2$).

4. Discussion

Beaver-felled trees supported more regrowth which was concentrated closer to the ground and therefore readily accessible to browsing

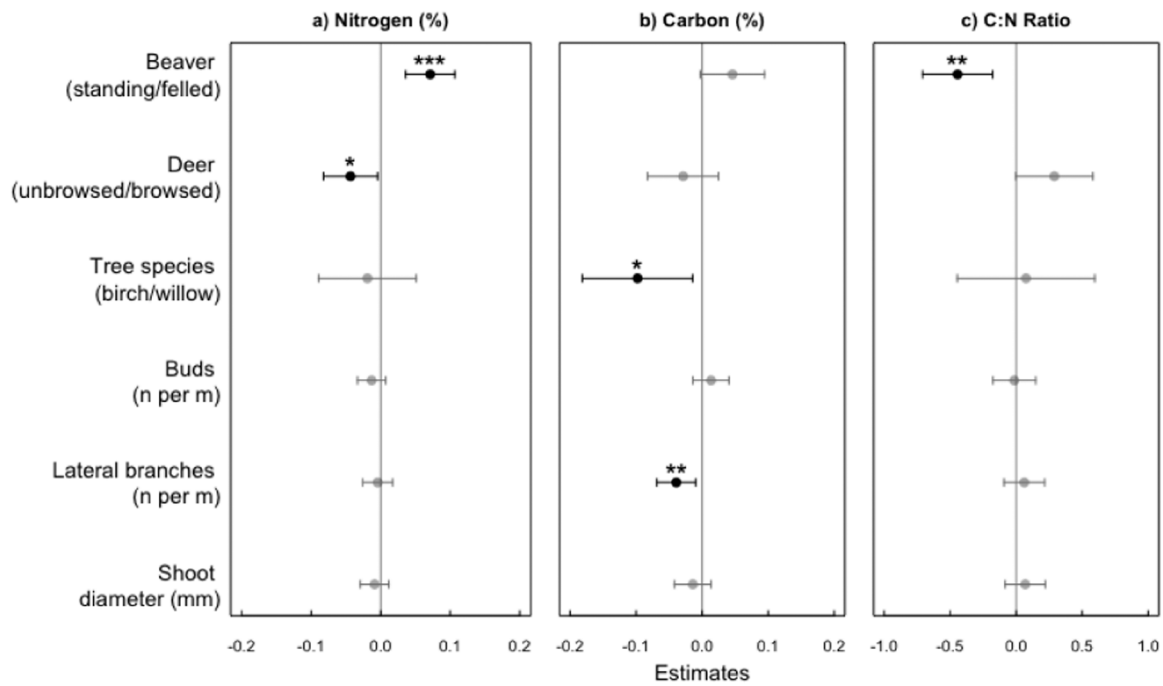


Fig. 7. Forest plot outputs from linear mixed models for response variables a) nitrogen (N) (%), b) carbon (C) (%) and c) C:N ratio of sampled shoots. For factors the first level named in brackets is the reference level. Predictors are coloured by significance (grey = not significant, black = significant). * $P=0.05$; ** $P=0.01$; *** $P<0.001$.

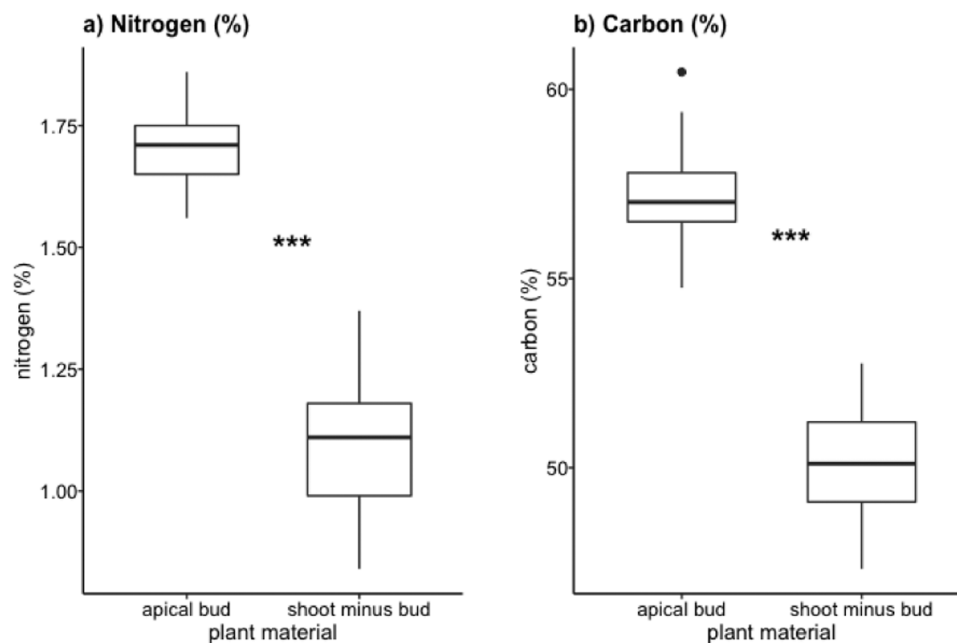


Fig. 8. The concentration of a) nitrogen (%), and b) carbon (%) in plant material (apical bud vs shoot minus bud) collected from an additional subset of unbrowsed sampled shoots. Stars indicate $P<0.001$ (full linear mixed model output in Appendix 3).

deer. Secondary shoots from resprouted beaver-felled trees were also of higher nutritional quality, containing more N than those from standing trees. However, shoots browsed by deer from all trees 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.

4.1. Beaver felling: implications for riparian woodland regeneration

The large proportion of beaver-felled trees (62%) we observed with resprouted secondary shoots is consistent with previous research in Scotland on a range of broadleaf species (Jones et al., 2009; Iason et al., 2014). In our study, it was evident that mature single-stemmed birch and willow trees were transformed into stumps with a multi-stemmed architecture of young resprouted secondary shoots. A similar effect is achieved through coppicing by humans, one of the earliest known forms

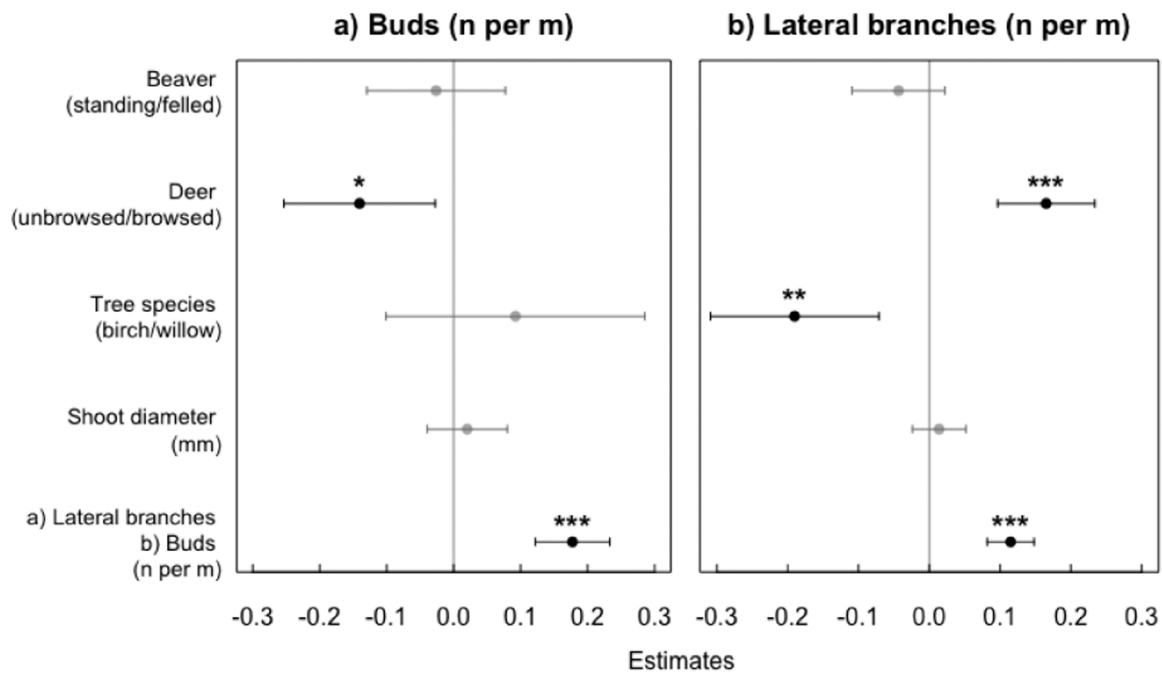


Fig. 9. Forest plot outputs from linear mixed models for response variables a) buds (n per metre), and b) lateral branches (n per metre). For factors the first level named in brackets is the reference level. Note that 'lateral branches' and 'buds' were included in the models for plot a and b respectively. Predictors are coloured by significance (grey = not significant, black = significant). * $P=0.05$, ** $P=0.01$, *** $P<0.001$.

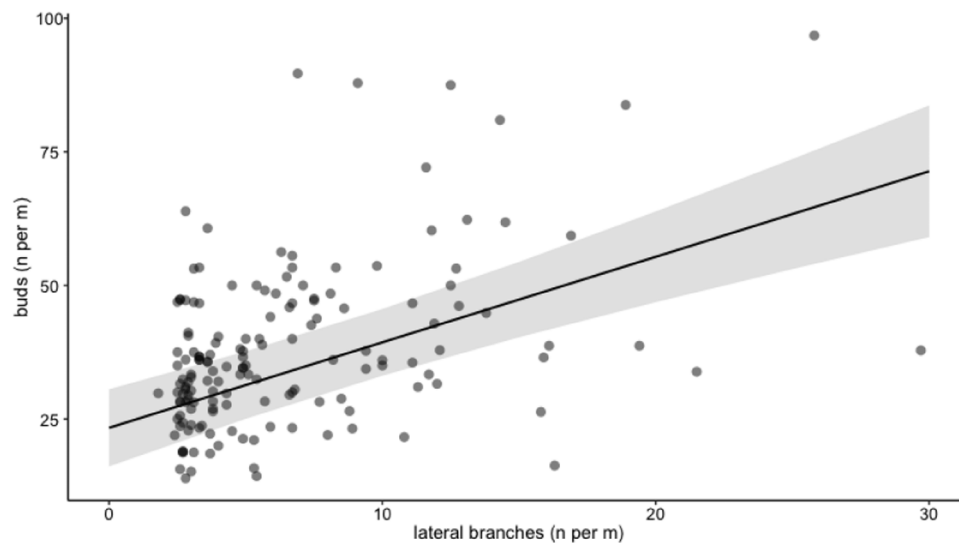


Fig. 10. Relationship between the buds (n per metre) and lateral branches (n per metre) on sampled shoots subjected to a range of beaver and deer browsing treatments. Points represent raw data values, and the line represents the predicted linear mixed model fit from Fig. 9a.

of woodland management (Buckley, 2020), with many broadleaved species sprouting vigorously following cuts or stress (Koop, 1987). Coppicing creates structural heterogeneity which is linked to high biodiversity and conservation value (Kirby et al., 2017). Our findings therefore highlight the value of beavers in a self-regulating woodland regeneration system.

4.2. Forage availability

Our results indicate that beaver herbivory significantly increases the forage available to browsing deer in riparian woodlands, confirming our first hypothesis. This result is expected due to the general shorter stature of beaver-felled tree stumps (typically 30–50 cm) compared to standing

trees. This height difference suggests a larger area for secondary shoots to emerge from standing trees, while concentrating those on beaver-felled trees close to the ground. Despite this, our findings still demonstrate a notable abundance of taller shoots in beaver-felled trees, even within the higher 100–150 cm height range, potentially suggesting a conservative interpretation of the findings.

4.3. Forage quality

Our hypothesis that secondary shoots from resprouted beaver-felled trees were more nutritious than those from standing trees was confirmed. High N concentrations typically occur in young, fast-growing tissues to support rapid protein synthesis during growth bursts (Mattson,

1980). Resprouted secondary shoots of Fremont cottonwood trees following felling by North American beaver 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 are consistent with our own despite differences in tree (and beaver) species. Future studies should consider quantifying the nutritional value increase of food sources per hectare whilst assessing the availability of alternative food sources for deer.

As N is an essential dietary nutrient and limiting element for herbivores (Mattson, 1980), deer are likely to prefer shoots with elevated N concentrations. Unexpectedly, we found that deer-browsed shoots were lower in N than unbrowsed shoots. From our study design, it is impossible to ascertain whether deer preferentially select shoots lower in N, or if 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, based on our separate analyses of bud and residual shoot tissue, we found that apical bud removal alone could not account for the lower N content in deer-browsed shoots. Furthermore, the number of buds on shoots also did not account for any variation of N content in our model.

Since the literature implies that roe deer actively select the most nutritious forage (P. Duncan et al., 1998; Mancinelli et al., 2015), the lower N content we observed in browsed shoots is most likely a physiological response by shoots to deer browsing indicative of compensatory regrowth (Utsumi and Ohgushi, 2009; Moyo et al. 2015). Removal by deer of the apical bud, which plays an important role in shoot growth through hormone regulation whilst acting as the main meristem (Muller and Leyser, 2011), may also have consequences for secondary shoots. However, the nutritional status of shoots would need to be assessed before and after deer browsing to explicitly determine cause and effect. The mechanistic basis of shoot response to herbivory is evidently an area that requires further study.

4.4. Forage morphology

While the drivers behind the selection of secondary shoots by deer is poorly understood, it is well known that overall 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 and Colin, 2003; Renaud et al., 2003). When offered saplings that were structurally ‘normal’ (control), ‘bushy-topped’ (top-heavy without apical dominance) and ‘five-shoot’ (a multi-stemmed coppice-like form), deer preferred the coppice-like structure.

In our study, contrary to one of our original hypotheses, individual shoots from resprouted beaver-felled trees did not differ morphologically in their number of buds or branches when compared to those on standing trees. However, our anecdotal observations suggest that the shoots from resprouted beaver-felled trees may, collectively contribute to significant differences in the overall morphology of a tree. For example, secondary shoots on these trees were significantly higher in density and had a distinct basally-centred, rather than evenly dispersed, height distribution. Therefore, whilst the morphology of individual shoots may not differ significantly from those on standing trees, we further predict that the unique, visually-striking arrangement of shoots will make beaver-felled trees more conspicuous to browsing deer and ultimately influence their attractiveness as a whole.

From our study design, we cannot distinguish whether deer selected branchier shoots with fewer buds, or if these shoots produced more branches and fewer buds in response to deer browsing. Research comparing fenced and unfenced plots of young oak (*Quercus petraea*) noted that trees browsed by large herbivores were significantly more branched (Drexhage and 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). Herbivore browsing has also been suggested to stimulate changes in morphology in birch trees, producing longer shoots with more leaves than unbrowsed shoots (Danell et al., 1985; Herder et al., 2009). This implies that differences in shoot morphology in our study may have occurred *after* deer browsing, potentially as a compensatory growth strategy, rather than a preference by deer for branchier shoots.

4.5. Implications

Habitat use by deer is strongly determined by the availability of food (Palmer and Truscott, 2003; Borowski et al., 2021), including search time (Nudds, 1980). By providing a nutritious resource of forage that would have been less common or conspicuous prior to the beaver's reintroduction, we anticipate that tree-felling by beaver may indirectly influence the spatial distribution of deer. However, any such effect is likely conditioned by the landscape, local and individual tree-level resource. For example, the spatial arrangement of an increased abundance of secondary shoots concentrated around the base of a beaver-felled tree may also help reduce forage search time for deer and increase feeding efficiency. Furthermore, canopy gaps created by beaver-felled trees in otherwise dense riparian woodlands, can lead to localised, well-lit patches that facilitate tree seedling recruitment (Nummi and Kuuluvainen, 2013). This, alongside an increased richness of graminoid species (Law et al., 2017), could further influence deer distribution.

Currently there is limited evidence to suggest that beavers can indirectly attract deer through a resource interaction, and roe deer have been shown to actively avoid areas with high beaver activity in Denmark (Pejstrup et al., 2023). However, Scotland's woodland resource is more fragmented than that of Denmark and around 56% of its riparian vegetation is in ‘poor condition’ with many stream reaches now lacking broadleaved trees altogether (Ogilvy et al., 2022). Under this scenario the potential implications of beaver-deer interactions are likely to be magnified.

5. Conclusions

Tree felling by beaver creates a heterogeneous habitat of mature trees and stumps with vigorous secondary shoot growth, and the potential for an indirect interspecific interaction with deer in riparian woodlands through a change in resource availability. It is unclear if this secondary shoot growth can completely replace the trees felled by beaver over time. However, our study confirms that beaver-felling promotes the growth of a multi-stemmed architecture of secondary shoots. Our finding that secondary shoots from beaver-felled trees were more abundant and nitrogen-enriched when compared to those of standing trees, in line with our hypotheses, also suggests that deer will be attracted to this resource. Whilst the morphology of secondary shoots from beaver-felled trees did not differ in comparison to those from standing trees, the conspicuous and unique basally-concentrated arrangement of shoots on beaver-felled trees is also likely to play a role in their use by deer. This marked change in resource availability could have significant implications for deer distributions and management (e.g. by diverting animals to more vigorously regenerating stands) or regeneration of riparian woodlands (e.g. necessitating supplementary planting or temporary stand protection) that merits longer term study of environments where beaver and deer interact.

CRediT authorship contribution statement

Kelsey A Wilson: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Alan Law:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Alison J Hester:**

Writing – review & editing, Methodology. **Martin J Gaywood:** Writing – review & editing. **Nigel J Willby:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. 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	Freshwater type	Location	Number of samples collected				
			BD	BND	NBD	NBND	(total)
1	loch	56° 42' 07.3"N, 04° 06' 18.0"W	5	5	5	5	20
2	river	56° 35' 59.6"N, 04° 15' 33.7"W	5	0	5	5	15
3	wetland	56° 37' 25.8"N, 03° 52' 17.4"W	5	3(7)	5	6(5)	31
4	river	56° 39' 32.8"N, 03° 40' 31.6"W	7	5	5	5	22
5	loch	56° 20' 55.1"N, 03° 49' 42.4"W	5	5	5	6	21
6	river	56° 34' 59.5"N, 03° 33' 45.6"W	2	5	5	5	17
7	river	56° 33' 40.6"N, 03° 35' 38.0"W	0	(6)	0	(5)	11
8	wetland	56° 38' 49.8"N, 03° 16' 04.1"W	0	8	5	6	19
		total	29	44	35	48	156

Appendix B. 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 (50–100 cm)	0.39	0.15	2.56	0.01
Height category (100–150 cm)	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 C. 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

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