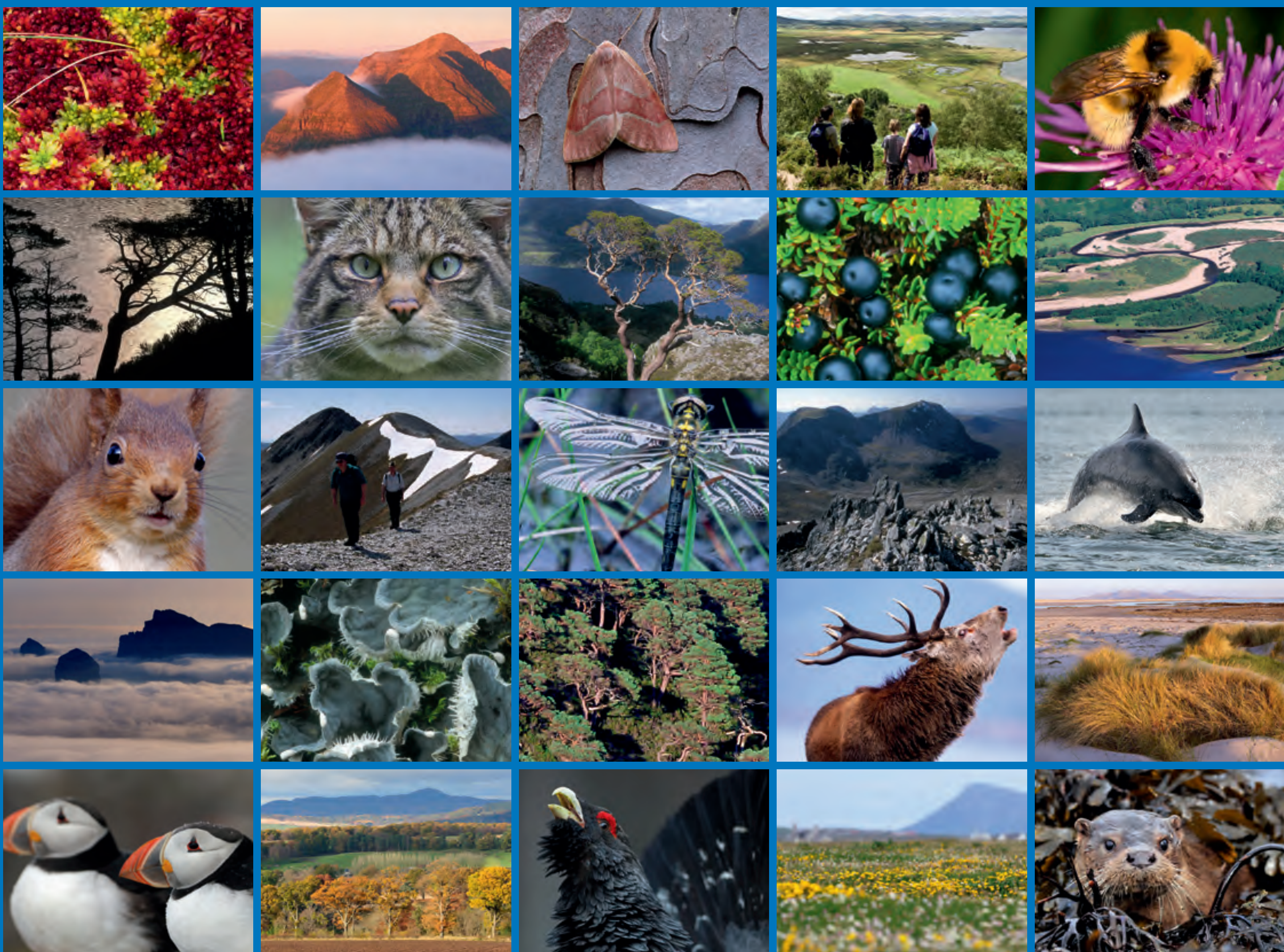
Scottish Natural Heritage
Commissioned Report No. 788

The Scottish Beaver Trial: Woodland monitoring 2009 – 2013, final report



COMMISSIONED REPORT

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COMMISSIONED REPORT

Summary

The Scottish Beaver Trial: Woodland monitoring 2009–2013, final report

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Keywords

Eurasian beaver; Knapdale; Scottish Beaver Trial; browsing in woodland; woodland regeneration; woodland monitoring.

Background

In 2008, the Scottish Government approved a licence to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), to undertake a five-year trial reintroduction of the European beaver (*Castor fiber*) to Scotland after an absence of more than 400 years. In May 2009, three beaver family groups were introduced to Loch Coille-Bharr, Loch Linne / Loch Fidhle and Creagmhor Loch / Un-named Loch (North) on land managed by Forestry Commission Scotland (FCS) at Knapdale, Argyll. Since 2009, additional releases have also taken place, and by November 2010, beaver groups were established in these three lochs and Lochan Buic. This is the final report that describes the effects of beavers on riparian woodland at Knapdale, and summarises effects observed up until November 2013. The first woodland monitoring took place in November 2009 and any impacts of beavers on trees in the few months prior to this, but following the first release of beavers, were assessed. These readily observable effects on trees were taken into account to form a survey baseline of the woodland composition of the area in April 2009, prior to release. Subsequent surveys of the permanently installed monitoring plots took place every April and November until November 2013.

Main findings

- Thirty one transects each comprising up to four permanent vegetation plots (4x10m) were established between the water's edge and 30m from the water's edge, on five lochs at Knapdale.
- Of the total of 111 plots, most of which were established in 2009, three have been excluded from the monitoring of ground vegetation, and three excluded from monitoring the effects on trees, making 108 sampling plots for each of the sets of measurements. These plots either became inaccessible due to beaver-induced flooding (2 plots, vegetation monitoring still possible in one), or were affected by road-widening for forestry purposes (2 plots, tree monitoring still possible in one). A total of 4,454 tree stems were individually marked, along with 139 marked logs or natural stumps. Any beaver-induced changes on these marked trees and logs were monitored along with the associated vegetation characteristics of the plots for four years from their establishment through to November 2013.

- Downy birch (*Betula pubescens*) was the dominant tree species on most plots, although black alder (*Alnus glutinosa*), hazel (*Corylus avellana)*, ash (*Fraxinus excelsior)*, rowan (*Sorbus.aucuparia)* and willows considered as a group comprising the genus *Salix,* also occurred as co-dominants or dominants with restricted distributions.
- In November 2013, 54 months after their release, beavers had directly affected trees in 51 out of the 108 (47.2%) continuously monitored vegetation plots. Of the individual trees marked in all intensively monitored study plots, 15.8% had been gnawed or felled. Because some of the intensively monitored plots were selectively located in beaver-used areas, in order to quantify their effects, an independent assessment of the percentage of trees gnawed or felled in the entire area of the beaver-occupied lochs at Knapdale was undertaken in early 2014. In 261 10m diameter circular plots, all within 30m of the water bodies, 8.6% of trees had been gnawed or felled.
- Plots used by beavers included more birch and willow, but less alder, than an average plot.
- Throughout the four years of the study there was no tendency for beavers to forage any further away from the water's edge, with most effects on trees being recorded within 10m.
- The stem diameter of trees gnawed by beavers varied among species, and changed across the four years of the study; for most tree species it increased.
- A comparison of the tree species used by beavers across the entire study period, with their numerical abundance, indicates that *Salix* were preferred, whereas *S. aucuparia, F. excelsior* and *C. avellana* tend to be only slightly preferred on this basis. *Betula pubescens* and *A. glutinosa* were avoided. However *B. pubescens* is both the most abundant species and the species most often used by beavers. On the basis of the basal areas used by and available to beavers it was selected in relation to its availability along with *Salix* and *S aucuparia.* The numbers of stems of all species newly gnawed or felled has reduced across the years with the exception of *C. avellana*, the use of which has increased.
- Plots containing preferred species were used less with increasing time since the trial reintroduction, suggesting they had been depleted of preferred trees, whereas plots containing un-preferred tree species were used more through time.
- The degree of browsing, its characteristics and any subsequent re-sprouting of beaver-cut stumps, are all important for the long-term dynamics and sustainability of the beaver interaction with woodland. An initial flush of re-sprouting from the remaining stumps of trees that had been directly affected by beavers has now declined. Of the stumps affected by beavers prior to November 2010, 58% had re-sprouting shoots, but this fell to 43% of stumps previously affected by 2011; only 26% of trees previously affected by beavers up to 2012, and 26% up to 2013 had current re-sprouted shoots.
- The most vigorous re-sprouting was observed on *F. excelsior* and *Salix*; poorer re-sprouting was observed on *B. pubescens* and *S. aucuparia*, and very poor re-sprouting was observed on *A. glutinosa*, although this latter species is rarely affected by beavers. In response to greater browsing in the last year of the study, the number of previously gnawed hazel shoots that had re-sprouted increased from 26% to 52%.
- Much of the vigorous re-sprouting from stumps that had resulted from beavers' activity, suffered heavy mortality that was attributed to over-winter frost damage in the early years of study. The re-sprouted shoots that remained were progressively longer than previously, suggesting good growth of survivors. In 2013, the final year of monitoring, for *B. pubescens*, *C. avellana*, *F. excelsior* and *Salix,* more than 68% of the stumps or tree stems that had produced re-sprouted shoots, had been browsed by deer suggesting that deer may inhibit future woodland responses to beaver felling and gnawing activity .
- It is not yet possible to ascertain definitively whether regeneration can ensure replacement of trees felled or damaged by beavers. This will require further study.
- In general the trees were equally affected by beavers in the summer months (April – October) and in the winter months (November – March).

- The effects of beavers on trees led to a more open woodland canopy which had a lower vertical density and visual impediment, and was associated with greater ground cover by graminoids and woody debris, and with less leaf litter.

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This project is part of the independent monitoring programme for the Scottish Beaver Trial coordinated by SNH in collaboration with a number of independent monitoring partners. For further information go to:
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Table of Contents **Page**

List of Figures **Page**

List of Tables **Page**

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1. BACKGROUND

1.1 Overall background to the trial release of beavers

The European beaver, *Castor fiber*, became extinct in Scotland by the end of the 16th century as a result of hunting combined with habitat loss (Kitchener and Conroy 1997). Over recent years the potential for restoring this species to the natural fauna has been investigated. These investigations have resulted in a suite of information about the scientific feasibility and desirability of conducting such a reintroduction. Relevant documents published by Scottish Natural Heritage (SNH) can be viewed at the 'Other work on beavers' page at:
http://www.snh.gov.uk/protecting-scotlands-nature/safeguarding-biodiversity/reintroducing-native-species/scottish-beaver-trial/other-work-on-beavers/.

Article 22 of the European Council Directive 92/43/EEC *on the Conservation of Natural Habitats and of Wild Flora and Fauna* (the 'Habitats Directive') requires the UK government to consider the desirability of reintroducing certain species (listed on Annex IV), including European beaver.

The Species Action Framework, launched in 2007 by Scottish Ministers, sets out a strategic approach to species management in Scotland, and 32 species, including the European beaver, were identified as the focus of new management action for five years from 2007. SNH worked with a range of partners in developing this strategy for which further information can be found at www.snh.gov.uk/speciesactionframework.

In May 2008, the Minister for Environment approved a licence to allow a trial reintroduction of up to four families of European beavers to Knapdale Forest, mid-Argyll. The licence was granted to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS), who are working as the 'Scottish Beaver Trial' partnership. The trial site, Knapdale Forest in Argyll, is managed by Forestry Commission Scotland (FCS). Animals were caught in Norway in 2008, quarantined for six months and released in spring 2009. The initial release sites were Loch Coille-Bharr, Loch Linne / Loch Fidhle and Creagmhor Loch. Further releases took place during 2010 at Un-named Loch (South) which resulted in animals becoming established at Lochan Buic (Figures 1 and 2).

One condition of the licence was that SNH coordinated an independently conducted monitoring programme in collaboration with the project partners. The trial has therefore involved a number of independent monitoring sub-projects in order to address the primary aims, and at the end of the trial the outputs of the monitoring will be assessed and a decision made by Scottish Government on the next stage. This is the final report on the woodland monitoring sub-project, which has been conducted by The James Hutton Institute (formerly Macaulay Land Use Research Institute) in partnership with Scottish Natural Heritage.

1.2 Summary of possible beaver impacts on woodland

Beavers are ecosystem engineers and can produce both direct and indirect effects upon woodlands (Rosell *et al.* 2005). The most obvious direct effect is felling of trees. In other parts of the species' range, particularly during autumn and winter, beavers gnaw and fell trees for food and to obtain timber for the construction of lodges and dams. In the short term at least, tree felling can reduce the biomass of standing, living trees and change the age and size structure of woodlands. Longer-term changes may involve a shift in tree species composition away from more preferred / less resilient species. Many riparian tree species in Europe and North America evolved in the presence of beavers and other browsing herbivores and, given suitable conditions, respond to browsing of woody stems by producing abundant new growth. This can lead to the production of denser stands of woody vegetation producing abundant foliage, which can offer a valuable food resource not only to beavers but also to browsing ungulates and herbivorous insects (Jones *et al.* 2009; Baker *et al.* 2012). However, the recovery of vegetation from beaver browsing and felling will be dependent upon the interaction of new shoots with subsequent browsing by both beavers and sympatric ungulate browsers (Hood and Bayley 2009). Some woody species may also respond to browsing by altering the nutritional and anti-herbivore defensive chemistry of new growth, which can alter the food quality of this plant material for herbivores, sometimes in unpredictable ways (Veraart *et al.* 2006).

Because plant species differ in their tolerance of browsing and their competitive abilities, as well as their palatability to herbivores, sustained browsing of riparian woodlands by beavers may also alter their species composition. As well as herbivorous animals, human interests can also be influenced by changes in the structure and floristic composition of riparian woodlands. For example, the appearance of loch and river shores can change, with significant aesthetic consequences. Access to the water from land, or ease of movement in riparian areas, may also be hindered or facilitated. This depends upon the extent to which beavers remove the felled material, and the nature and rates of decomposition of remnant felled material, and the density and nature of the remaining trees and their regrowth, if any. If the beaver activity alters the degree of shading at ground level, then this may in turn influence the community composition of the ground layer, which may also respond to changes in nutrient inputs from decomposing remnant shoot material and decomposing root material of felled trees. If the degree of shading changes close to the water's edge, then this may influence water temperatures particularly in smaller watercourses, which in turn could, affect the reproduction and survival of fish species, some of which might be of commercial or recreational value.

Many internationally important species of lichen rely on a continuity of old tree stems in open woodland. By maintaining a cycle of felling and re-growth, beaver activity may result in a loss of this habitat in riparian zones, or at least suppress the future development of such habitat.

The most obvious indirect effect of beaver activity on loch-side woodlands is flooding caused by beaver dams. Beavers build dams which raise the water level of lochs and watercourses, expanding their potential foraging area into inundated woodlands and other habitats. Most tree species are intolerant of sustained flooding, and so flooding can increase the amount of standing dead timber but possibly also favour flood-tolerant species such as willows and alder. These structural changes to aquatic systems may potentially also affect the abundance and composition of invertebrates and movement and abundance of fish (Kemp et *al.* 2012; Malison *et al.* 2014).

2. AIMS AND OBJECTIVES

The overall aim of the Scottish Beaver Trial, as set out in the licence application submitted by RZSS and SWT was:

"To undertake a scientifically monitored trial re-introduction of the European beaver to Knapdale, mid-Argyll, for a five year period in order to:

- Study the ecology and biology of the European beaver in the Scottish environment
- Assess the effects of beaver activities on the natural and socioeconomic environment.
- Generate information during the proposed trial release that will inform a potential further release of beavers at other sites with different habitat characteristics.
- Determine the extent and impact of any increased tourism generated through the presence of beaver.

- Explore the environmental education opportunities that may arise from the trial itself and the scope for a wider programme should the trial be successful”

The overall aim of the work reported here was to monitor the effect of the introduced beavers on woodland in the area of the trial release. It thereby directly addressed the first three of the overall aims of the trial, and will help to inform any future decisions and plans for the species in Scotland.

The specific objectives of this monitoring work were to:

- Carry out a sample-based assessment of the composition and structure of the loch-side woodlands around the beaver release site;
- Assess the nature and extent of beaver effects on the loch-side woodlands, again based on a representative sample of survey plots;
- Assess seasonal variation in the effect of beavers on woody vegetation.

In addition to these objectives, the duration of the monitoring programme from 2009-2013 enabled us to identify any changes in the beavers’ effects on the woodland with time since the release of beavers, along with the woodlands’ responses to the beaver activity. We assessed temporal changes in:

- The nature of foraging activity and impact as compared to that observed immediately after beaver release (i.e. changing preferences for tree species and size classes within locations).
- The spatial location of impacts.
- The appearance of and use of newly sprouted shoots by beavers and other herbivores, from trees that had been previously affected by beavers.

This report covers the monitoring of beaver effects on woodlands undertaken at two sampling times (April and November), in each year from November 2009 - November 2013 inclusive. It therefore quantifies the effects of beavers up to a point 54 months after their release. Primarily, it uses data which were collected on a common standardised set of plots which were sampled on all occasions, plus an additional survey of the entire area to give an estimate of the proportion of the total trees affected by beavers.

It was not intended to try to assess the detailed effect of beavers on the woodland ground flora at the species level, or on epiphytic species. It is likely that the presence of beavers will affect these species, either directly through grazing or indirectly through changing the woodland structure, but confidently demonstrating such an effect was deemed to be extremely difficult and would have demanded greater resources than were available (Armstrong *et al.* 2004). Much of the loch-side vegetation in the trial area had been managed prior to the trial reintroduction to improve the habitat in preparation for the trial beaver release. As a result, in some areas, the ground flora is already developing in response to this management prior to the release of the beavers. Distinguishing any change which may result from beaver activity from this background change would be challenging, especially over such a short period as five years. However, gross changes in the main components of the ground cover, such as grasses, bryophytes and litter were assessed in relation to beaver effects on the trees in the locality. The effect of the beavers on the epiphytes of hazel (*Corylus avellana)*, and the beavers use of aquatic macrophytes have been reported by other sub-projects of the trial reintroduction.

3. METHODS

3.1 Site description and beaver releases

The loch-side and riparian woodland at Knapdale has been described by Armstrong *et al.* (2004) (Loch Linne and Loch Fidhle) and Brandon-Jones *et al.* (2005) (all loch-side and riparian woodland within the FCS land at Knapdale). Most of the release sites (excluding Lochan Buic and Un-named Loch (South)) lie within the Taynish and Knapdale Woods Special Area of Conservation (SAC; EU code UK0012682), which comprises 44% broadleaved woodland as well as water bodies, extensive conifer plantations and smaller areas of bogs, marshes, water-fringed vegetation, fens, heath and scrub. One main reason for the designation of the area as an SAC is the presence of "Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles". In the years leading up to the Scottish Beaver Trial, extensive areas of conifer plantation have been cleared from Knapdale, particularly near the lochs, and in most places, dense downy birch *Betula pubescens* regrowth has taken their place.
A decision was taken to restrict woodland monitoring with permanent plots to the strip of woodland within 30 m of loch shores, as it was anticipated, based on other studies of *C. fiber*, that most beaver effects would occur in this zone (Haarberg & Rosell 2006). Most woodlands in this zone at Knapdale are dominated by mature and regenerating *B. pubescens* and common or black alder (A*lnus glutinosa*). In many areas, willow species, particularly goat willow (*Salix caprea*) are abundant and rowan (*Sorbus aucuparia*) is widespread throughout the area, both as mature and sapling trees. Hazel (*Corylus avellana*) and ash (*Fraxinus excelsior*) are also common in some areas around the loch shores. Aspen (*Populus tremula*) is highly favoured by European beavers elsewhere, but is very rare at Knapdale and only occurs on rocky terrain, where it was assumed that it would be largely inaccessible to beavers. *Quercus petraea* is common and widespread at Knapdale, but within 30m of the water it is limited to steep, often rocky terrain where the shore is precipitous and usually unsuitable for beavers.

Three family groups, comprising eleven beavers, were released at Knapdale in late May 2009. One group was released in each of Loch Coille-Bharr (four animals), Loch Linne/Loch Fidhle (four animals; these lochs are continuous with one another) and Creagmhor Loch (three animals). Beavers were released into artificial straw bale lodges situated in areas that were expected to provide suitable browsing habitat nearby and minimise the likelihood of disturbance to the animals, although ultimately they were rarely used. These artificial lodges were located at the southern ends of Loch Coille-Bharr and Creagmhor Loch and on the island in Loch Linne/Fidhle. Subsequently, one Loch Linne beaver died, and all three beavers disappeared from Creagmhor Loch, although the adult male was subsequently recaptured and returned to the site. Prior to April 2010, the male at Creagmhor Loch was removed on welfare grounds because of ill health, and subsequently died at Edinburgh Zoo. By this time, the family from Loch Coille-Bharr had established themselves in a lodge on the eastern shore of the small Dubh Loch to the east of Loch Coille-Bharr. These animals had also dammed the point where the Dubh Loch naturally drains to Loch Collie-Bharr, flooding the surrounding broadleaved woodland and significantly expanding the area of Dubh Loch.

To reach the trial's aims of having established four pairs of beavers at Knapdale, two new pairs were released in 2010. Firstly, in May one pair was released onto a small un-named lochan just to the south of Lochan Buic (Figure 2), called Un-named Loch (South) for the purposes of this report. This loch lies outwith the Taynish and Knapdale SAC but within the Forest Enterprise Scotland land-holding. Secondly, in June 2010 a further pair was released onto Creagmhor Loch. The male from the Un-named Loch (South) pair died a few days later and the female moved herself to the nearby Lochan Buic. Another male beaver was released into that loch in September 2010. In anticipation of the 2010 releases, a number of additional monitoring transects were established around Un-named Loch (South) and

Lochan Buic in April 2010, and no new sampling areas have been established since (see 3.2.1 below).

As at November 2010, there were beaver pairs/families established on four loch complexes at Knapdale: Loch Coille-Bharr/Dubh Loch, Loch Linne/Loch Fidhle, Creagmhor Loch/Un-named Loch (North) and Lochan Buic/Un-named Loch (South) (Figures 1 and 2). The first two families each successfully produced at least one kit in 2010. These same families also produced a further kit each during the summer of 2011, although only that produced by the Loch Linne/Loch Fidhle pair has survived. During the summer of 2011 the pair of non-breeding beavers on Creagmhor Loch built a further lodge at the south-eastern end of the small loch to the east of Creagmhor Loch, referred to here as Un-named Loch (North) (Figure 1). In the summer of 2012 the pairs/families at Loch Linne/Loch Fidhle and Lochan Buic/ Un-named Loch (South) produced one kit each and the pair at Loch Coille-Bharr/Dubh Loch produced three kits. The only kit to have definitely survived is that at Lochan Buic/Un-named Loch (South) as the kit born at Loch Linne/Loch Fidhle has been found dead and the three born at Loch Coille-Bharr/Dubh Loch have not been seen since autumn 2012. Further kits were produced by the Lochan Buic and Dubh Loch families in 2013, although none are confirmed to have survived. Full details of the released animals and the established family groups are given in (Harrington *et al.* 2014 and in prep).

Overall, the number of beavers throughout the area of the trial release has been approximately constant with about eight adults. Those at three of the four centres (Loch Linne/Loch Fidhle, Lochan Buic/ Un-named Loch (South) and Loch Coille-Bharr/Dubh Loch) have been consistently producing kits, that accompany them during the summer for some months before disappearing in the autumn or winter due to mortality or dispersal.

3.2 Field Methods

3.2.1 Location of transects and plots

Field sampling of the vegetation in the broad area designated for beaver release could not feasibly be established prior to the release, since their range locations or sizes could not be predicted. Seventeen transects, each comprising from one to four plots, with 65 plots in total, were established at Knapdale in November 2009 (Moore *et al.* 2010). Those transects were positioned, radiating perpendicularly from the water's edge, around all lochs known to have been used by beavers at that time, so that all shores, other than those considered to be too steep to be readily accessible by beavers, were included. By November 2009, the lack of beaver field signs suggested that some of these areas were yet to be visited by beavers. To increase the likelihood that a reasonable number of transects would subsequently be visited by beavers, and to provide the opportunity to monitor their local effects, the choice of locations of further transects was guided by the position of active beaver lodges and the distribution of existing signs of beaver herbivory. A further 13 transects (43 plots) were established in April 2010, and one further transect (3 plots) established in November 2010, making a total of 111 plots across 31 transects. Most transects established in 2010 were positioned to monitor the impact of the newly released beavers at Un-named Loch (South)/Lochan Buic. Two of the 111 plots, including a single plot transect, have since been accidentally destroyed or otherwise affected by human road-building activity, and two more have been flooded due to the activity of beavers. These losses (specified by plot in Appendix 4), have led to the reduction of the number of plots such that the sampling of impacts on trees and on ground vegetation characteristics is now reduced to 108 plots, although not precisely the same 108 plots for both tree and vegetation monitoring. The 108 tree monitoring plots contained a total of 4454 marked stems and 139 marked logs or natural stumps (Table 2). Plot locations are indicated in Figures 1 and 2.

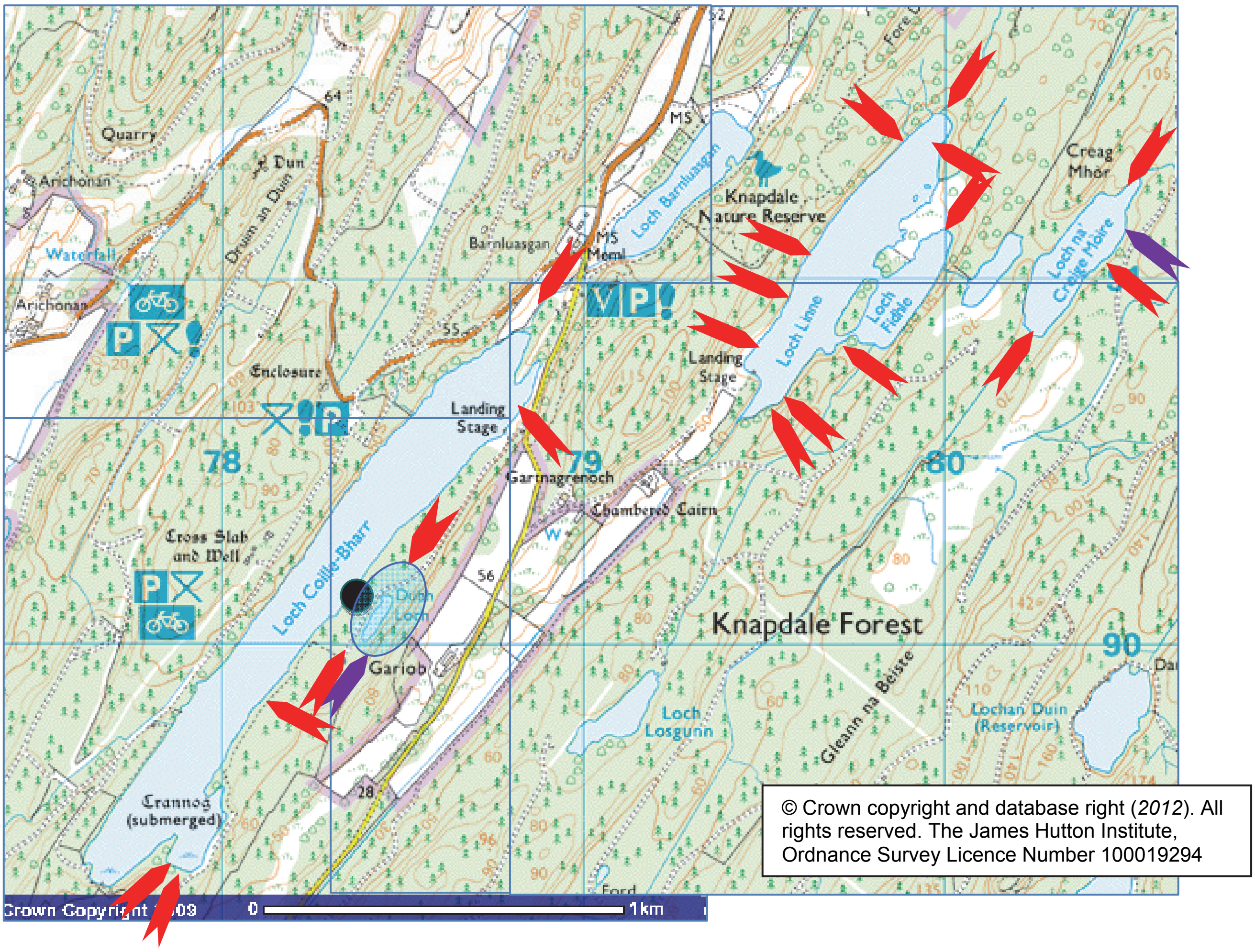


Figure 1. Locations of monitoring transects (red arrows) around Loch Coille-Bharr/Dubh Loch, Loch Linne/Loch Fidhle and Creagmhor Loch/Un-named Loch (North) in November 2013. The excluded transect is shown as a black dot and the two transects with excluded plots are shown in purple. No further sampling plots have been added since November 2010.

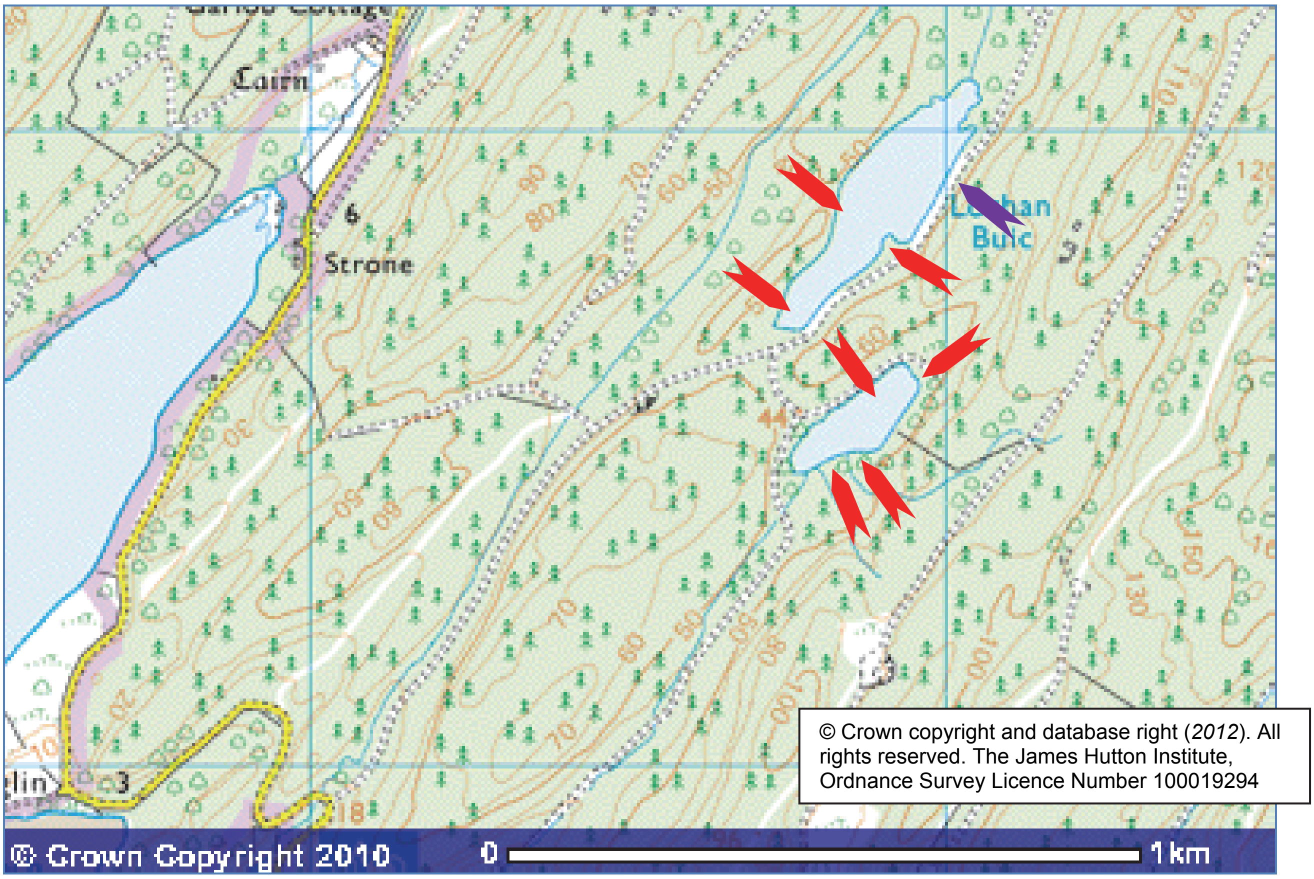


Figure 2. Locations of monitoring transects around Lochan Buic/Un-named Loch (South) in November 2013. See text for explanation of symbols. The transect with excluded plots is shown in purple.

Complete transects were established such that they extend perpendicularly from the water's edge for 30m (Figure 3). In most cases, four rectangular plots were positioned along each transect, each 10 m long (with their long side parallel to the water's edge) and 4m wide (with this short side parallel to the transect and perpendicular to the water's edge). Plots were placed along the transect from 0–4m, 6–10m, 16–20m and 26–30m from the water. All four corners of each plot were marked with permanent wooden posts, and one post was marked with a numbered aluminium tag (at point A, Figure 4). The geographic coordinates of each plot were also recorded at this point using a global positioning system (GPS). Where the loch shore is indented or projects into the loch beyond a straight line along the edge of the first plot, all land and trees up to the water's edge was considered to be part of the plot, and if necessary the position of the plot was adjusted such that its total area remains $40m^2$. In sites where the woodland was flooded due to beaver activity, it was not always possible to access, or to identify the edge of the loch. In these instances, the transect was started at the closest point to the water body that allowed safe working.

On some sections of loch shore, deciduous broadleaf woodland extends for less than 30m from the water before conifer plantations, paths, roads or inaccessible terrain are encountered. In these cases, transects included fewer than four plots. Where transects crossed small paths, it was occasionally necessary to shift a plot one or two metres towards or away from the water.

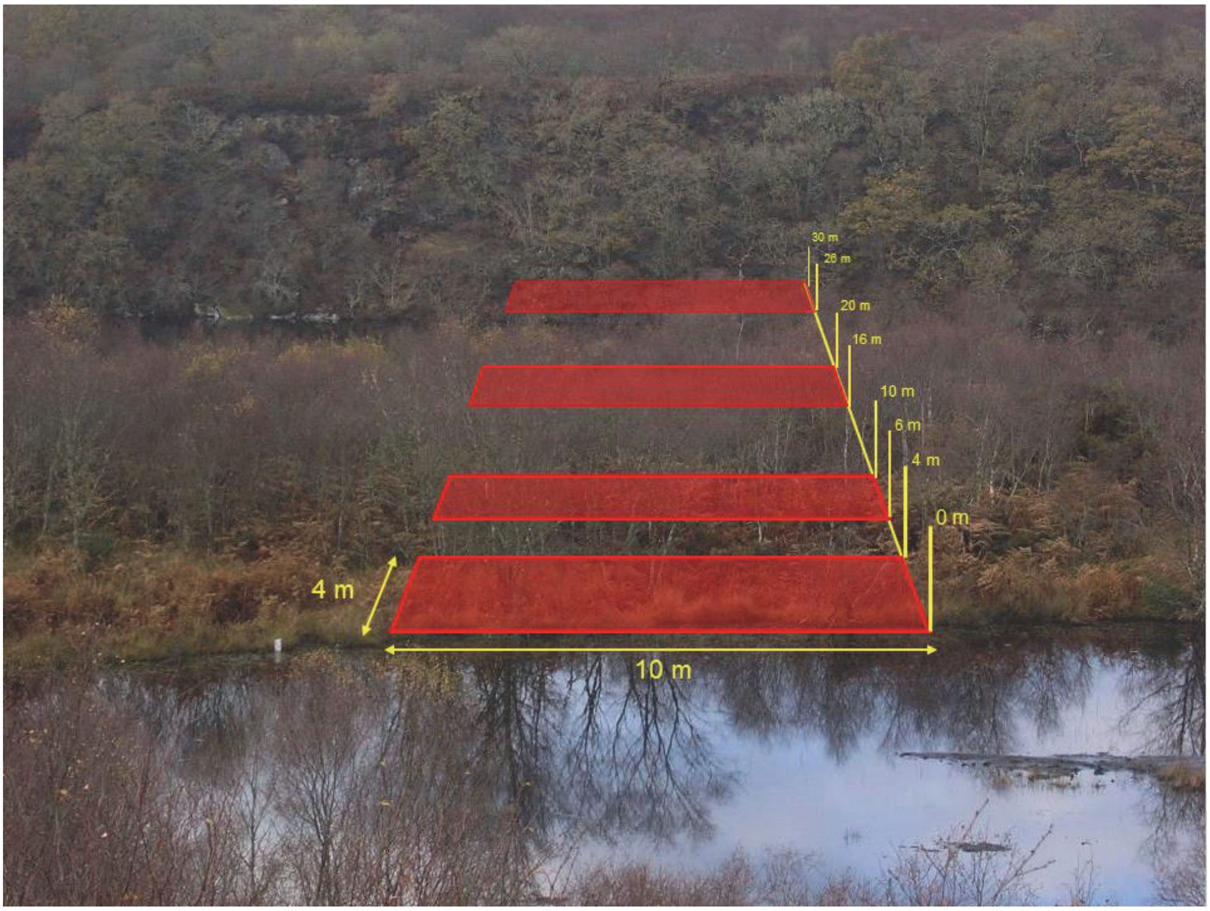


Figure 3. Photograph showing a superimposed typical monitoring transect.

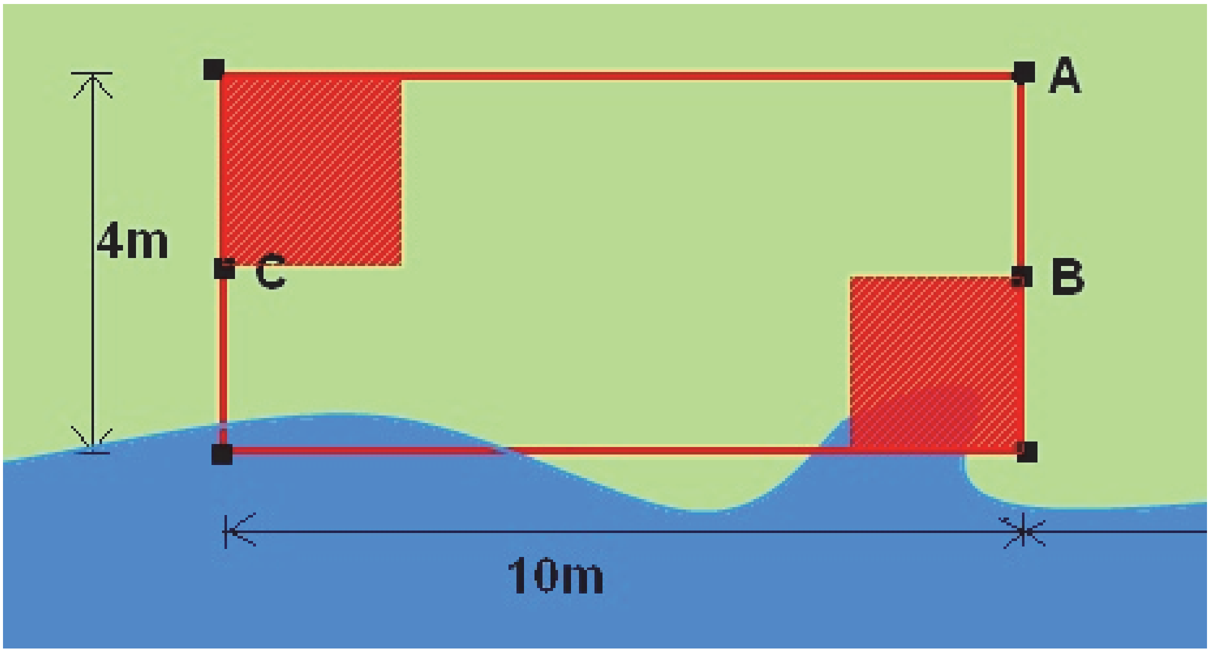


Figure 4. Dimensions of permanent vegetation plot, position of subplots for ground cover description within the plot (solid red squares) and several point locations referred to in the text.

3.2.2 Plot measurements

The slope of each plot, from its lowest to highest point, was measured at the time of establishment (this varied between plots, as explained in 3.2.1 above) using a clinometer, and where this was greater than zero, the aspect of the slope was also measured using a compass. The canopy cover estimated as the percentage of each plot that was beneath a tree canopy of greater than 2m in height, and the percentage of the ground surface of each plot covered by standing water, were estimated to the nearest 5% on each sampling occasion. Vertical density of the vegetation was measured in April and November visits across the plot from point B (Figure 4) by estimating the percentage area obscured of a 50×50cm white board held by an assistant standing at point C and facing the observer at point B (Figure 4). This was repeated with both the board and the observer's eyes at four different levels above the ground: 0–50cm, 50–100cm, 100–150cm and 150–200cm. At each visit, in each plot, one photograph was taken from point B, facing across the plot towards point C, with a camera supported 1.6 m above the ground by a monopod. The camera used was a Nikon Coolpix 5400, with its zoom set to the widest lens angle possible (28 mm). All photographs are archived at The James Hutton Institute and SNH and provide a sequence of photographs showing visual changes to each plot over the course of the Scottish Beaver Trial. The assessment of canopy cover and vertical density at four heights that was conducted during all April and November surveys, was repeated during the summer of 2013, when trees were in full leaf.

3.2.3 Subplot measurements of ground cover

Ground Cover was described in two subplots within each plot. Subplots measured 2×2m and were positioned in the near right-hand corner and far left-hand corner of the plot (when facing the plot from the water) as illustrated in Figure 4. For each sub-plot, percentage cover of the following was estimated to the nearest 5%:

- Graminoids (grasses, sedges or rushes)
- Leaf litter of deciduous trees
- Woody debris (from small twigs to logs)
- Ferns (including browned-off bracken)
- Bryophytes (mainly mosses and a very small proportion of liverworts)
- Dwarf shrubs (primarily *Calluna vulgaris, Myrica gale* and *Vaccinium* spp.)
- Herbs
- Rock
- Bare earth or mud
- Standing water

Because more than a single category can overlie the same point on the ground, for example litter, grass and bryophytes, the sum of all estimates in a plot was allowed to exceed 100%. Tree seedlings less than 1.3 m in height were also counted in each subplot.

3.2.4 Measurements of woodland and the effects of beavers on trees

All trees greater than 1.3m in height, regardless of stem diameter, were marked and recorded in each plot, along with stumps and fallen timber from trees which would originally have met this criterion. Working from one end of the plot to the other, each stem, or in the case of easily grouped clumps of smaller stems of a single species, each clump of stems was permanently marked with a uniquely numbered aluminium tag. Tags were affixed as close to the ground as possible, using either a small aluminium nail or, for some smaller stems, a length of wire encircling the stem. For each stem, stump or group of stems, an observer recorded the species; measured the diameter at height 20cm (or lower if a bifurcation occurred at 20cm or if beavers had severed the stem below 20cm) of each stem or stump, using calipers; recorded whether the stem or stump was alive, dead or indeterminate; and assigned the stem(s) to one of 13 categories, listed below in Table 1 in approximate order of frequency (See Appendix 1 for examples). The signs of beaver felling and gnawing which were readily identifiable from the clean appearance of the slicing tooth marks and the resultant sliced wood chips were also recorded.

Table 1. Categorisation of the status of individual trees recorded.

1	Up	Upright tree, unaffected by beaver gnawing, NB trees need not be vertical to qualify, some 'upright trees' are inclined at angles as low as 10 degrees from the ground
2	BStump	Stump of a tree felled by beavers
3	LogUp	Upright stems growing from a log or horizontal tree trunk previously felled by beaver
4	Base	A base is the stem of a multi-stemmed tree, above which one or more of the multiple stems have been affected by beavers
5	BP	Tree partially felled by beavers i.e. the xylem has been incompletely severed, some phloem remains continuous between the stump and the upper part of the tree, but the upper part of the tree has fallen over and is resting on the ground or on other trees
6	NLog	Naturally fallen log
7	BUp	Upright tree gnawed by beavers; this included trees with a single bite-mark through to trees that are near toppling
8	BLog	Large log felled by beavers
9	NStump	'Natural' tree stump – resulting from windfall or decay, but also including stumps sawn by humans
10	Bent	Trees that have been pushed over by part of beaver felled or partially felled tree
11	BCut	Site on a tree where a minor branch has been removed by beavers, typically overhanging the water
12	NP	Naturally partially fallen tree
13	Gone	Trees that had previously been tagged but which could not be found on subsequent visits

In a number of cases, trees branched at a point closer to the ground than the height at which stem diameters were measured (20cm). In these cases diameters were recorded for all stems at that height. Instances were also observed where trees branched at a point higher than 20cm, but beavers severed the branched stems above the branching point. In those cases, in addition to the 20cm diameter observers also measured the diameter where the stem was severed by beavers, and recorded this hierarchy of branching (see Appendix 1 for details). In some instances, secondary and even tertiary branching events were recorded below beaver gnawing.

Some tree stems and logs were leaning, either naturally, or because they had been incompletely gnawed and partially felled by beavers or because they had been completely severed by beavers but were still supported above the ground by surrounding vegetation. The angle these stems made with the ground was recorded. From trees and stumps that had been gnawed by beavers, observers recorded the percentage of the circumference of the stem that had been gnawed. In the case of stumps of trees felled by beavers, this was almost always 100%. From stumps felled by beavers and partially felled and upright trees gnawed by beavers, observers also recorded the height above the ground at which gnawing had occurred. For stumps, this was taken from the highest part of the stump remaining.

From upright trees, this was taken from the vertical midpoint of the gnawing. The lengths and diameters of any logs lying within the plot were also recorded, but only that part of the log lying within the plot boundary was included.

Observers also recorded any coppice re-sprouting from stumps or trees gnawed by beavers. All new shoots were counted and recorded separately as:

- "low shoots": shoots originating from stumps or below the gnawing damage on trees gnawed but not felled by beavers, or
- "high shoots": shoots originating from logs or above the gnawing damage on the stems of upright or partially felled trees gnawed by beavers.

A series of illustrations of trees that have experienced a variety of beaver effects and an example datasheet recording all required data about these trees was produced for observers' reference in the field. Many permutations of tree growth form and beaver effect are more easily described by these illustrations than in text. These sheets are included as Appendix 1 and 2 at the end of this report.

The average and maximum shoot lengths were both recorded. Where coppice re-sprouting had occurred and it had subsequently been browsed, observers recorded the extent of browsing effects on these shoots attributable to deer (roe deer *Capreolus capreolus*, red deer *Cervus elaphus* and sika deer *Cervus nippon* are present at Knapdale) and/or to beavers on a three-point scale: 0 = none; 1 = detectable, less than half of shoots browsed; 2 = substantial, more than half of shoots browsed. Although we might expect to be able to distinguish deer-browsed from beaver-browsed shoots on the basis of the shaggy versus clean cut stems respectively, no browsing on the re-sprouted shoots was attributed to beaver browsing. Re-sprouting shoots remained fairly small and narrow within the time-span of this study. Previous bark stripping by deer was evident on the trunks of many willows throughout Knapdale.

3.2.5 Timing of measurements

The fieldwork reported here was conducted between November 2009 and November 2013. After establishment of permanent plots in November 2009, field visits were undertaken in each November and April so that observers were able to assess the full extent of coppice re-sprouting throughout the growing season from trees and stumps felled by beavers, as well as any beaver and deer herbivory that the originally marked shoots or any re-sprouted shoots had suffered. This timing of survey also allows partitioning of the intensity of beaver gnawing among the two periods of the year: November-April and April-November. These periods coincide approximately to the periods of dormancy and growth of trees respectively. It was anticipated that spring fieldwork would reveal the full extent of tree felling and bark feeding that had occurred on dormant trees through the preceding winter and that autumn fieldwork would also allow the determination of the net gain of new shoots resulting from the interaction of growth and browsing.

3.2.6 Assessment of impacts of beavers on trees throughout the entire study area

Due to the selection of locations of the intensively monitored sites (section 3.2.1), it was not possible to estimate the proportion of trees in the Knapdale release area as a whole, that had been affected by beavers. Consequently in January-February 2014, as series of additional transects was walked around each of the four main loch systems (Loch Coille-Bharr/Dubh Loch, Loch Linne/Loch Fidhle, Creagmhor Loch/Un-named Loch (North) and Lochan Buic). At this time of year, when trees were not in leaf, the signs of any beaver activity were most visible. Along each route around these lochs at approximately 100m intervals, in each of a block of three circular plots each with a 10m diameter, the proportion

of trees that were visually affected by beavers by felling or gnawing was estimated as either zero, less than 5% (coded as 2.5% for statistical analysis), 5%, 10%, 15% ….100%. The first of the three plots in each block was centred 5m from the loch-shore and the two further contiguous circular plots of 10m diameter, were centred at 15m and 25m from the water. For each plot, the dominant tree species was assessed on the basis of projected canopy cover, since actual canopy cover was impossible to measure in the winter sampling period. Eighty seven blocks of three sampling plots were distributed around the lochs as follows:
Loch Coille-Bharr/Dubh Loch (39), Loch Linne/Loch Fidhle (22), Creagmhor Loch/Un-named Loch (North) (15) and Lochan Buic .(11). No record was made at six of the possible 261 plots due to either inaccessibility to the recorders or the presence of a road or track at the location.

3.3 Analysis and presentation of results

The abundance of trees within plots was recorded in two ways. First, the number of stems was counted, and second, the basal area of each stem was calculated (basal area = $\pi \times$ stem radius^2) and these were summed to give a total stem basal area (at height 20cm) for each plot. These records were made during first monitoring of the plots that began in November 2009. Any impacts of beavers on trees in the few months prior to this, and following the first release of beavers, were assessed. These readily observable effects on trees were taken into account to form a survey baseline that provides a very close approximation of the woodland composition of the area in April 2009, prior to the release.

The dominant and sub-dominant tree species in each plot were determined at the outset on the basis of the number of stems of each recorded. This may overestimate the abundance of the individuals of *C. avellana* and to a lesser extent *Salix*, because for these species in particular, numerous stems may have been recorded from a single stool or plant.

Where comparisons were made between trees directly affected by beavers and the total tree sample, the former category included all trees gnawed by beavers, whether they were still standing or whether only a stump remained. Where possible, data are analysed in order to provide an analysis of temporal changes in the effects of beavers since release or between years of observation.

3.3.1 Statistical analyses

A range of statistical methods was applied according to the specific requirements of the analysis, but Generalized Linear Mixed Models (GLMMs) were mainly applied, as appropriate, using Genstat (VSN International 2011). The statistical probabilities of rejecting a particular result under a null hypothesis are presented in this report, and the detailed methods of all statistical analyses are presented in Appendix 3. Although exact probabilities (P) are available in many instances, for consistency we present statistical significance as probabilities of obtaining a result by chance as $P<0.05$, $P<0.01$ and $P<0.001$ or *NS* (not significant), unless otherwise stated. For all analyses the plot, or the transect and plot within transect, were entered as random variables. For sub-plot based measurement of the different components of percentage ground cover, then sub-plot within plots were treated as random variables. For model construction, the fixed effects estimated were entered sequentially with subsequent alteration of the order of entry to investigate any inter-dependencies and identify main effects, and further by subsequent removal from the model. Higher order interaction effects were removed from the models when they were not significant. The fixed effects entered usually included those of year (2010-2013), tree species and plot distance from water's edge (0m, 6m, 16m, 26m). The extent of beaver impact in each plot was quantified as the proportion of the total number of trees in the plot, irrespective of species, that had been directly affected by beavers (beavimp). This parameter was used to assess the effect of beaver activity on the components of the ground cover, canopy cover and vertical density. For analyses of the location of plots in which beavers were foraging, whether the dominant tree species or species combination in the plot was 'preferred' or 'un-preferred' was entered as an explanatory variable, along with year and the possible interaction effects. 'Preferred' communities were defined on the basis of their composition of species in relation to the degree of selection of number of stems and basal area expressed by beavers across the entire period of survey (Figure 6). Any plots containing *Salix* as the dominant or sub-dominant species were considered to represent a preferred plot type, along with those dominated by *B. pubescens* either alone or in combination with the species that were neither strongly preferred nor avoided in relation to their basal area, namely *F. excelsior* and *S. aucuparia* (Section 4.4.1 – below). All other plots were considered to contain an un-preferred community; the communities present are listed in Appendix 4. All potentially subjective measurements were conducted in the November sampling period, by one of two observers (David Sim on 62% of occasions and Ben Moore on 38%), and in order to correct for possible observer bias in these measurements, the observer identity was entered first into the analyses of ground cover, canopy cover and vertical density.

The use of tree species in relation to their numerical availability was analysed using binomial GLMM of the number of marked stems of each species newly felled or browsed by beavers during the preceding year, in relation to the number of un-browsed stems available at the start of that particular year. This analysis used data recorded in November of each year 2010-2013 inclusive, and the fixed effects assessed were tree species, year and their interaction. A similar GLMM was used to analyse the proportion of the available basal area of each tree species at the start of any year that had been eaten by beavers in the subsequent year. This proportion was logit transformed prior to analysis.

The browsing by deer of re-sprouted stems that grew from stumps formed from previous beaver activity was analysed using an ordinal regression of the intensity of deer re-browsing (0,1,2, representing no browsing, low or high proportion of re-sprouted shoots browsed; Figure 14). This Generalized Linear Modelling approach entered plot as the first variable in the model and tested the effects of tree species, the number of re-sprouts per stem, and the average length of re-sprouts, each after accounting for all other statistically significant variables.

4. RESULTS

4.1 Details of transects and plots

The locations of the 31 transects and 111 plots established by November 2010 are listed in Appendix 4 and their locations are illustrated in Figures 1 and 2. As previously mentioned Transect 25 Plot 2102 and Transect 27 Plot 2705 have been excluded from all monitoring. Ground cover measurements are no longer recorded in Transect 13 Plot 261, and tree measurements are no longer recorded in Transect 6 Plot 232. Seven different species were recorded as dominant or co-dominant tree species in at least one plot, however it should be noted that plot 244, which was dominated by *Q. petraea*, included only a single tree. Two of the marked plots, plots 285 and 290 did not contain any trees. *Betua pubescens* was dominant in the majority of vegetation plots. Note that species dominance presented in Appendix 4 has been determined on the basis of number of stem diameters recorded.

4.2 Vegetation composition and structure in plots

The initial numbers of stems of tree and shrub species, and their basal areas, in the constant set of plots that were established by November 2010, and used throughout the analyses in this report are shown in Table 2. These represent a consistent baseline dataset of availability of trees to beavers, against which future comparisons can be made. Fourteen tree and shrub species were identified in the vegetation plots. However, because trees were not in leaf during establishment of the plots then the willows could not all be identified to the nearest species, and although most *Salix* at Knapdale is believed to be *Salix caprea*, the willows are referred to collectively as '*Salix'* throughout this report. Numerically, *B. pubescens* was clearly dominant, and *only A. glutinosa*, *C. avellana*, *Salix* spp. and *S. aucuparia* could also be considered abundant (Table 2). When total basal area was considered however, the dominance of *B. pubescens* over *A. glutinosa* was less marked. This result can be largely explained by the widespread occurrence of dense thickets of young, small *B. pubescens* trees which have grown in place of recently cleared conifer plantations throughout Knapdale. The substantial contribution made by *A. glutinosa* to the total basal area despite its more modest stem count, reflects the fact that this species most commonly occurs as large trees at the water's edge.

The tree species codes given in Table 2 are used to annotate the figures throughout this report. The category 'Other' was not used for analysis of ecological effects since the numbers and basal areas of this mixture of species were very small and few inferences could be made. 'Other' was included in descriptions of the site. Note that '*Salix'* refers to the genus rather than a single species.

Table 2. Total number of upright stems and total basal area of all tree and shrub species recorded in the 108 plots prior to release of the beavers. Asterisked species indicate the minor species categories that were summed and treated as a single category (called 'Other') in data summaries and descriptions of the numbers and species present. No. of plots is the number of the total of 108 plots in which the species occurs.

Common name	Code	Species	No. of plots	Stem Count	Total basal area (cm^2)	Median diameter (cm)
Sycamore*	ACEPSE	*Acer pseudoplatanus*	1	2	4	1.5
Black alder	ALNGLU	*Alnus glutinosa*	34	518	116,175	5.0
Downy birch	BETPUB	*Betula pubescens*	91	2792	117,297	3.0
Hazel	CORAVE	*Corylus avellana*	16	374	11,534	3.0
Hawthorn*	CRAMON	*Crataegus monogyna*	3	5	162	2.0
Ash	FRAEXC	*Fraxinus excelsior*	14	60	10,919	7.0
Holly*	ILEAQU	*Ilex aquifolium*	1	1	79	10.0
Bog myrtle*	MYRGAL	*Myrica gale*	2	11	37	2.0
Sitka spruce*	PICSIT	*Picea sitchensis*	14	20	6,185	5.0
Sessile oak*	QUEPET	*Quercus petraea*	4	6	1,444	2.0
Wild rose*	ROSACI	*Rosa acicularis*	1	1	1	1.0
Willow	SALIX	*Salix* spp.	35	371	10,776	3.0
Rowan	SORAUC	*Sorbus aucuparia*	33	284	6,242	2.0
Western hemlock	TSUHET	*Tsuga heterophylla*	2	4	909	5.5
Unidentified*				5	15	2.0
TOTAL				4,454	278,779	

Because beavers are expected to have the greatest effect on woodland near to the water's edge, different tree species may vary in their susceptibility to beaver herbivory if their distributions differ in relation to distance from water. Figure 5 shows how the abundance of each tree species differs with distance from the water. The numerical density of *A. glutinosa, C. avellana* and *F. excelsior* decreased and the density of *B. pubescens* and to a lesser extent *Salix*, increases with distance from water. Most large *A. glutinosa* were found near the water's edge. *Salix and B. pubescens* were most abundant in the plots furthest from the water whereas *C. avellana* and *A. glutinosa* showed the opposite trend (Figure 5a). The basal area of almost all species was greater within 4m of the water's edge when compared with those at greater distances from the water (Figure 5b).

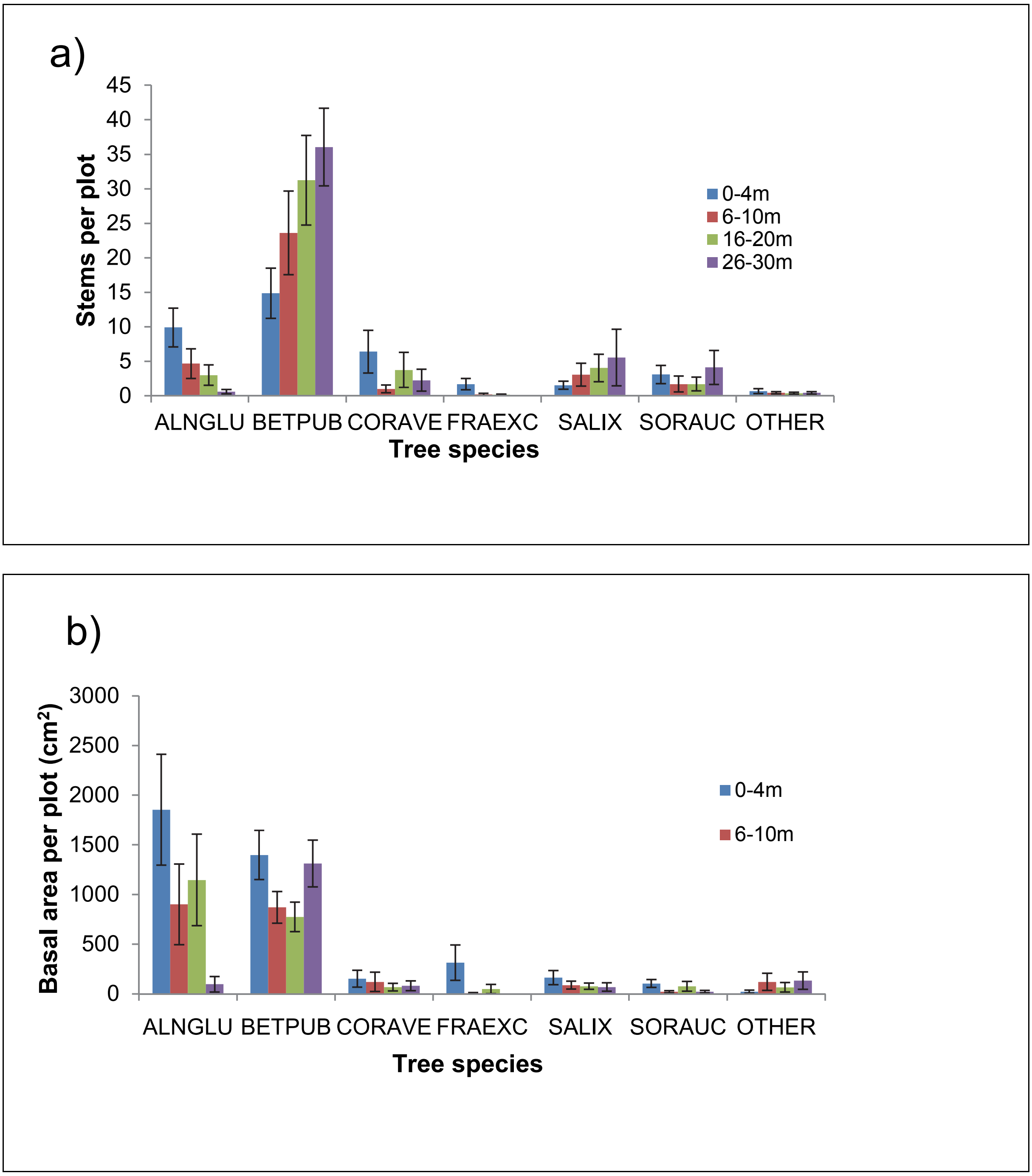


Figure 5. (a) Mean number of stems per plot and (b) mean total basal area per plot for seven common tree species in plots located at increasing distances from the water's edge before the trial reintroduction of beavers. Error bars indicate 1 standard error.

4.3 The effects of beavers

4.3.1 Use of tree species by beavers

Different tree species differ in their abundance and spatial distribution at Knapdale but also in their suitability as food sources, or construction materials for beavers. Consequently, it is expected that the proportional use of preferred species should be greater than their proportional availability and conversely that of avoided species should be less than their availability. It is clear that the majority of direct beaver effects so far observed at Knapdale have been on *B. pubescens* and *Salix* (Figure 6).

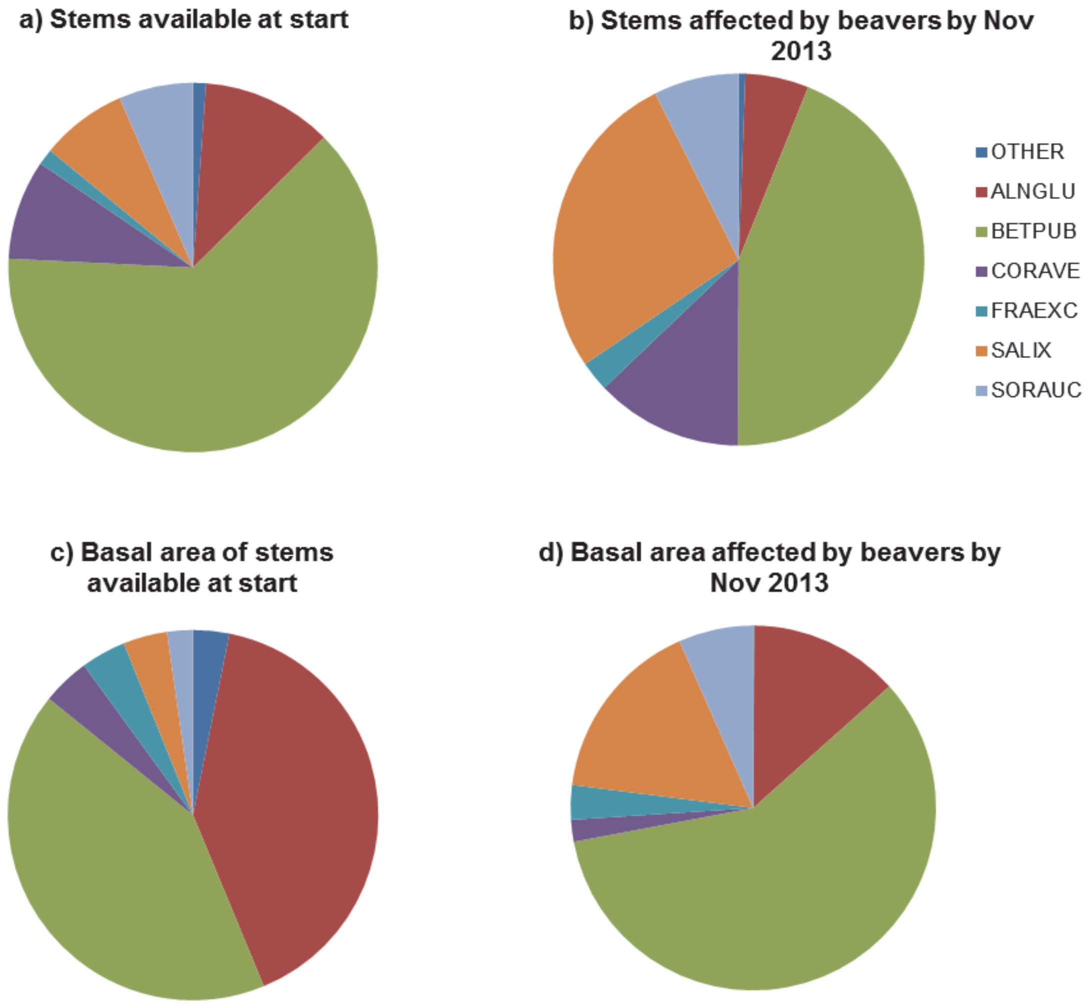


Figure 6. Proportional composition by species of (a) total number of stems in the standard set of 108 plots at Knapdale prior to the trial and (b) total number of these stems gnawed by beavers attributable to major tree species, and proportions of (c) total summed basal area of stems in plots at Knapdale and (d) total summed basal area of these trees directly affected by beavers. These data include all trees recorded up to and including November 2013. Species codes can be found in Table 2.

Figure 6 shows that although fewer individual stems of *B. pubescens* were browsed than suggested by its availability, the total basal area of browsed *B. pubescens* was greater than expected. This finding suggests that beavers tended to favour large birch trees over the small birch trees typical of dense stands of *B. pubescens* growth. Figure 6 also strongly suggests that *A. glutinosa,* and large trees in particular, were avoided by beavers, while

Salix was strongly preferred relative to its availability, both on the basis of tree numbers and basal area. *F. excelsior* and *S. aucuparia* were used in approximate proportion to their abundance but on the basis of basal stem area the latter was slightly positively selected relative to availability. *C. avellana* was used roughly in proportion to its availability, but when it was used, only very small stems were gnawed. It should be noted however that the availability of *C. avellana* is somewhat misleading, because it is less widespread than other tree species. Where it occurs, very large numbers of small stems were often recorded growing from only a small number of stools.

The use made of tree species in relation to their availability is important to the prediction of the impacts of beavers on the tree species in other circumstances. The pattern of selection of these three species relative to availability changed with time differently for the different species (species x year interaction: F=3.42 df 15,767, P<0.001; Figure 7). There was an overall tendency for the percentage of available trees newly affected by beavers to diminish with increasing time since the release in all species except for *C. avellana* (Figure 7). The large error bars for *F. excelsior* and *C. avellana* reflect the relatively small numbers of plots in which they occur (Table 2). Analysis of the patterns of change of the logit proportion of the available basal area of the different species in each year very closely matched the patterns seen for the number of stems affected (Figure 7).

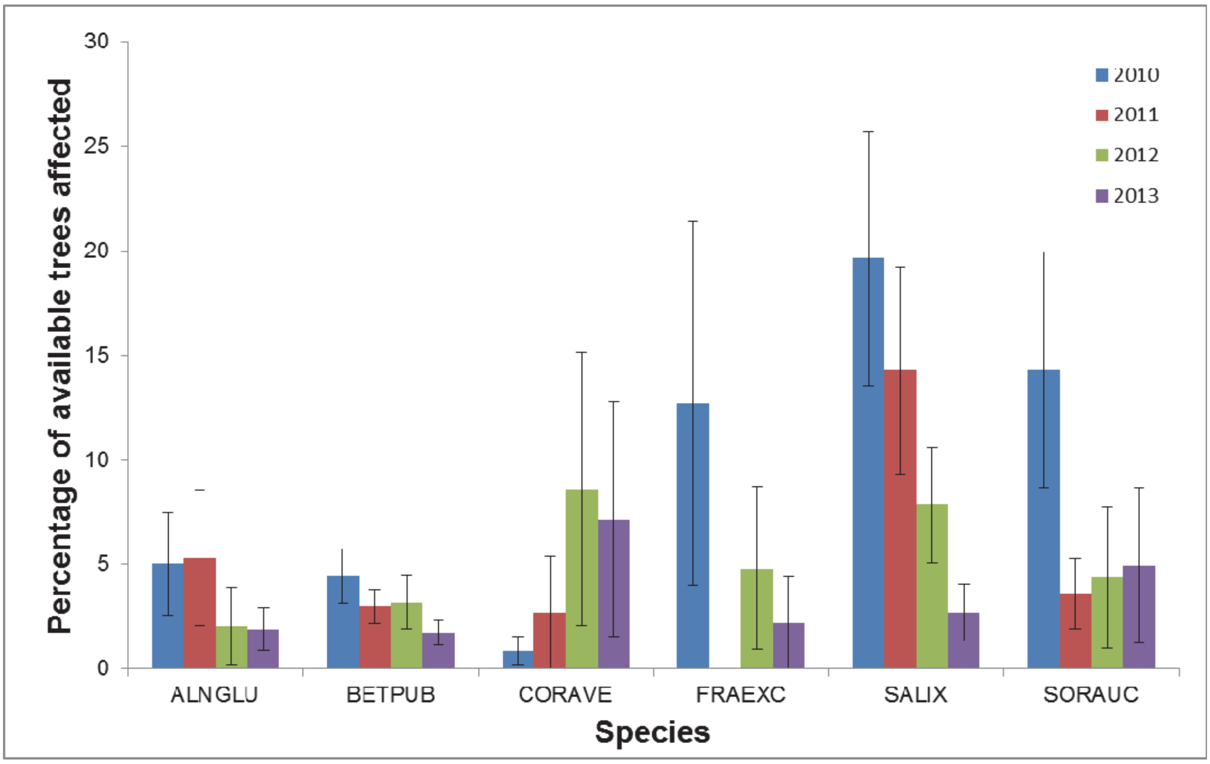
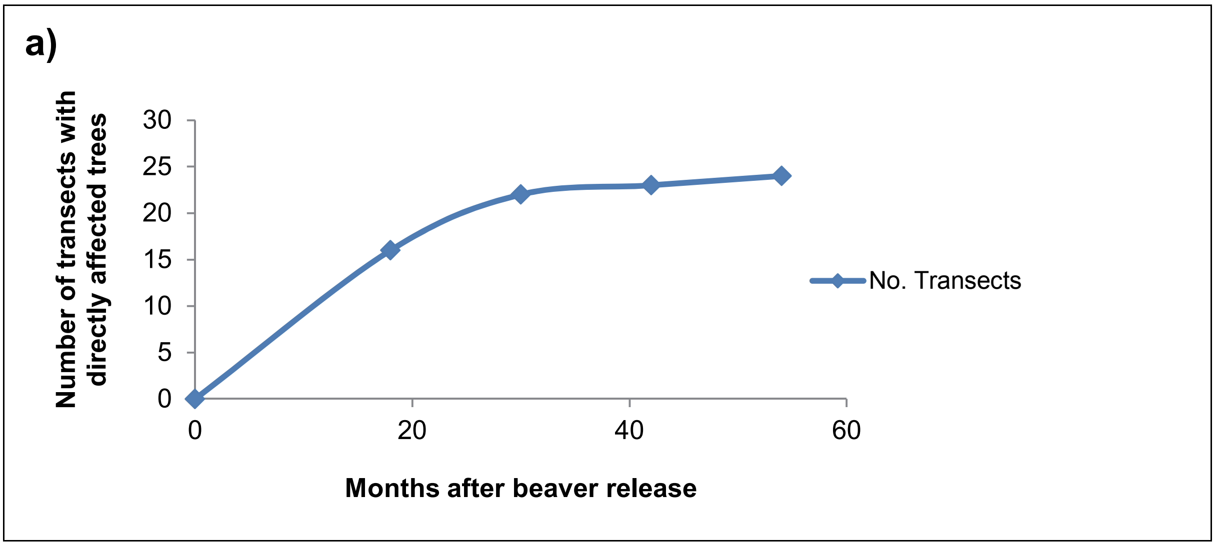


Figure 7. The mean percentage of available trees of each species affected by beavers in each year since the trial reintroduction began. The mean and standard error of the values for plots in which each species occurs are shown. The numbers of plots for each species, and species codes are given in Table 2.

4.3.2 Use of transects by beavers

The establishment of transects was partly guided by existing beaver effects, making these data unsuitable for a formal analysis of the factors influencing beaver preferences for vegetation communities present in different transects. Up to November 2010, 16 of the 30 (53.3%) transects included trees that had been gnawed by beavers. By November 2011 that had risen to 22 (73.3%) and one hitherto unused transect was added in each of the two subsequent years giving a figure of 23 (76.7%) and 24 (80.0%) for November 2012 and November 2013 respectively (Appendix 4; Figure 8a). The intensity of beaver effects on each transect remains variable.



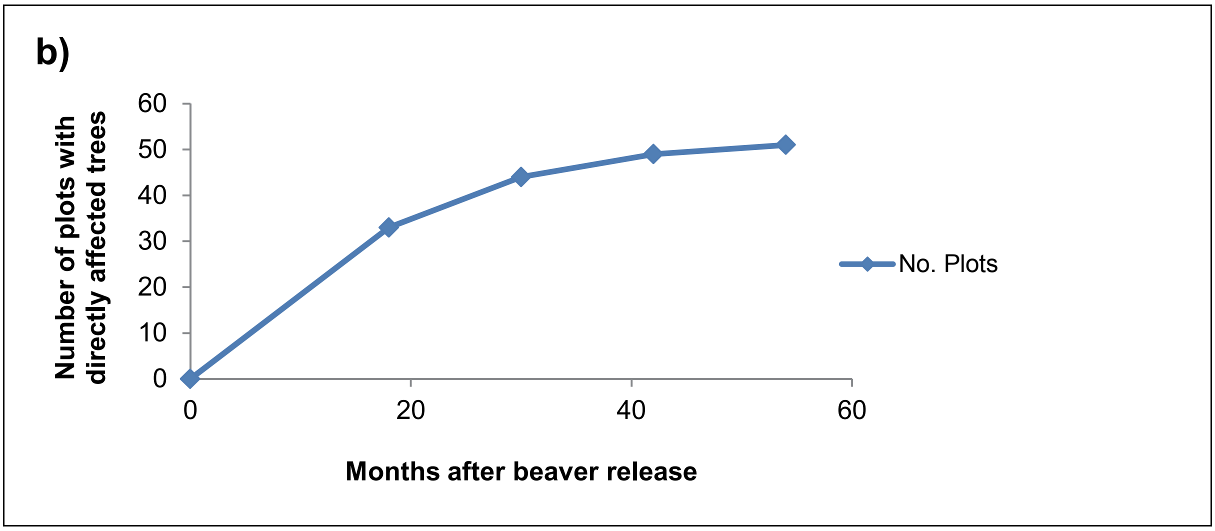


Figure 8. Number of a) transects and b) plots with trees directly affected by beavers since release up to November 2013.

4.3.3 Use of plots by beavers

Approximately one and a half years after their release, by which time all the monitoring plots had been established, beavers had directly affected trees in 33 of the 108 (30.6%) vegetation plots. After two and a half years that had risen to 44 (40.7%). After three and a half years that had risen to 49 (45.3%) and after four and a half years (by November 2013) it had risen further to 51 (47.2%) (Appendix 4, Figure 8b).

The dam at Dubh Loch has substantially expanded the area of that water body into the surrounding woodland and across a nearby FCS road and walking track. Since November 2009, the beavers continued to improve the dam, consequently expanding the flooded area as reported previously (Moore *et al.* 2010, 2011, 2013). This flooding has prevented access to some of the plots established in that area (Appendix 4).

The effects of beavers varied with the plots' proximity to water, there being more browsing in the plots 0-4m and 6-10m from the water (*F*=4.53, *df* 3,60, *P*<0.01; Figure 9). The number of new incidences of beaver browsing per plot varied between years (*F*=11.32, *df* 3,332, *P*<0.001), but the propensity for foraging closer to the water was greatest during the first and the last years (year x distance interaction; *F*=7.66, *df* 9,334, *P*<0.001), suggesting no progressive spread in impact at greater distances from water, following the trial reintroduction of beavers. Beavers used the marked plots containing preferred species more in the earlier years (year x 'preferred' interaction: *F*=11.53, *df* 3,336, *P*<0.001).

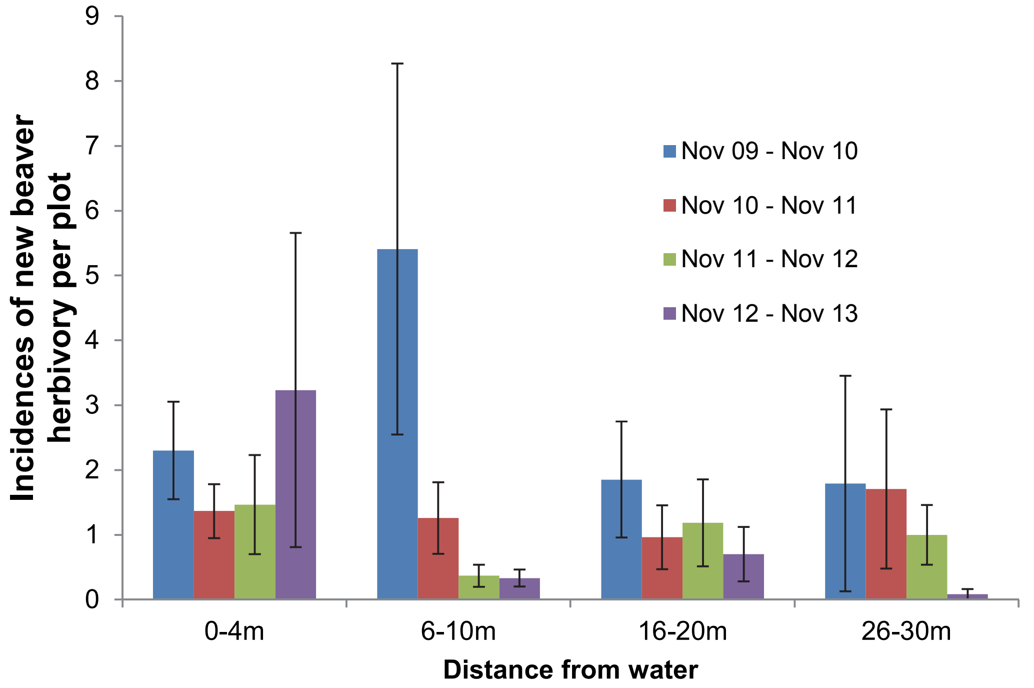


Figure 9. Distribution of beaver effects, expressed as mean number of new incidences per plot, with plot distance from water's edge, in each year since the trial reintroduction began. Error bars indicate 1 standard error.

A second important facet of the spatial distribution of the effects of beavers on trees is the possibility that the distance at which they forage from their lodges would increase as the preferred food types that are close to them are depleted. The consistent recording of the set of plots at Loch Linne/Loch Fidhle and Lochan Buic in November of each year from 2010 through 2013 permits a comparison of the distance of beaver foraging from the nearest beaver lodges, and how this has changed over time and in relation to the plot characteristics. The construction of a new lodge on Loch Coille-Bharr in 2013 and the movement of the beavers between this lodge and their previous lodge on Dubh Loch means that they are only included for November 2010, 2011 and 2012 in this aspect of the report. Similar movements by the Creagmhor Loch family into a new lodge on Un-named Loch (North) in July 2011 means that they are only included for November 2010 and 2011. Figure 10 shows that beavers exploit the woodland resources by using plots containing preferred species that are closer to their lodges. This is likely facilitated by careful selection of the location of the lodge close to preferred species. These results suggest that beavers had not depleted the preferred species close to the lodges, despite expressing a strong preference for *Salix* (Figures 5,6,7).

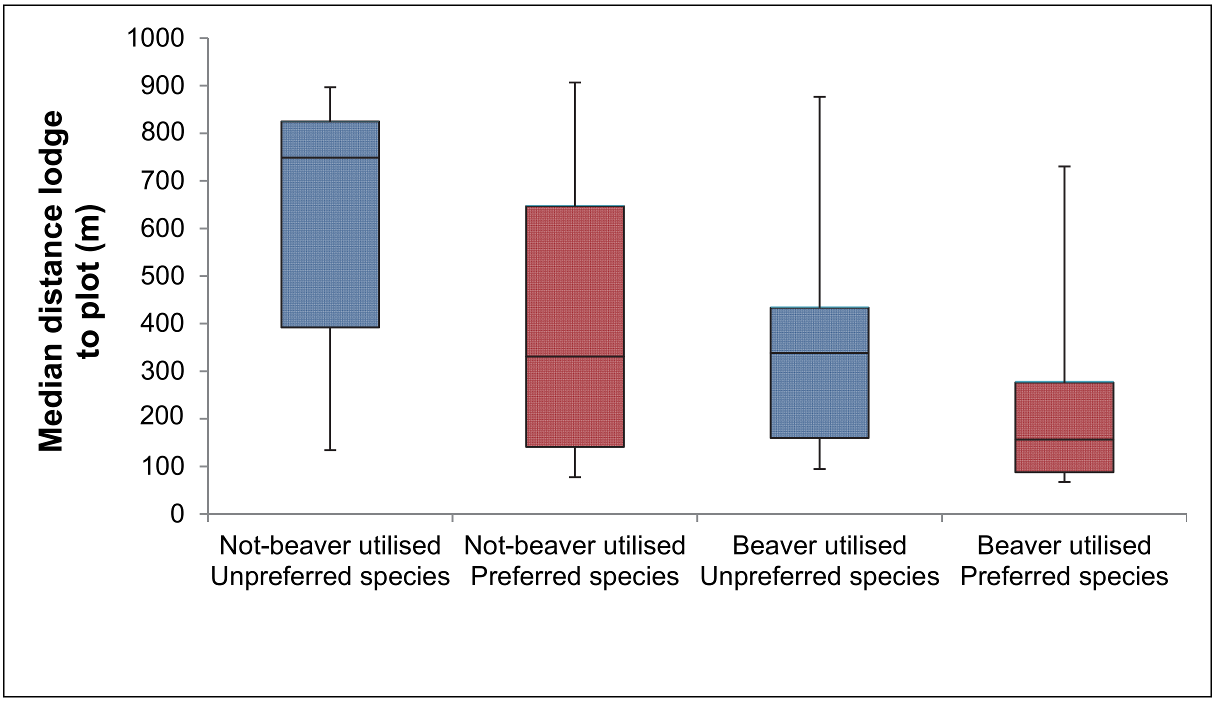


Figure 10. The median distance from the three main beaver lodges to their corresponding monitoring plots in relation to whether or not the plots were utilised by beavers and whether the plot consisted of a dominant tree species that was unpreferred (blue bars) or preferred (red bars). The data cover the periods up to November 2013. Bars represent upper and lower quartiles, whiskers are ranges.

The statistical analysis of the use of plots in different years according to their distance from the nearest lodge and whether the dominant tree species in the plot is a 'preferred' species, showed a complex three way interaction between the fixed effects of distance, whether a 'preferred' species dominated, and whether utilised by beavers (F= 3.55, df 3,190, P<0.05), with this effect being largely due to a strong interaction between year x 'preferred' (F=6.21, df 3,185, P<0.001). This was again due to a reduction in the use of preferred plots within the sample in the later years, and plots comprising or dominated by unpreferred species being used more in later years.

4.3.4 Use of individual trees by beavers

The majority of marked and measured stems in the plots in November 2012 were standing trees unaffected by beavers. However, stems, stumps and branches were recorded in all status categories (Section 3.2.4, Table 1). By November 2010, 7.1% of trees in the plots had been directly affected by beavers, however these accounted for only 4.9% of the total basal area. By November 2011 the figures had increased to 10.4% and 7.2% respectively, by November 2012 to 12.9% and 9.2% and by November 2013 a further increase to 15.8% and 11.3% respectively (Table 3, Figure 11). There was considerable variation among the plots in their intensity of use by beavers, which, in November 2013 ranged between 0 - 70% of trees affected. The ultimate effect of beavers on woodland structure at Knapdale will be strongly influenced by which individual trees beavers fell. Figure 12 compares the distribution of stem diameters available at the start of the trial reintroduction amongst all trees measured in the vegetation plots and among trees gnawed or felled by beavers in the four individual years November to November, from 2009 to 2013. Numerically, the vegetation surrounding the lochs at Knapdale is dominated by small trees, reflecting the extensive areas of recent regrowth of birch, in particular, described by Brandon-Jones *et al.* (2005).

Beavers use very small trees (diameter ≤ 2 cm) less than their availability would dictate, and mostly use trees of diameter 2–6 cm (Figure 12b). Trees larger than 6 cm diameter were gnawed approximately in proportion to their abundance. Overall, there was a significant tendency for the mean stem diameters gnawed to increase across the four years (F= 5.06, df 3,705, P<0.01) and there were strong differences among species (F= 7.99, df 5,650 P<0.001; Figure 12c). However, any changes in the mean diameter of the stems gnawed by beavers in the years following the trial reintroduction differed among the species (species x year interaction F= 1.67 df 14,688, P=0.057, Figure 12c). The mean diameters of gnawed *Salix* and *S. aucuparia* were greater in the last year, and the diameter of gnawed *A. glutinosa* was greatest in the last two years whereas the diameter of the *F. excelsior* gnawed tended to decrease, although relatively few of this species were present or gnawed. The diameters of birch gnawed remained constant. In our sampling plots, very few trees of diameter ≥ 20 cm were observed to have been directly affected by beavers. However, trees of this size and considerably larger were commonly observed both as stumps and partially felled trees throughout the trial area more widely, particularly close to the water.

Table 3. Thirteen status classes used to classify trees and tree parts in the plots, codes used to record them, and the numbers of each class recorded in vegetation plots in November of each year 2010-2013 inclusive.

Status	Code	Count				Total Basal Area (cm^2)			
		2010	2011	2012	2013	2010	2011	2012	2013
Upright tree, unaffected by beavers	Up	4031	3888	3772	3641	264715	261531	252908	246977
Stump of tree felled by beavers	BStump	237	345	421	527	6130	7712	9393	10879
Upright stems growing from a log	LogUp	103	98	98	98	2703	2657	2657	2657
Base of Affected Tree	Base	23	38	51	68	1914	5096	7638	10957
Tree partially felled by beavers	BP	29	36	50	48	3636	4094	4965	4994
Naturally fallen log	NLog	38	43	46	47	13946	12919	12990	12994
Upright tree gnawed by beavers	BUp	21	34	39	44	2037	3215	3507	4571
Log felled by beavers	Blog	27	35	39	41	2323	2470	2540	2631
Natural tree stump	NStump	7	26	31	32	223	558	618	634
Tree pushed down by beaver tree	Bent	13	13	21	26	82	82	104	137
Site where a minor branch removed from standing tree	BCut	7	10	23	57	5	35	86	236
Naturally partially fallen tree	NP	1	2	2	2	1810	1829	1829	1829
Tagged but subsequently missing 2011	Gone	16	63	114	165	467	704	770	1643
Total trees affected by beavers		4553	4631	4707	4796	299991	302902	300005	301139
TOTAL (excl. ‘Gone’)		4537	4568	4593	4631	299524	302198	299235	299496

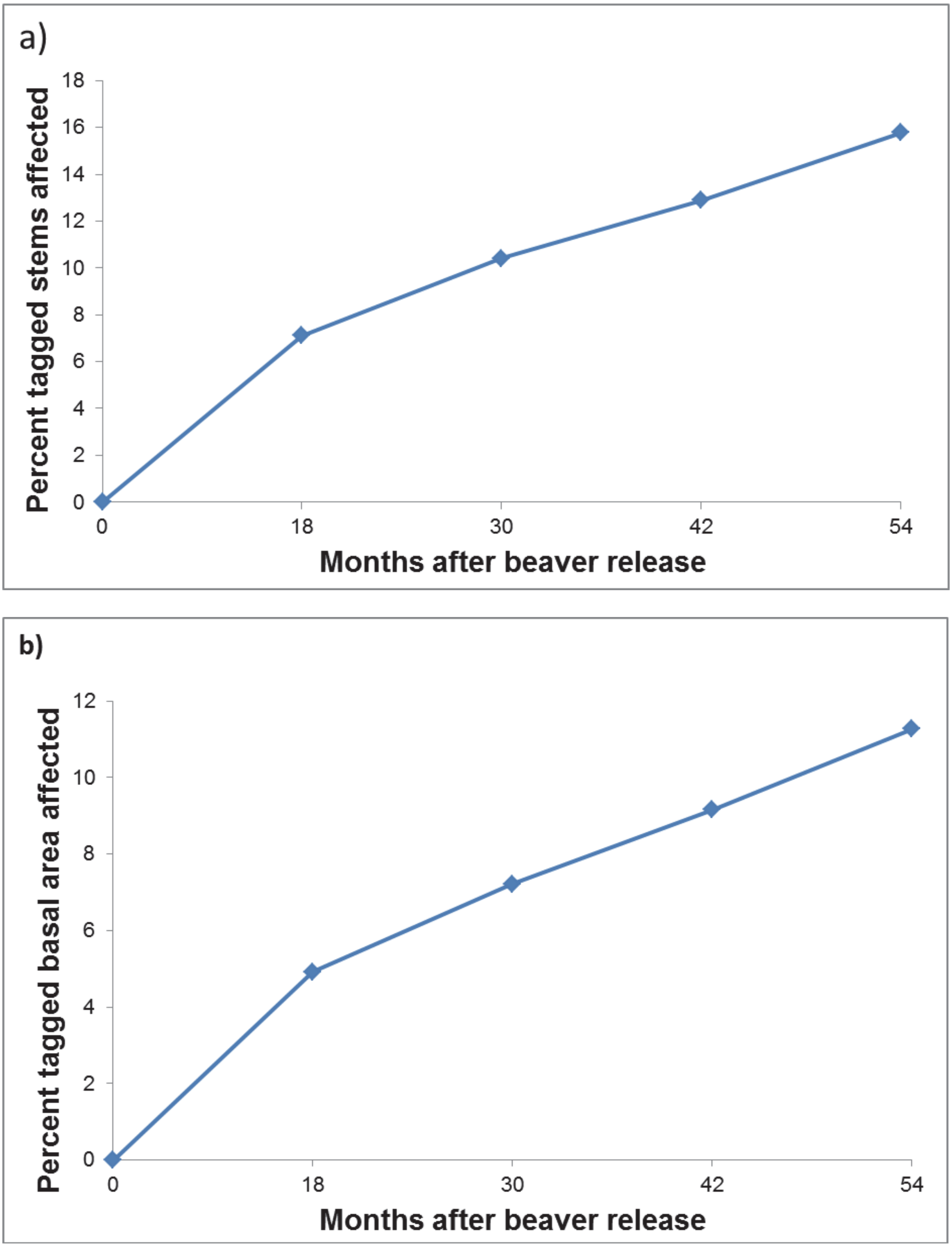


Figure 11. The cumulative percentage of a) the number of individually marked stems and b) basal area of stem affected by beaver activity since their release.

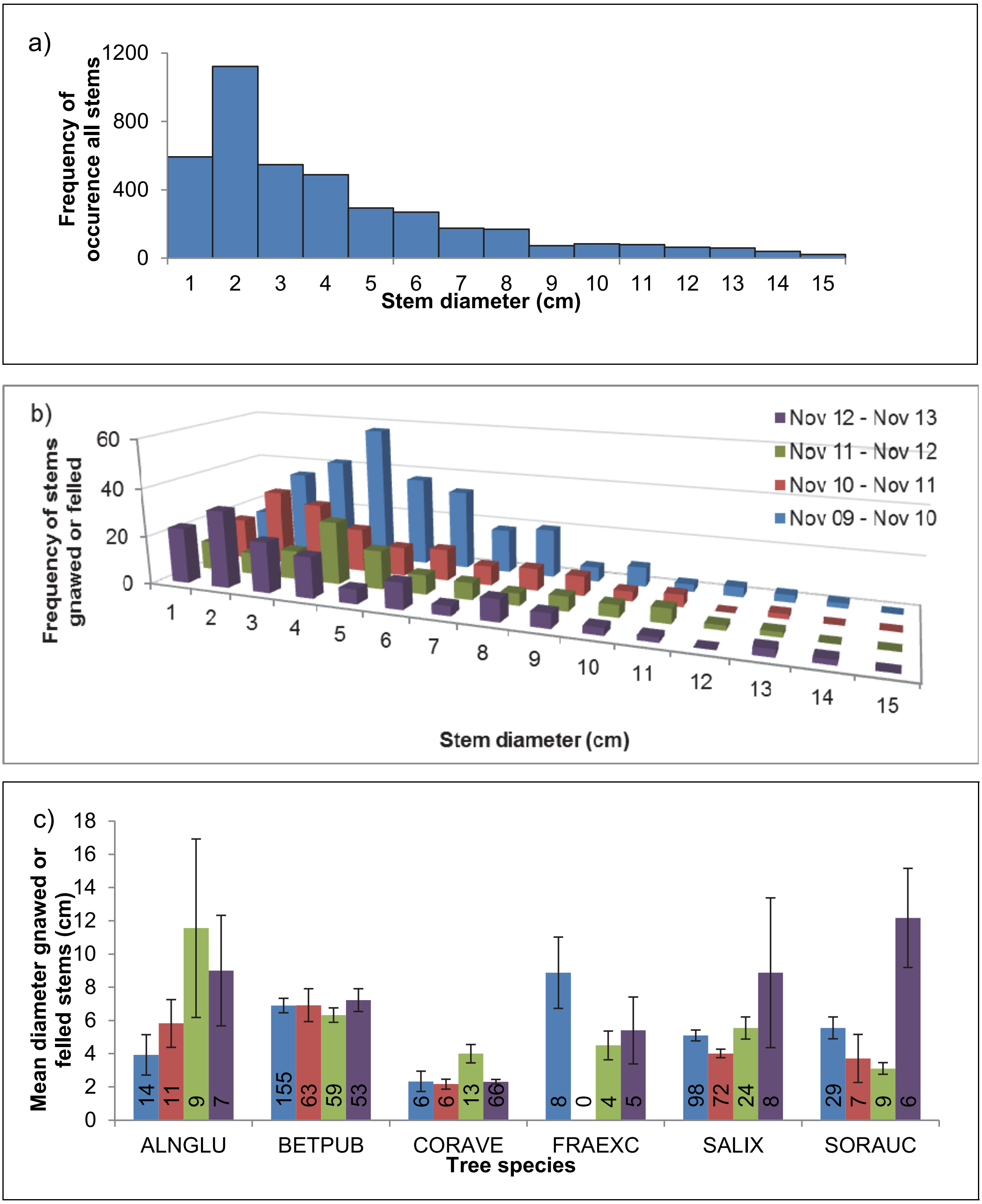


Figure 12. Frequency histograms illustrating a) the distribution of stem diameters of all trees recorded in plots at Knapdale at the start of the trial reintroduction of beavers; b) the frequency distribution of stem diameters of all trees newly gnawed or felled by beavers in each of the four periods November 2009 to November 2010, November 2010 to November 2011, November 2011 to November 2012 and November 2012 to November 2013 in the plots; c) the mean diameter of stems of each species newly gnawed or felled by beavers in each of the four years (colours are as given in Figure 12b). The numbers inside the bars are the numbers of newly gnawed trees measured in each time period. The frequency histograms in a) and b) are truncated; beavers also use some trees larger than 15 cm diameter.

4.4 The effect of beavers on canopy cover and vertical density

The extent of beaver activity (beavimp - measured as the proportion of the total number of trees in the plot, irrespective of species, that had been directly affected by beavers), was strongly negatively associated with both logit-transformed canopy cover (F=16.13, df 1,140, P<0.001; slope = -2.350, SE 1.016) and vertical densities at heights 150cm and 200cm in the annual November measurements (F=16.96, df 1,126, P<0.001; slope = -0.93, SE 1.00, and F=15.90, df 1,105, P<0.001; slope = -0.36, SE 0.896). There were minor differences among years, only for vertical density at 200cm height, and no effects of beaver activity on vertical density at the two lower heights of 50 and 100cm were detected.

Plot structure was assessed visually and photographic records were taken in each April and November over the 48 months of monitoring. These pictures have provided an interesting visual record of how horizontal vegetation structure has changed as a result of the effects the beavers have had on the plots. Examples of these are illustrated in Appendix 5. The changes in plot structure that were assessed visually in April and November provide only a limited impression of the effects of beavers, because at these times of year the trees are not in leaf and consequently a clear view across the plot is usually obtainable. Consequently these measurements were repeated during the summer of 2012, and again in the summer of 2013, in order to help us investigate more fully the beaver effects on both horizontal vegetation density and plot canopy cover. The assessment of canopy cover and vertical density in summer 2013 showed a very similar pattern. In plots that were used by beavers, there was a significantly negative relationship between beaver impact and the canopy cover (F=6.25, df 1,41, P<0.05; slope = -1.20, SE 1.488) and the vertical density at 150cm height (F=5.62, df 1,41, P<0.05; slope = -2.03, SE 1.075), although there was no effect detected on vertical density at 200cm height in summer. The visible contrast between seasons is also illustrated in Appendix 5.

The activity of beavers and its impact in terms of removing or damaging trees is clearly associated with an opening of the canopy, reducing its cover. It also reduces the vertical density of the woody vegetation above 150cm, but does not affect the vertical density closer to the ground.

4.5 The effect of beavers on ground cover

Results for ground cover estimates and seedling counts in the two subplots in each vegetation plot in November of each year are presented in Appendix 6. It was not anticipated that any major changes in ground vegetation would take place across any single year, due to the likely slowness of the vegetation responses to any changes implemented by beavers. There were likely to be differences among years in some measurements such as percentage cover of litter, grasses, standing water due to inter-annual difference in the weather, affecting the timing of vegetation growth and the fall of leaf litter. However the most ecologically significant results are considered to be the effects of the extent of beaver impact on trees in the plot (beavimp). The interaction effect of beavimp with different years was also considered as important because it was hypothesised that there was likely to be a lag in response of the ground cover following beaver activity in a plot.

Statistical analysis of the percentage cover of the main components of the ground cover shows that there was a significant interaction effect between beavimp and year on the percentage cover of grass, leaf litter, ferns and bryophytes. The effect of beaver impact in plots led to an increase in grasses, presumably due to an opening of the tree canopy or reduction of the density of understory trees permitting more light to reach the ground level and favouring the competitive advantage of the graminoids. The strength of this effect accumulated with progressive years following the release (Table 4). There was a concomitant switch from an initially positive relationship between beaver impact and percentage cover of leaf litter as assessed in the autumn of 2010, to a negative relationship, reflecting a positive association of beavers with tree-dominated plots (Table 4). This changes as trees are affected by beavers, leading to a subsequent reduction in the cover of leaf litter with increasing beaver impact in those plots. As expected, where the beavimp x year interaction was not significant for particular variables (percentage cover of: woody debris, shrubs, and herbs), then there were constant, significant differences among years in the percentage cover of these components. In the case of percentage cover of woody debris, there was a significant main effect of beavimp overall, with the percentage cover of woody debris in the plots being positively associated with beaver impact (Table 4). This is likely to be due to direct beaver activity, but the presence of this effect equally across all years indicates that a possible contributory factor is the selection of the plots by beavers that contain a greater cover of trees themselves.

Table 4. The effects of the interaction between the impact of beavers in plots (beavimp) and year of the study on components of the ground vegetation. Where this interaction effect was not statistically significant, then the main effect of beavimp across all years is given. The effects presented are parameters and their standard errors of estimate (SE) calculated on logit-transformed data on the proportion of ground covered by each component.

	Constant	*SE*	Effect of Beaver Impact overall or by individual year				*SE*	*F*	*df*	*P*
			2010	2011	2012	2013				
%Grass	0.542	0.156								
Beavimp x Year			0.002	0.081	0.561	1.109	0.515	3.03	1,664	<0.05
%Leaf litter	-0.160	0.097								
Beavimp x Year			0.702	-.750	-1.042	-1.209	0.382	3.99	3,668	<0.01
%Woody debris	-1.629	0.085								
Beavimp x Year								2.11	3,672	NS
Beavimp			1.608				0.511	7.44	1,274	<0.01
%Fern	-1.558	0.146								
Beavimp x Year			0.477	-0.661	-0.320	-0.007	0.428	3.01	3,664	<0.05
%Bryophytes	-0.874	0.136								
Beavimp x Year			-.0211	-.564	0.283	-.1766	0.516	3.66	3,666	<0.05
%Shrubs	-2.197	0.120								
Beavimp x Year								1.59	3,667	NS
Beavimp			0.297				0.515	0.40	1,612	NS
%Herbs	-1.925	0.108								
Beavimp x Year								0.78	3,672	NS
Beavimp			-0.332				0.527	3.58	1,406	NS

It should be borne in mind that the results of these ground cover surveys are very season-specific, and quite different results might be returned at other times of the year. A maximum of only 62 seedlings of woody plants (range 0-8 in any one plot) was recorded across all plots in the final year of survey, 2013.

4.6 Re-sprouting and subsequent deer and beaver browsing

An important factor likely to influence the effects of beavers on riparian woodland in the medium to long-term is the re-sprouting of stumps of trees felled or otherwise affected by beavers. The key rationale for conducting two monitoring sessions in the woodland each year was to estimate both rates of browsing by deer and beavers on new shoots during the non-growing season as well as rates of browsing and net growth during the growing season.

In November 2009, no new sprouts were observed on beaver-felled stumps in the permanent plots, and little significant re-sprouting was observed elsewhere in the trial site (Moore *et al.* 2010). As expected this situation had changed little by April 2010, as the intervening winter period was not favourable for plant growth. A larger number of the beaver-damaged trees showed signs of re-sprouting by November 2010 and 2011 (Moore *et al.* 2011, 2013). Of those trees that produced re-sprouted shoots following some form of beaver damage, the number of shoots they produced was fewer in the later years of the study (Figure 13b). This was true of all species, the only notable exception being *B. pubescens*. However, those re-sprouted shoots that remained as at November 2013, had in most species, grown to a longer length (Figure 13c). The data reported in Figure 13 and 14 are cumulative in that re-sprouted shoots recorded in any year could have been produced in any of the previous years. However, the mortality of these shoots means that the number present does not necessarily increase in successive years. The re-sprouting of beaver-damaged trees is strongly species-dependent; *F. excelsior*, *Salix* and *S. aucuparia* are reliable re-sprouters which generally produce large numbers of thick shoots. The proportion of beaver damaged stumps with re-sprouted shoots had declined from the 2010 measurement through to November 2013, with the exception of *C. avellana* and to a lesser extent *F. excelsior* which had increased by proportion in 2013 (Figure 13a), whilst contributing relatively few re-sprouted shoots in absolute terms. This is due largely to their scarcity within the study area, particularly in the case of *F. excelsior* (Table 2).

Much of the re-sprouting from stumps caused by beavers in the early years suffered heavy mortality that was attributed to over-winter frost damage of small re-sprouted shoots rather than deer browsing. The winters of 2009-2010 and 2010-2011 were colder with lower minimum temperatures than the two latter years of the study[1]. In the early years of monitoring up to 2012, relatively few data concerning deer browsing of re-sprouts were available and only in sufficient quantity in *Salix*, *S aucuparia* and *B. pubescens*. However, in 2013 information on more re-sprouted shoots was available for more species (Figure 13b). These data collected at the end of the monitoring period were analysed to examine whether or not the stumps that had developed re-sprouted shoots and had been subsequently browsed by deer. The ordinal regression of browsing intensity class (0,1,2), showed that the intensity of browsing varied significantly among species (F [Deviance ratio]=8.89, df 5,164, P<0.001). The proportion of stumps that had re-sprouted shoots that had been subsequently browsed is shown in Figure 14. In 2013, the final year of monitoring, for *B. pubescens*, *C. avellana*, *F. excelsior* and *Salix,* more than 68% of the re-sprouted shoots had been browsed by deer, whereas only a small proportion of re-sprouted stumps of *A. glutinosa* and *S. aucuparia* were browsed by deer. In addition to this effect of species, the intensity of browsing by deer increased with increasing number of re-sprouted shoots per beaver affected stump (coefficient = 0.123, SE 0.054, F = 8.42, df 1,162, P<0.001), but was not affected by the length of the shoots.

[1] http://www.metoffice.gov.uk/climate/uk/stationdata/dunstaffnagedata.txt.

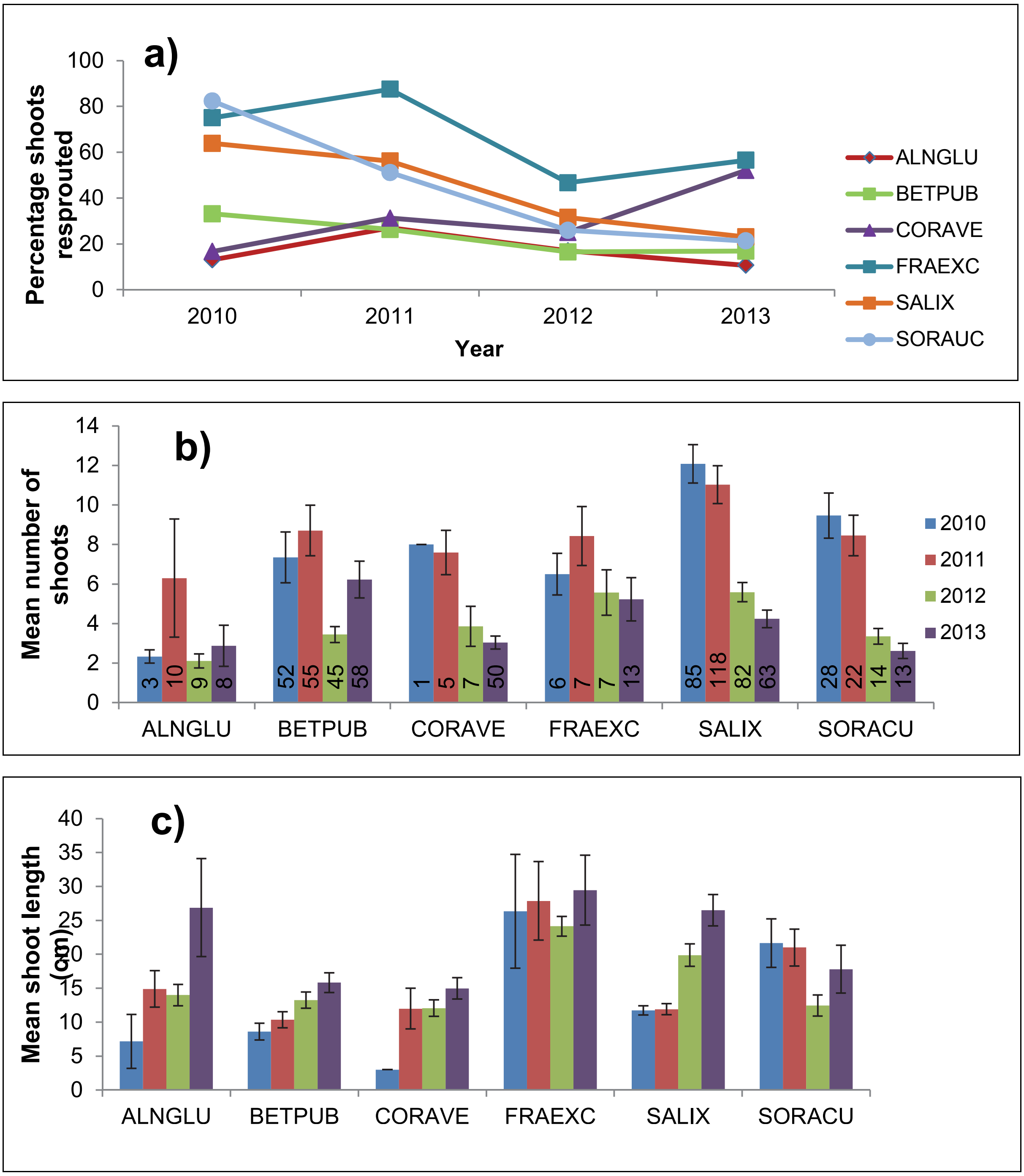


Figure 13. a) Percentage of stumps resulting from beaver activity that had new re-sprouting shoots at the same time points; b) Mean number of shoots re-sprouting from those trees of each species that had re-sprouted after having been directly affected by beavers measured in November 2010, November 2011, November 2012 and November 2013 and c) Mean length of extant living shoots (in cm) re-growing from the stumps and base of trees gnawed by beavers at the same time points as in b. The numbers of trees in the samples for b) and c) are given in b).

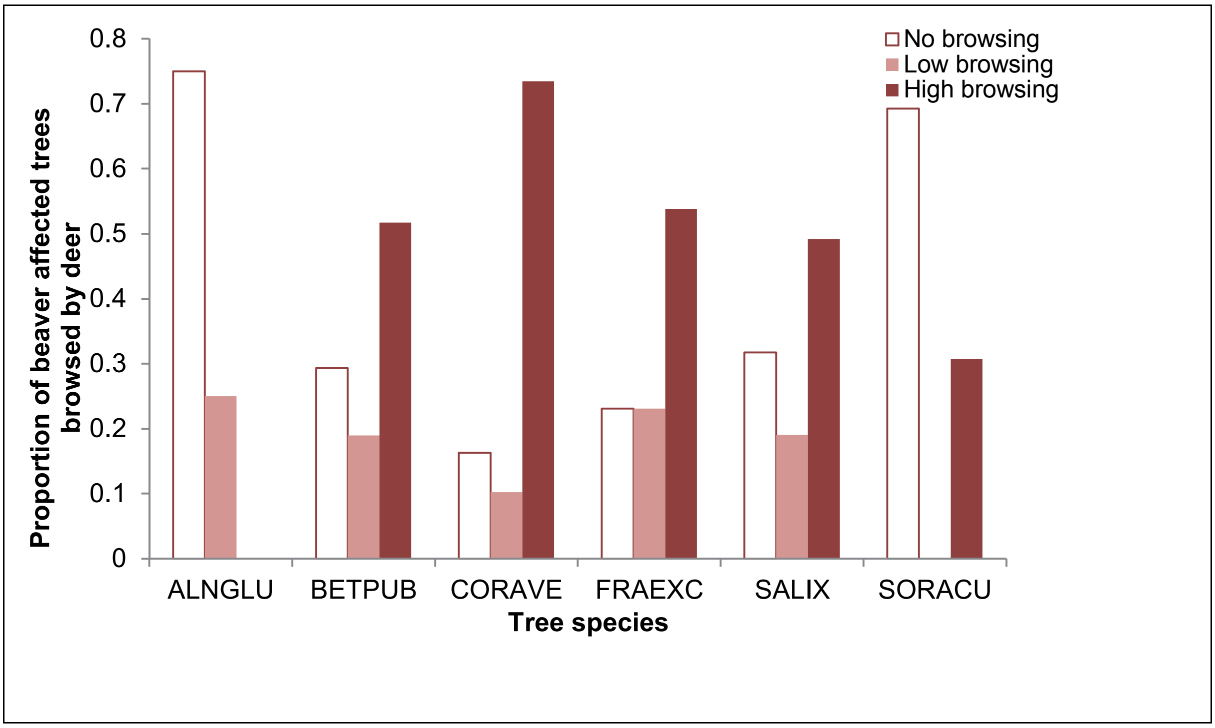


Figure 14. The proportion of trees of each species that had produced re-sprouted shoots following beaver activity and which had been subsequently browsed by deer (Low browsing: <50% of re-sprouts browsed, High browsing: >50% of re-sprouts browsed) or not browsed (No browsing). The data shown are from the records collected in November 2013 for all trees summed across all plots.

4.7 Seasonal differences in beaver effects

Because trees in the plots were individually permanently marked and monitored for the duration of this study, all beaver effects that occurred after initial marking of these trees could be detected.

Because of the constancy of the composition of the sample of plots recorded in April and November 2010 - 2013, the seasonal variation in the effects of beavers on the trees can be assessed by comparing the frequency of effects of beavers in the summer and winter seasons, between these dates. During summer and autumn, beavers are expected to feed more on forbs and aquatic macrophytes in addition to the foliage of deciduous trees, and to direct their diet more towards the bark and small twigs of woody vegetation as other foods become less available through winter (Krojerová-Prokešová *et al.* 2010). November-April coincides with the period of winter dormancy of the vegetation and April-November represents the summer growth period. Overall there were no significant season (F=1.41, *df* 1,1664, *NS*), nor season x species interaction effects (F=0.69, *df* 5,1694, *NS*). The slight and non-statistically significant tendency for greater beaver activity affecting trees in summer rather than winter may be contributed to by the longer period of the summer (seven months). However, the main effect of species (F=9.68, *df* 5,1693, P<0.001) was statistically significant and reflects the strong preference for willow by beavers (Figure 15).

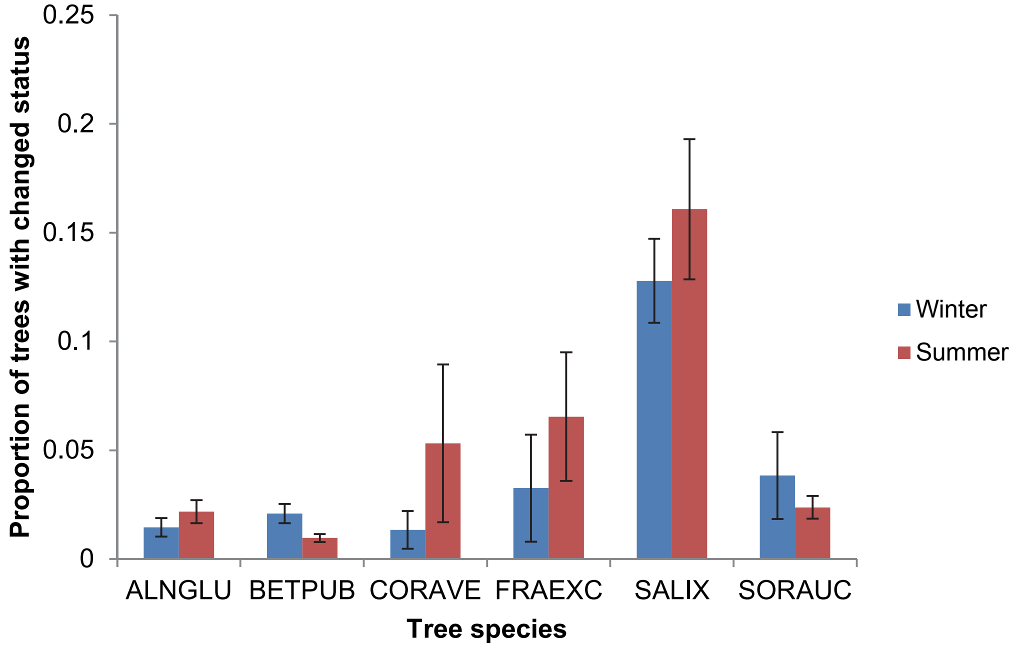


Figure 15. The proportion of stems of each species that changed status (i.e. were affected by beavers) between successive monitoring sessions over four winters (November 2009 - April 2010, etc. until April 2013) and four summers (April 2010 – November 2010 etc. until Nov 2014). Data are the mean (and SE) of the proportion of trees that changed status across the four years.

4.8 Beaver impacts on woodlands throughout the wider area of the trial release

In the 255 sampling plots distributed around the four main beaver-occupied lochs, the survey estimated that 8.6% of trees had been felled or browsed by beavers. This estimate of total beaver impact varies strongly between localities with 160 of the 255 plots (62.7%) being unaffected by beavers.

The percentage of trees affected by beavers varied in relation to the dominant species present in the sampling plots (F=9.46, df 6,240, P<0.001; Table 5). *F. excelsior* (1 plot), *S. aucuparia* (2 plots) and *Fagus sylvatica* (Beech – 3 plots), and one other plot containing an unidentified tree species were included in the 'other species' category. These all individually represented insufficient plots to estimate means for a species or include in the analysis. *Quercus petraea* (26 plots) was included separately in this analysis, as were 'conifers' which comprised *Tsuga heterophylla*, *Pinus sylvestris*, and *Picea sitchensis,* which collectively dominated 41 plots. However, very few conifer or *Q. petraea*-dominated plots showed signs of beaver use (Table 5).

The mean percentage of trees affected by beavers declined with increasing distance from the loch-shore (F=23.72, df 2,180, P<0.001; 5m: 13.5% (SE 1.53), 15m: 9.3% (SE 1.44), 25m; 6.3% (SE 1.43)). This confirmed the result of the intensive tree-based sampling (Section 4.3.3, Figure 9).

There was surprisingly little difference among the four lochs in the overall percentage of trees affected by beavers (F=2.63, df 3,89, NS). This measurement for any given loch is likely to be influenced by the number of beavers, their duration of occupancy and the length of the loch-shore.

Table 5. The mean percentage of trees affected by beavers in plots according to the dominant tree species or species grouping in the plots sampled throughout the area of the trial reintroduction occupied by beavers. For the composition of the 'Conifer' and 'Other species' categories, see text.

Dominant Species/ Tree grouping in plots	Mean % trees affected by beavers	SD	Number of plots	% of plots affected by beavers
Alnus glutinosa	14.6	3.411	13	69.2
Betula pubescens	10.78	1.053	137	47.4
Conifer	1.36	1.933	41	7.3
Corylus avellana	8.78	2.432	26	42.3
Quercus petraea	1.82	2.412	26	15.4
Salix spp	36.02	5.499	5	80.0
Other species	4.3	4.648	7	28.6

5. DISCUSSION

Beavers are semi aquatic mammals with a renowned capability for ecosystem modification (Rosell et al. 2005). As ecosystem engineers, through their dam building and browsing on aquatic and riparian vegetation, beavers can affect a range of environmental characteristics at the interface between aquatic and terrestrial systems (Czerepko *et al.* 2009; Milligan & Humphries 2010; Rosell *et al.* 2005). Several studies have attempted to predict the food and habitat selection of Eurasian beavers (Pinto *et al.* 2009), including in areas where they have been reintroduced or are colonising (e.g. France, Bavaria, Poland). Few generalities are possible (Fustec & Cormier 2003), and earlier assessments suggested that much of Scotland was not particularly suitable for the establishment of beavers (Collen 1995). Predicting beaver habitat use should consider not only forage availability but also the physical environmental factors such as bank and river characteristics necessary to locate a lodge with a suitable entrance, and presence of construction materials, which may differ from foraging material (Fustec & Cormier 2007).

The effects of beavers at Knapdale already include the flooding of a substantial area due to the construction of a beaver dam at Dubh Loch, and significant vegetation changes can be expected in this flooded woodland. Flood-tolerant species such as willows and alders may survive there while less flood tolerant species have died, but may persist for some time as standing dead timber. Ultimately, the vegetation may shift from broadleaf deciduous woodland to swamp or bog. It is to be expected that the capacity of beavers to modify both woodland habitat structure and species composition will have a strong effect on associated communities of organisms (Humphrey *et al.* 1999; Kerr 1999 Ciechanowski *et al.* 2011), and therefore the quantification of these effects is an important step towards prediction of their overall impact. This report describes the effects of beavers on the woodland environments of Knapdale, and includes the effects of their gnawing and felling of trees on the trees themselves and the associated terrestrial vegetation.

5.1 Woody vegetation at Knapdale

Since the initial survey undertaken in November 2009 (Moore *et al.* 2010), the number of monitoring plots at Knapdale has been almost doubled, however the mixture of woodland types included in the sample has not changed substantially. The set of vegetation plots onto which all comparisons in this final report have been standardised, show that the most numerous tree species recorded, by a considerable margin, was *B. pubescens*. Dense stands of young regrowth of this species, as well as larger, old trees, occur throughout the area. In many places birch has rapidly colonised areas from which conifer plantations were removed to meet Natura Special Area of Conservation obligations in earlier years. These early successional woodlands are dynamic communities and it is likely that the presence of beavers will alter the trajectory of their development. *Alnus glutinosa* is also widespread and common at Knapdale, but in contrast to *B. pubescens*, it occurs primarily as large trees at the water's edge, and for this reason accounts for a similar large proportion of total tree basal area. *Salix spp*., *C. avellana*, *F. excelsior* and *S. aucuparia* were also common in plots and have previously been identified as important components of Eurasian beaver habitat elsewhere in Europe (Haarberg & Rosell 2006, Macdonald *et al.* 1997).

5.2 Beaver browsing preferences and effects

5.2.1 Beaver selection of trees

Because the positioning of transects was partially guided by pre-existing beaver herbivory, the plots selected are not an unbiased sample of loch shore. They do however permit a thorough analysis of local selection of tree sizes and species by beavers. The number of transects established at Knapdale was such that all vegetation types were represented and a clear picture of beaver preferences has emerged. From November 2010 - November 2013 the beavers have affected a progressively increasing number of the 108 standard monitoring plots. 15.8% of trees in those plots have now been affected, representing 11.3% of the basal area although there is large variation locally among plots. The proportion of trees affected ranges from 0 to 70% of stems affected by beavers. As expected the assessment of the percentage of trees gnawed or felled by beavers across the entire range of perimeters of the lochs at Knapdale that were occupied by beavers (8.6%) was less than the figure calculated from the intensively monitored plots.

The beavers' preference for *Salix* species, which has been found in other studies, was confirmed at Knapdale. *Salix* is used both for lodge construction (Fustec & Cormier 2007) and is a favoured food (Haarberg & Rosell 2006). The stems that were most utilised in relation to their availability in the environment were of *Salix,* and to a much lesser extent *S. aucuparia*, particularly in the first year after the release of beavers, suggesting that these were most preferred. *F. excelsior* and *B. pubescens* are used overall approximately in proportion to their availability in the environment, but *B. pubescens* remains easily the species that is numerically most utilised by beavers, due to its abundance, whilst *F. excelsior* is far less abundant and forms only a very minor component of the species used by beavers. Another study found that uncommon or rare species, including *F. excelsior*, were selected more intensively than expected by chance, and this was attributed to the beavers maintaining intake of particular nutrients that the species contains, or trying to maintain a mixed diet to avoid any such deficiencies (Nolet *et al.* 1994). The proportion of the available *C. avellana* stems utilised by beavers increased in the third and fourth years of the study compared to the earlier two years, due to a large number of stems being browsed in two plots. This reflects the local abundances of stems of *C. avellana*, the basal area of which is often very small. Because only about 37% of sample plots in the wider area of the beaver-occupied lochs were used by beavers, there are presumably many local areas of woodland not yet visited or used by beavers. The progressive use of these previously un-exploited plots may explain the pattern of usage of *C. avellana* in the later years of the study. In Telemark, Norway, the source of the reintroduced beavers, they fed preferentially on *Salix*, *S. aucuparia* and birches, although alders dominated their diet (Haarberg & Rosell 2006). Beavers' species preferences in that study could be ordered willow > rowan > birch >*Prunus*> others > alder > conifers, which is consistent with patterns observed at Knapdale (see section 6). Note that the alder present in Telemark was *Alnus incana,* not *A. glutinosa*.

Based upon a comparison of the sizes of trees used by beavers with those available, the most frequent tree size used by beavers was from 2–6 cm diameter, and smaller trees were less preferred, although still commonly used. A study of foraging by beavers in Telemark, Norway found that beavers there used trees in approximately the same diameter class as those used by the beavers at Knapdale, (Haarberg & Rosell 2006). The mean diameter of stems eaten by beavers varied among the years of monitoring with a tendency to increase in the later years of the study for most species. However, the stem diameter gnawed and its variation among years is species-specific. The diameters of gnawed trees in any one year are likely to have been connected with availability which is linked to the possible depletion of preferred size classes of stems of preferred species. This is particularly likely in the case of willow, the most depleted species, and preferences are also likely to change in relation to requirements for lodge and dam construction versus foraging. During the period of this study, and since their initial colonisation, beavers have continued to actively enhance their lodges and a large dam, both of which use mainly poles from harvested stems, rather than large tree trunks. However, outwith the plots, many larger trees were also observed to have been affected by beavers. Despite mainly felling small-stemmed trees, it is clear that beavers will fell or attempt to fell even very large trees.

Herbivory of the upper parts of trees would be expected to yield greater energy and nutrient gains during the summer when they are in leaf and some of the harvested material is likely to have been cached underwater by beavers. Food-caching is a behavioural characteristic that is advantageous to beavers that regularly experience harsh winters and for which access to food resources or travel opportunities may be restricted by ice for long periods, or the costs of swimming at low temperatures become too high (Nolet & Rosell 1994). However, there was no evidence of a consistent or significant seasonal difference in the proportion of stems that were affected by beavers between the summer and winter seasons. The proportion of the beavers' diet that comprises food from other sources such as grasses, forbs and shrubs, or aquatic vegetation is unknown, but also likely to be higher during the summer due to greater availability and quality.

5.2.2 Spatial aspects of beaver foraging and impacts at Knapdale

As beavers are central-place foragers (Haarborg & Rosell 2006), the decision of where to locate a lodge would seem to be very important as it determines the future costs of foraging and their proximity to food of the required quality. The data suggest that beavers focus on plots containing preferred communities, close to their lodges, and that these were used progressively less in later years. However, there remain un-utilised plots containing preferred species, at similar distances from the lodges as the utilised plots containing un-preferred species (Figure 10). This suggest that although certain plots are being depleted of available and suitable trees, the beavers continue to have options to forage fairly close by on preferred communities, within the period of this study. Central place foraging can impose distance-dependent depletion on their food supply (Fryxell 2001), which is likely to change with time since occupancy of the lodge. This may contribute to abandonment of lodges and the building of new or alternative lodges by several of the beaver families, for example the Creagmhor beavers which moved to another lodge in 2011. It has been suggested that beavers move to occupy sub-optimal habitat following the initial colonisation of and depletion of prime habitats (Frantisek *et al.* 2010), although without further extensive quantification of spatial distribution of available preferred trees species this can neither be confirmed nor refuted. Whilst resource depletion is a possibility, the contrast between the quality of primary and secondary occupied habitat cannot be tested here since our monitoring data include only plots foraged by those beavers that remain in the same lodges.

We might expect a tendency for the effects of beavers on trees to occur slightly further from the water's edge with increasing years since the release. Beavers prefer to forage close to water, which permits escape from predators, but as they deplete their preferred food sources at these locations, they might be forced to forage further inland. In the first year following the release of beavers, the majority of beaver effects on trees were within 10m of the water's edge. There was, however, no sign that they moved systematically to forage further from the water's edge with increasing time, as they foraged closer to the shore in the fourth year after release. Although it has been shown that inter-annual variation in weather variables can lead to changes in forage quality due to direct growth responses to temperature and rainfall, or via localised waterlogging (Campbell et al 2013), this is not a likely explanation in this case. Rather, the result was attributable to the beavers at Lochan Buic alone foraging intensively close to the edge of the loch in the final year, and not due to a more widespread effect. Because relatively few individual trees of some species were newly foraged in the final year of study, we could not systematically explore the relationship between foraging at different distances from the water's edge, as it changed through time for the different tree species. For example only five, eight and six trees were recorded as newly foraged in November 2013 for *F. excelsior*, *Salix* and *S. aucuparia* respectively.

Where conditions allow, beavers will feed from the water on overhanging branches and trees growing right at the water's edge. Opportunities for this type of feeding seem to be limited at Knapdale, as loch shores are sometimes steep or rocky and often are vegetated with large mature trees such as birch and *A. glutinosa*, rather than by dense thickets of the strongly preferred tree species such as willow or aspen. Many parts of Knapdale are not suitable for assessing how far beavers forage from the water, because the narrow strip of broadleaf woodland along the edges of the lochs is hemmed in by dense conifer plantation, which was hardly used by beavers.

5.2.3 Beaver effects on woodland structure and its consequences

In most areas, much of the felled biomass has been removed for construction, caching or eating elsewhere, or consumed on the spot by beavers. Even some very large trees have been almost entirely removed. As a consequence, the riparian woodland is not generally becoming strewn with dead wood, although an increase in coarse woody debris in the ground cover measurements was recorded in plots with a greater use by beavers for gnawing and felling trees. Plots with greater beaver effects on the trees had a greater cover of grasses and less leaf litter and more open canopies due to tree removal. There were also lower vertical densities of stems and foliage in both autumn and summer when the trees were in leaf. Where beavers use plots more intensively, then they have significant, visibly detectable impacts on the vegetation structure, but also on their composition of associated ground vegetation communities and probably also on their ecological functional processes such as nutrient transfers.

5.2.4 Regeneration of woodland following browsing

Re-sprouting directly from beaver-cut stumps or from root suckers after felling or other forms of beaver damage, is a characteristic that varies strongly among tree-species. *S aucuparia*, *F. excelsior* and *Salix* species are the strongest re-sprouters, and *A. glutinosa* and *B. pubescens* appear to be fairly poor re-sprouters. *C. avellana* was almost un-browsed in the first year after release of the beavers but re-sprouted in response to browsing in later years. The regeneration rates of their woody food plants can be an important influence on the longer-term food supply to a beaver population (Jones *et al.* 2009). The overall pattern of dynamics of re-sprouted shoots is that following browsing an initial flush of re-sprouting occurs, which could potentially replenish the populations. However, in this study, these re-sprouts suffered heavy mortality in a particularly cold winter, and this was attributed to frost damage (Figure 16a). While surviving shoots grew progressively longer, those growing on birch appeared to be very thin and wispy and suffered a high mortality. Subsequently, we detected significant browsing by deer on the re-sprouted shoots, and during the course of this study, none of the re-sprouts reached the 2cm diameter favoured by beavers.

Consequently the sustainability of a beaver population that might be facilitated by generation of its food supply is doubtful when the regenerating stems are significantly depleted by deer browsing. A further factor that may influence the re-sprouting from beaver-damaged trees is the mortality of the remaining stumps, which despite initially re-sprouting, were seen on occasions to subsequently die and/or become rapidly colonised by moss (Figure 16b).

Figure 16. a) Frost damage causing browning to re-sprouting shoots and b) a stump over-grown by moss.

5.3 Assessment of monitoring methodology

The monitoring fieldwork reported here was conducted for a period up to 54 months after the initial release of beavers to Knapdale in late May 2009. Over the period of study there has been some instability in the numbers and locations of beavers (Harrington *et al.* 2014, in prep.), so any interpretation of trends in beaver foraging patterns should still be treated with some caution, and considered in relation to the presence of beavers numbers that foraged in that locality. The tree sampling plots contributing results to this report represent a sub-sample that comprises most of the plots established, with the exception of a few which have been destroyed by routine forestry activity or have become impossible to access due to flooding caused by beavers. The results presented here have been standardised to the same sample plots across all years, and within these plots, the species and size composition at the outset of the trial have been estimated. Ideally, this woodland monitoring program would have commenced with a survey of baseline vegetation conditions in the plots before beavers were reintroduced. However, uncertainty surrounding several aspects of the releases made this impractical. For example, the precise locations of the artificial lodges used for the releases was not known long in advance and the use of space by beavers post-release could not be confidently predicted, making the prior siting of transects too speculative to be justified. The initial location of the sampling plots does not provide an unbiased reflection of the use of habitat by beavers as they were located at the lochs on which beavers were initially established or were considered likely to establish subsequently. The proportion of trees affected (15.8%) reflects the use of trees by beavers locally in the plots and in the areas in which they are established rather than their selection from a wider population of all available trees. A rapid survey method that systematically covered the entire circumference of all the Knapdale beaver-occupied lochs and counted the proportion of trees affected by beavers, provided a suitably objective estimate of the proportion of trees affected in the overall study area.

Despite the absence of baseline data prior to release, the persistence of stumps of trees felled by beavers prior to the first survey allowed the reconstruction of a complete picture of woodland structure and species composition prior to the release. All stumps of trees felled by beavers in vegetation plots were identified, tagged and measured. Estimates of stem density and total basal area in each plot will only differ from the true baseline figures if trees branched above the site of beaver gnawing but below 20cm. Other measures that may have changed from their baseline values since the beavers' introduction include estimates of canopy cover, estimates of horizontal vegetation density and estimates of ground cover, particularly where beavers had caused flooding or canalisation. Any direct effects of beavers on trees that have occurred since monitoring plots were established will have been detected.

Overall, the permanent woodland monitoring plot methodology served its purpose well, with the woodland of 47.2% of plots being used by beavers. Tree tags and plot markers have proven to be sufficiently robust and durable for the duration of this monitoring. Some transects established on Un-named Loch (South) and Loch Coille-Bharr are arguably of marginal interest now that beavers have established patterns of movement focussed on other lochs. However beaver activity continued to be detected on these lochs until the final sampling period, and the plots may be utilised by beavers in future.

6. CONCLUSIONS

Some main conclusions arising from this monitoring of Knapdale beavers are summarised below. The overall pattern of browsing by beavers was that they preferred to browse within 10m of the water's edge and on *Salix* where possible, although they also used other species present. The overall percentage of trees affected by beavers in the area as a whole was 8.6%, although 36% of trees were affected in plots dominated by *Salix*. In some areas they locally depleted their food supply, by affecting 70% of the trees present. Forage depletion appeared not to force the beavers to forage further from the water's edge with increasing years since the beaver release. This may be due to the preferred species in the preferred size categories not being distributed close to the water's edge but them also occurring at some distance from the edge. A further manifestation of the effect of local depletion of forage was that the beavers used plots dominated by un-preferred species to an increasing degree, and by preferred species less, in later years.

The specific results revealed by this monitoring program are listed below along with a commentary. Those results that are currently considered to comprise general principles that might be applicable as predictors of beavers' effects on woodlands elsewhere are highlighted in bold type. There then follow two sections that specifically address prediction of future effects of beavers at Knapdale, should they establish and persist (Section 6.2) and prediction of the effects of beavers on riparian woodlands should they establish or be established elsewhere (Section 6.3). The outcome of the beaver-woodland interaction is dependent upon the species composition of the woodland. Consequently any prediction of the effects of beavers on woodland in any area of Scotland or the remainder of the UK that they may colonise, would need to be tailored in the light of the woodland resources present. This means that the predictability of the beaver-woodland interaction elsewhere is low relative to our knowledge of the possible woodland vegetation responses at Knapdale.

6.1 Overall conclusions

We measured beaver effects on woodland up to 30m from the shore. This does not represent an upper limit of distance from water of their effects, but from the results produced here and elsewhere, is likely to include a very large proportion of their effects. Within this 30m distance from the shore of the lochs, **beaver activity and the effects on trees diminished markedly with increasing distance from the water's edge.**

All aspects of beaver woodland utilisation are strongly dependent on the tree-species.

Overall the beavers have expressed a consistently strong selection for *Salix* in relation to its availability (Figure 6). An initial preference for *Sorbus aucuparia* waned with time, and *Corylus avellana* was eaten more relative to its availability in the last two years of the study. This may be because a small number of plots containing *C. avellana* were latterly discovered by beavers. Only six tree species occurred in substantial numbers in our sample of plots. These were *Betula pubescens, Alnus glutinosa, C. avellana, Fraxinus excelsior, S. aucuparia* and *Salix* spp. Most plots were dominated by *B. pubsecens*, often in conjunction with one or more other species, and the birches remain numerically the species most used by beavers. Conifers and *Quercus petraea* were fairly abundant in the area but little-used by beavers. **Species that are not especially preferred by beavers (eg. *B. pubescens* in this study or alders in the study of Haarberg & Rosell (2006)) can form a significant component of the trees used by them, where they occur in abundance.**

The order of selection of tree species by beavers in relation to their abundance of stems was:
Salix > F. excelsior > S. aucuparia > C. avellana > B. pubescens > A. glutinosa

On the basis of basal stem area it was:
Salix > S. aucuparia > B. pubescens > F. excelsior > C. avellana > A. glutinosa

The position of *F. excelsior* in this hierarchy is uncertain as its low abundance meant that relatively few data were available for it. Although *Q. petraea* and conifers were in low abundance in the intensively sampled plots, they were present in the wider area of the lochs used by beavers and where they were dominant species there was only a small proportion of trees affected by beaver felling and gnawing, indicating that they are not preferred species.

By November 2013, beavers had been present at Knapdale for 54 months **and had produced noticeable effects on woody vegetation and in the wider area of the lochs used by beavers 8.6% of trees had been affected by them.** Most effects were observed on transects less than 500m from active beaver lodges. Trees had been gnawed or felled by beavers in 45.3% of the 108 plots that were intensively monitored. **Many localities of the lochs used by the beaver families remain unaffected by them including 62.7% of the 161 monitoring plots used to assess their impacts over a wider area of the beaver-used lochs. Within the intensively monitored plots that were used by beavers, in some, only one or two stems were affected whereas in others over 70% of the stems present had been affected.** Plots used by beavers included more *B. pubescens* and *Salix* (Fustec *et al.* 2001), but less *A. glutinosa* than an average plot. **Beavers favoured trees of diameter 2-6cm.**

For the prediction of beaver habitat use and impacts, special attention should be paid to understanding the location of lodges (Campbell *et al.* 2005; Hartmann & Axelsson 2004). This facet of habitat selection is likely to have long-lasting effects on the beaver-vegetation interaction. **Approximately 45% of the *Salix* present in the sampling plots had been browsed by beavers in the first four years. Depletion within certain localities (plots) may be causing beavers to forage elsewhere in their range accessible from the same lodge or causing them to forage elsewhere accessible from a different lodge.** Among the beavers using their original lodges, there appears to have been no detectable shift by them towards using plots that are farther from the lodges or from water's edge. They did however use plots closest to their lodge that were dominated by more preferred species in the earlier years since their release, whilst in later years, they increased their use of plots nearer to their lodge that were dominated by less preferred species. This suggests localised depletion of preferred plots that was not yet sufficient to necessitate a major shift in foraging range. Some family groups did however build new lodges elsewhere, the foraging implications of which cannot yet be ascertained. The Creagmhor beavers have built a new lodge on a neighbouring loch and the Dubh Loch family distribute themselves between two lodges, **indicating some flexibility in the construction and use of lodges. A fairly small beaver population can have locally large effects especially on preferred tree species within a short time after reintroduction.**

It has been hypothesised that any impact of beavers on woodland via direct effects on trees would be offset by re-sprouting from the gnawed or felled stump, and by regeneration from seed produced by mature trees. **In general the tree species most preferred by beavers are those most suited to re-sprouting. *Salix*, *F. excelsior, S. aucuparia* and *C. avellana* were particularly vigorous re-sprouters;** *B. pubescens* also re-sprouted but the shoots were narrow and wispy and not vigorous. **The re-sprouts of *B. pubescens* were, along with those of the strongly re-sprouting species *Salix, F. excelsior* and *C. avellana,* significantly eaten by deer which are a likely inhibitory factor to the recovery of these species following beaver browsing.** We found little evidence of regeneration from seed; few seedlings were found to be establishing (only 64 were recorded in November 2013).

In areas where beavers have felled trees, they have influenced the structure of the woodland causing an opening-up of the canopy and a reduction in the vertical density, which is associated with greater ground cover of grasses and less leaf litter and more coarse woody debris.

6.2 Possible future effects of beavers at Knapdale

This section contains speculation based upon the main results and conclusions summarised above, as to the effects on trees of beavers in Knapdale, should they continue to occupy the area. Any future effects will be dependent upon their future numbers and distribution, which are currently unknown.

In general should an equivalent or increased number of beavers continue to live in the area of Knapdale, we would expect to see a steady progression of their influence by affecting trees in some of the areas around the occupied lochs, that they do not currently occupy. Although only 8.6% of trees around the beaver-occupied lochs have been affected by beavers this is predicted to progressively increase. Of the abundant species present only willow has been significantly depleted. As this depletion continues we would expect this to cause beavers to forage initially in other unused foraging areas to seek the willows, and subsequently to forage more on alternative less preferred species. So far, since the release of beavers they have tended to gnaw or fell slightly wider-stemmed trees in successive years, and this trend would be expected to continue until such time as significant replenishment of stems is provided by regrowth from previously browed trees. It is predicted that beavers would shift their lodges to allow them ready access to currently less exploited areas of the loch shores. Whilst beavers have the option of foraging further from the shores of the loch at Knapdale they have been reluctant as yet to do this, but may do so in future, although in many areas the unfavourable steep topography is likely to discourage them from foraging far from the water's edge. Their avoidance of areas of coniferous trees seems unlikely to change.

Given the slowness of regeneration both from the stumps formed by beavers and from seed of the woodland at Knapdale, then it is likely that changes in woodland community composition will result from the beavers' activity. The structure of riparian woodland at Knapdale in the future will be strongly influenced by the interaction between the growth of new shoots from beaver stumps and subsequent browsing of these shoots by deer and beaver (Jones *et al.* 2009). Results suggest that although re-sprouting was initially profuse, it may take longer than anticipated for it to generate regrown stems of sufficient size to be utilised by beavers.

Although the re-sprouting and growth rate of new shoots can offset any losses of stems due to beaver felling and gnawing (Jones *et al.* 2009), this appears to be a slow process and many of the re-sprouted shoots at Knapdale are susceptible to browsing by the deer populations. Overall 8.6% of trees had been affected by beavers in the area of the beaver-occupied lochs. In November 2013, approximately 26% of these had re-sprouted in some way and of these about 68% had a proportion of the re-sprouted shoots browsed by deer. In many cases the majority of the re-sprouted stems were browsed by deer (Figure 14). These processes are all tree-species specific. The re-sprouting is likely to be attractive to sika and roe deer which utilise more woody browse than red deer, although this species also browses woody shoots at certain times of year. The greater proportion of grasses that appear in the ground cover in response to beaver utilisation and opening up of the woodland habitat structure is likely to serve to attract red deer, which are 'grazing' rather than 'browsing' herbivores, to the loch-shore areas. It is not known whether the beaver-altered food resource is of sufficient magnitude to influence deer populations via reproductive performance, but it is likely to make the loch-shore vegetation more attractive to them and to result in changes in their distribution causing them to spend more time in these areas, potentially adding to any effects of beavers on the vegetation. In areas where beavers overlap with deer species, then deer management should be integrated with predicted effects of beavers on woodland, either by adjusting deer culling to prevent additive effects on the vegetation, or by considering means of constructively using the potentially attractive beaver-induced food resource to facilitate management by culling of the existing deer populations. The continued monitoring of re-sprouting and woodland structure should be an important component of any future work.

The greater use of *C. avellana* in the two latter years of this study, and heavy browsing of its re-sprouting shoots by deer suggest that this species may, like willow, ultimately be reduced in its abundance, and that the remaining trees will have a preponderance of smaller younger shoots, which would form less suitable habitats for epiphytic communities, than the trunks of larger trees (David Genney *pers comm*). The general reduction in older dead wood may ultimately have ecological effects in reducing the biodiversity and functioning of the decomposer food chain, although beaver activity was associated with an increase in the amounts of coarse woody debris on the woodland floor, whilst reducing the amount of leaf litter.

6.3 Using results obtained in Knapdale to predict impacts of beavers elsewhere

The extent to which trees were felled or gnawed by beavers, the extent to which they re-sprout following this, and the extent of browsing on the re-sprouted shoots by deer were all species-specific. Consequently, the likelihood of beavers colonising any other area of

Scotland or the UK, be this by assisted colonisation or more natural spread, the subsequent impact of beavers and the response or recovery of the trees is highly likely to be dependent upon the species present in the area. We have good information on the likely preference of beavers for particular tree species, and of the tree traits that determine their response to beaver browsing and their subsequent attractiveness to other herbivores, notably deer.

The landscape at Knapdale consists of fairly continuous forest, which has been exploited by beavers in a patchy manner. This similar pattern would be expected elsewhere, but should the landscape contain only patchily distributed woodlands, then beaver activity is expected to be focused on these patches where they comprise acceptable tree species.

The most preferred species is often considered to be *Populus tremula* but in the case of Knapdale, where *P. tremula* is absent, the willows are clearly the most preferred tree species. The high level of impact of beavers on the preferred species is likely to recur in the presence of beavers elsewhere. This is predicted to result in shifts in the composition of woodlands, leading to a younger age distribution of shoots (if the beaver-browsed species readily re-sprout, as most do), or a shift away from browsing intolerant species towards more browsing resilient species. If the most preferred species become depleted in abundance, then the beavers are predicted to switch to alternative tree species. The time needed for this process would depend on the abundance of the preferred species in the area colonised by beavers. A strong preference for a particular species, such as a species of *Salix*, is manifested as a greater degree of impact on that species. Despite expressing preferences for certain species, beavers appear also to be able to harvest and use large quantities of species that are not particularly preferred, such as *B. pubescens*. This means that they are also likely to be able to successfully colonise and use a wide range of different woodland communities. Given that Knapdale provides a wide range of choice of tree stem diameters and a wide range of sizes are affected by beavers, the preponderance of very small 2-6cm diameters among those felled or gnawed probably leads to the expectation that this size range would be the most affected, should beavers colonise elsewhere. Because of the decline in beaver activity with increasing distance from the water body, there is no reason to think that colonisation of other areas by beavers would lead to direct impacts by them on trees that are distant from water courses.

Because beavers are central place foragers, the location of the beaver lodge provides a long-acting constraint on their subsequent foraging, determining where each night's foraging activity begins and ends. An ability to predict the location of lodges would be a major step in prediction of their impacts.

Within the fairly short time of monitoring at Knapdale, beavers significantly affected the structure of the woodland. The activity of beavers and its impact in terms of removing or damaging trees is clearly associated with an opening of the canopy, reducing its cover and facilitating light reaching the ground level and affecting the ground vegetation. It also reduced the vertical density of the woody vegetation above 150cm, but did not affect the vertical density closer to the ground. These effects are to be expected to occur everywhere that beavers are present.

One of the major effects of beavers evident at Knapdale is the flooding of the area between Dubh Loch and Loch Coillie Bharr due to construction of a dam. The consequences of this for the woody and other vegetation is profound, and would be so at other sites, where only flood-tolerant trees would be expected to persist.

In summary, beavers are selective foragers that are likely to exert effects on woodland species composition, age structure and ecological functioning via their effects on their preferred species and on stems that are fairly small (2-6cm). Although their effects are likely to be focussed fairly closely on the riparian zone, within this area, they are flexible enough in their foraging strategy to also exploit both less preferred species that are abundant, and larger individual trees. Regeneration of the woodlands from the beaver-affected trees is dependent upon the tree species' propensity for re-sprouting, and is likely to depend upon the density of the deer species present. As well as affecting the regeneration from the beaver affected stumps, the deer are a likely influence on tree-regeneration from seed, and their population management should be considered as integral to the prediction of the effects of beavers in any areas of future beaver colonisation. Because of their effects on woodland structural openness, colonising beavers will have a significant impact on the woodland floor vegetation close to the water's edge where they forage. An important predictor of the future impact of beavers, in any area of colonisation, is where they choose to site their lodges, the basis for which remains largely unknown.

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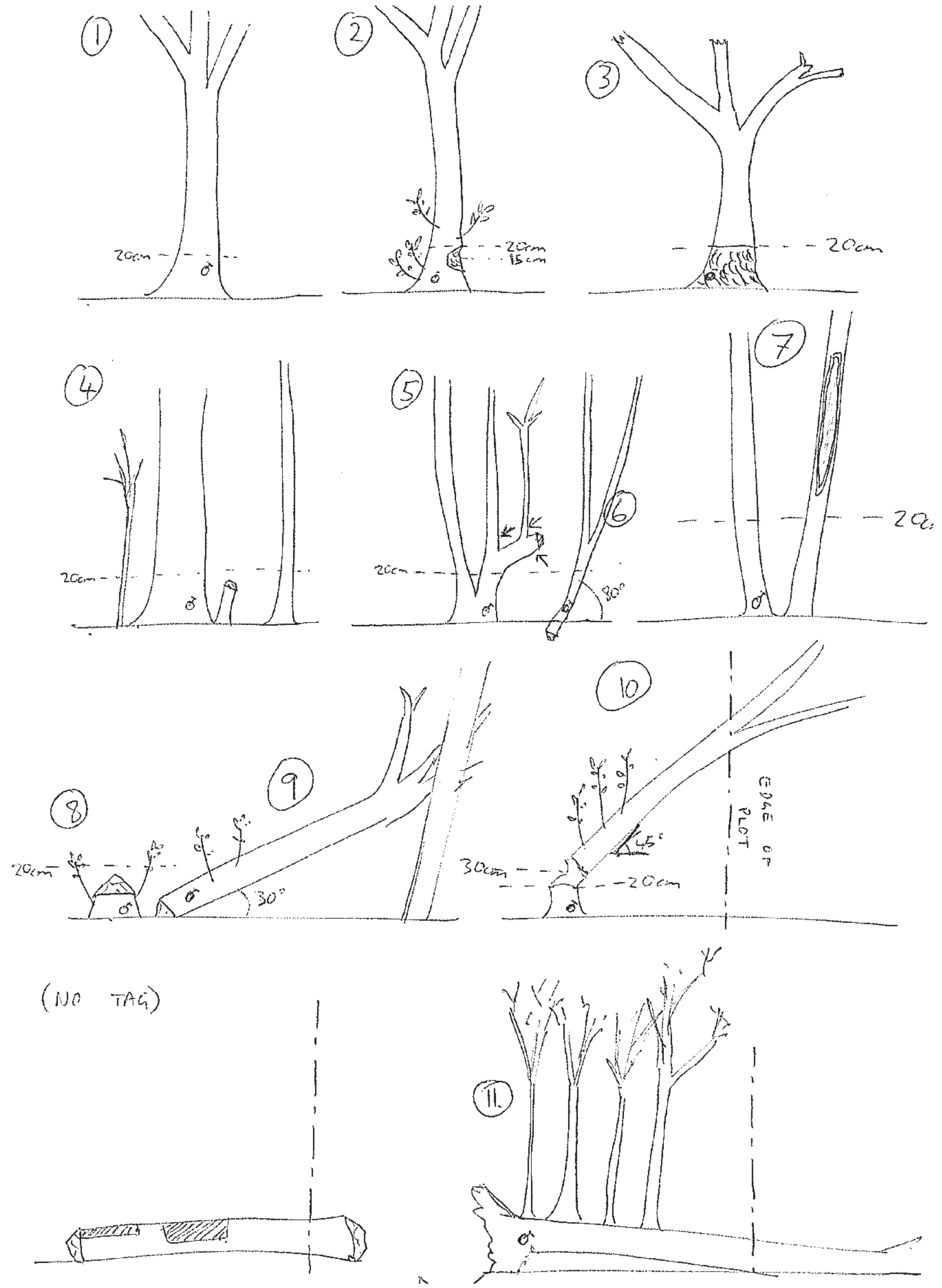
APPENDIX 1. REFERENCE ILLUSTRATIONS USED IN THE FIELD

Reference illustrations used in the field encompassing most tree, stump and log forms encountered with various types of beaver effect. Accompanying example data sheet with entries corresponding to numbered illustrations (Appendix 2).



APPENDIX 2. EXAMPLE FIELD RECORDING SHEET

Scottish Beaver Trial: Woodland Monitoring. C610460. Version 6. Loch________________________Transect____________Date__

Plot No.	Tag No.	Species or count	Squ	Diam. (20cm)	Status	Angle	Alive Y/N	bark rmvd	Height chopped	log length	low shoot	high shoot	max shoot	avge. shoot	Deer	Beav
	#[a]	CODE	1-10	cm	[b]	deg	Y/?/N	%[c]	cm	m[d]	count[e]	count[f]	cm	cm	0/1/2[g]	0/1/2[g]
1	1	SORAUC	1	15	Up		Y	-	-	-	-	-	-	-	-	-
1	2	BETPUB	1	10	BUp		Y	50	15	-	2	2	20	15	0	0
1	3	QUEPET	2	20	BUp		N	100	20	-	0	0	0	0	0	0
1	4	BETPUB	2	15	Up		Y	-	-	-	-	-	-	-	-	-
		"		3	Up		Y	-	-	-	-	-	-	-	-	-
		"		1	Up		Y	-	-	-	-	-	-	-	-	-
		"		2	Bstump		Y	100	15	-	0	0	0	0	0	0
1	5	SALIX	3	5	Up		Y	-	-	-	-	-	-	-	-	-
		"		8	Base											
		"		*5	Up		Y	-	-	-	-	-	-	-	-	-
		"		*3	Up		Y	-	-	-	-	-	-	-	-	-
		"		*6	Bstump		Y	100	30	-	0	0	0	0	0	0
1	6	SALIX	3	4	Blog	80	Y	0	-	3	0	0	0	0	0	0
1	7	SORAUC	5	4	Up		?	-	-	-	-	-	-	-	-	-
		"		4	Up		?	deer	-	-	-	-	-	-	-	-
1	8	ALNGLU	7	15	Bstump		Y	100	15	-	2	0	30	20	1	0
1	9	ALNGLU	7	15	Blog	30	Y	0	0	3	0	2	30	20	1	0
1	10	SORAUC	10	20	BP	45	Y	100	30	2.7	0	3	65	50	0	0
		BETPUB	10	25	Blog	0	?	20	1.9	-	-	-	-	-	-	-
1	11	FRAEXC	10	30	Nlog	0	Y	0	-	3.8	-	-	-	-	-	-
				*3	Up		Y	-	-	-	-	-	-	-	-	-
				*3	Up		Y	-	-	-	-	-	-	-	-	-
				*4	Up		Y	-	-	-	-	-	-	-	-	-
				*5	Up		Y	-	-	-	-	-	-	-	-	-

a: * indicates a level above a Base or Log; b: For stumps, logs & partially felled, indicate B (beaver) or N (natural) then Up=upright; St=stump; P=Pole; Log; c: % of circumference or % of log w/in plot, "deer" for old deer bark stripping; d: within plot boundaries; e: <30cm; f: >30cm; g: 0=none, 1=detectable, 2=significant;

APPENDIX 3. STATISTICAL METHODOLOGY

Using the general approach given in section 3.3.1 of the main report, the following statistical analyses were carried out using Genstat (VSN International 2011).

The use made of tree species in relation to their availability is important to the prediction of the impacts of beavers on the species in other circumstances. The selection of tree species may vary across the four years of the study and this was tested using a binomial Generalized Linear Mixed Model (GLMM) with a logit link function. It analysed the number of marked stems of each species newly felled or browsed by beavers during the preceding year, in relation to the number of un-browsed stems available at the start of that particular year. This analysis used data recorded in November of each year 2010-2013 inclusive, and was conducted at the plot level, treating plot as a random variable. The fixed effects assessed were Tree Species and Year and their interaction. A similar GLMM was used to analyse the proportion of the available basal area of each tree species at the start of any year,that was eaten by beavers in that year. This proportion was logit transformed prior to analysis:

Logit proportion = Log_{10} ((proportion + 0.001)/(1- (proportion – 0.001)))
The addition and subtraction of 0.001 from the numerator and denominator respectively precluded the probability of zero values.

In order to avoid large numbers of missing cells in the data owing to there being few tree species present in each plot, only the species present in each plot were included.

Beaver foraging at different distances from the water's edge was analysed using a GLMM, which used a binomial approach with a logit link function, to analyse the number of or newly eaten stems in each plot out of the total number of previously uneaten trees available in each particular year. The transect and plot within transect were entered as random variables and the fixed effects estimated were, sequentially, those of Year (2010-2013), Distance from water's edge (0m, 6m, 16m, 26m), whether the dominant tree species or species combination in the plot was 'preferred' (preferred or un-preferred), and all the possible interaction effects. The third order interaction term was not significant and was dropped from the model. Preferred communities were defined on the basis of their composition of species in relation to the degree of selection of number of stems and basal area expressed by beavers across the entire period of survey (Figure 6). Any plots dominated by or containing *Salix* as sub-dominant were considered to represent a preferred plot type, along with those dominated by birch either alone or in combination with the species that were neither preferred nor avoided in relation to their basal area namely *F. excelsior* and *S. aucuparia (Section 4.3.1 – below).* All other plots were considered to contain an un-preferred community; the communities present are listed in Appendix 4.

Any changes in the pattern of beaver foraging in relation to distance from their lodge were analysed by using a similar binomial GLMM analysis with a logit link function, of the number of stems showing signs of having been newly eaten, out of the total of previously un-eaten stems available in each plot. The fixed effects of Year (2010-2013), shortest distance to the plot from the beavers lodge (measured along the lake shore), whether the dominant tree species or species combination in the plot was 'preferred' (preferred or un-preferred), and all possible interactions of these explanatory variables were entered sequentially. The terms Lodge identity, transect and plot within transect were entered as random terms in the analysis.

The seasonal difference in beaver impacts on trees between summer and winter was quantified by recording changes in status to extant trees and comparing the proportion of trees having changed status (summed across the entire monitoring period) at the April versus the November monitoring events. The logit transformed proportion of trees changing status was analysed using fixed effects tree species and season and their interaction, whilst transect and plot within transect were treated as random variables.

Changes in the components of the ground cover measured in each November 2010 – 2013 described in section 3.2.3 were analysed using a Linear Mixed Model for each component of ground cover that considered the transect, plot within transect and sub-plot within plot as a random term, within which the fixed effects of observer, year, the beaver activity within the plots (Beavimp; the extent of beaver impact in each plot quantified as the proportion of the total number of trees in the plot, irrespective of species, that had been directly affected by beavers) and the Year x Beavimp interaction were considered sequentially. Where the interaction term was not statistically significant then the main effects of Year and Beavimp were assessed separately after inclusion of the observer term. The proportion of each component of the ground cover was logit transformed as above.

The Canopy cover expressed as the proportion of the ground area of each plot covered by a tree crown of greater than 2m height as assessed in November of each year 2010-2013 inclusive using an GLM which treated plot as random variable, and which sequentially assessed the fixed effects of Observer, Year (2010-2013) and the beaver activity on the trees in each plot ('Beavimp' see above), and the interaction of these two. The distance from the shore was explored by adding this term to the model.

The Vertical density of the vegetation represented by the proportion of the area of a white board that was invisible across the plots at the different heights 0–50cm, 50–100cm, 100–150cm and 150–200cm height, was assessed using an GLMM. The logit of the proportion (above) invisible at each height was analysed using plot as a random variable with of Observer, Year (2010-2013) and the beaver activity on the trees in each plot ('Beavimp'), entered sequentially with the interaction of these effects, plus the effect of distance from the loch shore as fixed effects.

The use of different stem diameters by beavers in different years was analysed treating the logarithm of the diameter of stems browsed in each plot in each year as the dependent variable, using a GLMM with plot as a random variable with Year (2010-2013) and species and their interaction as fixed effects.

The browsing by deer of re-sprouted stems that grew from stumps formed from previous beaver activity was analysed by an ordinal regression of the intensity of deer re-browsing (0,1,2) of stems on the stumps. This Generalized Linear Modelling approach entered plot as the first variable in the model and tested the effects of tree species, the number of re-sprouts per stem, and the average length of re-sprouts after accounting for all other statistically significant variables. The intensity of re-browsing on a particular stump was scored as no browsing (0), less than 50% of re-sprouts browsed (1) or more than 50% of re-sprouts browsed. Only data collected in the final sampling period in November 2013 was analysed in this way due to few data in the early years of the study which were only sufficient in *Salix*, *S aucuparia* and B. *pubescens*.

The proportion of trees affected by beavers in the 255, 10m diameter, circular plots in 87 blocks of three distributed around each of the four main beaver-occupied loch-systems, was logit transformed as above. It was analysed using a GLMM with block as a random variable and the effects of distance from loch (5m, 15m and 25m), loch identity (Lochan Buic, Creagh Mohr, Loch Coille-Bharr, Loch Linne) and the dominant species in each plot, as fixed effects. Dominant species was included after recoding minor species into an 'other species' category. Analysis of interactions was not possible due to uneven-ness in the distribution of species among lochs and with distances from loch shores.

All potentially subjective measurements but notably ground cover, canopy cover and vertical density, were conducted by one of two observers (D Sim or Ben Moore), and in order to correct for possible observer bias, the observer identity was entered first into analyses of these variables.

APPENDIX 4. DETAILS OF INDIVIDUAL MONITORING PLOTS

Numbers and date of establishment of each transect/plot and the permanent tag numbers, British National Grid reference, distance of plot from the water's edge, dominant woody species and presence or absence of previous beaver browsing, recorded in each plot in November 2010, 2011, 2012 and 2013.

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species%	Beaver sign# 2010	2011	2012	2013
1. Dubh N	11/09	211	NR 78494 90138	0 m	BETPUB	Y	Y	Y	Y
		212	NR 78500 90140	6 m	BETPUB	Y	Y	Y	Y
		213	NR 78509 90139	16 m	BETPUB	N	N	N	N
		214	NR 78512 90162	26 m	BETPUB/SORAUC	N	N	Y	Y
2. Linne SW	11/09	3015	NR 79461 90798	0 m	BETPUB	Y	Y	Y	Y
		3016	NR 79457 90799	6 m	ALNGLU/BETPUB	Y	Y	Y	Y
		217	NR 79450 90808	18 m	ALNGLU/BETPUB	Y	Y	Y	Y
		218	NR 79445 90814	26 m	BETPUB	N	Y	Y	Y
3. Coille-Bharr SE	11/09	219	NR 77900 89380	0 m	BETPUB/ALNGLU	N	N	N	N
		220	NR 77899 89375	6 m	BETPUB	N	N	N	N
		221	NR 77892 89369	16 m	BETPUB	N	N	N	N
		222	NR 77885 89361	26 m	BETPUB	N	N	N	N
4. Creagmhor S	11/09	223	NR 80271 90836	0 m	BETPUB	N	N	N	N
		224	NR 80272 90834	6 m	BETPUB	Y	Y	Y	Y
		225	NR 80265 90823	16 m	BETPUB	N	N	N	N
		226	NR 80258 90815	26 m	BETPUB	N	N	N	N
5. Fidhle N	11/09	227	NR 80014 91133	0 m	BETPUB	N	N	N	N
		228	NR 80018 91141	6 m	BETPUB	N	N	N	N
		229	NR 80021 91149	16 m	BETPUB	N	N	N	N
		230	NR 80027 91157	26 m	BETPUB	N	N	N	N
6. Dubh S	11/09	231	NR 78360 89946	0 m	BETPUB	N	N	N	N
		232	NR 78359 89946	6 m	Salix/BETPUB	-	-[a]	-[a]	-[a]
		233	NR 78353 89929	16 m	Salix/BETPUB	Y	Y	Y	Y
		234	NR 78355 89924	26 m	Salix/BETPUB	Y	Y	Y	Y
7. Linne SW	11/09	235	NR 79588 91016	0 m	BETPUB/ALNGLU	Y	Y	Y	Y
		236	NR 79576 91020	6 m	Salix/BETPUB	Y	Y	Y	Y
		237	NR 79575 91022	16 m	Salix/BETPUB	Y	Y	Y	Y
		238	NR 79592 91033	26 m	BETPUB	N	N	N	N
8. Linne W	11/09	239	NR 79665 91103	0 m	CORAVE	Y	Y	Y	Y
		240	NR 79665 91097	6 m	CORAVE	N	Y	Y	Y
		241	NR 79645 91126	16 m	CORAVE	N	N	N	N
		242	NR 79640 91118	26 m	CORAVE	N	Y	Y	Y
9. Coille-Bharr SSE	11/09	243	NR 77851 89397	0 m	ALNGLU/BETPUB	N	Y	Y	Y
		244	NR 77846 89391	6 m	QUEPET	N	N	N	N
		245	NR 77843 89387	16 m	BETPUB	N	N	N	Y
		246	NR 77823 89384	26 m	BETPUB	N	N	N	N
10. Creagmhor E	11/09	247	NR 80471 91047	0 m	BETPUB/FRAEXC	Y	Y	Y	Y
		248	NR 80472 91039	6 m	BETPUB	Y	Y	Y	Y
		249	NR 80475 91031	16 m	BETPUB	Y	Y	Y	Y

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water[*]	Dominant species[%]	Beaver sign[#] 2010	2011	2012	2013
		250	NR 80484 91026	26 m	BETPUB	N	N	N	N
11. Coille-Bharr E	11/09	251	NR 78195 89908	0 m	ALNGLU/SORAUC	N	N	N	N
		252	NR 78202 89905	10 m	BETPUB/SORAUC	N	N	N	N
		253	NR 78209 89899	20 m	BETPUB/SORAUC	N	N	N	N
12. Creagmhor N	11/09	254	NR 80555 91267	0 m	BETPUB	N	N	N	N
		255	NR 80561 91273	6 m	BETPUB	Y	Y	Y	Y
		256	NR 80567 91281	16 m	ALNGLU/BETPUB	Y	Y	Y	Y
		257	NR 80574 91285	26 m	BETPUB	N	N	N	N
13. Creagmhor NE	11/09	258	NR 80492 91072	0 m	BETPUB/SORAUC	Y	Y	Y	Y
		259	NR 80493 91073	6 m	BETPUB	N	N	N	N
		260	NR 80501 91064	16 m	BETPUB	N	N	N	N
		261	NR 80510 91058	26 m	BETPUB	N	N[d]	N[d]	N[d]
14. Linne N	11/09	262	NR 80026 91434	0 m	ALNGLU	N	N	N	Y
		263	NR 80029 91439	6 m	BETPUB	N	N	N	N
		264	NR 80037 91451	16 m	ALNGLU/BETPUB	N	N	N	N
		265	NR 80043 91459	26 m	BETPUB	N	N	N	N
15. Linne SE	11/09	269	NR 79466 90614	0 m	ALNGLU/BETPUB	Y	Y	Y	Y
		270	NR 79463 90611	6 m	BETPUB	Y	Y	Y	Y
16. Linne SE	11/09	271	NR 79503 90635	0 m	BETPUB	Y	Y	Y	Y
		272	NR 79506 90626	6 m	BETPUB	Y	Y	Y	Y
		273	NR 79512 90619	16 m	BETPUB	Y	Y	Y	Y
		266	NR 79518 90614	26 m	BETPUB	Y	Y	Y	Y
17. Coille-Bharr N	11/09	276	NR 78867 90853	0 m	ALNGLU	N	N	N	N
		277	NR 78873 90863	6 m	ALNGLU	N	N	N	N
		278	NR 78877 90863	16 m	ALNGLU/Salix	N	N	N	N
		279	NR 78882 90873	26 m	BETPUB	N	N	N	N
18. Lilly NW	4/10	201	NR 78851 88572	0 m	ALNGLU/Salix	N	Y	Y	Y
		202	NR 78849 88578	6 m	ALNGLU	N	Y	Y	Y
		203	NR 78844 88583	16 m	BETPUB	N	N	N	N
19. Linne NE	4/10	204	NR 79994 91278	0 m	BETPUB	Y	Y	Y	Y
		205	NR 79998 91276	6 m	BETPUB	Y	Y	Y	Y
		206	NR 80007 91276	16 m	BETPUB	N	N	N	N
		207	NR 80017 91276	26 m	BETPUB	N	N	N	N
20. Lilly N End	4/10	280	NR 78965 88611	0 m	ALNGLU	N	N	N	N
		281	NR 78968 88615	6 m	ALNGLU/BETPUB	N	Y	Y	Y
		282	NR 78975 88619	16 m	ALNGLU	N	N	N	N
		283	NR 78986 88623	26 m	BETPUB	N	N	N	N
21. Linne NW	4/10	284	NR 79879 91366	0 m	ALNGLU/CORAVE	Y	Y	Y	Y
		285	NR 79877 91369	6 m	-	-	-[e]	-[e]	-[e]
		286	NR 79870 91374	16 m	CORAVE	N	N	N	N
		287	NR 79864 91381	26 m	CORAVE	N	N	N	N
22. Lilly SE	4/10	288	NR 78879 88477	0 m	Salix	N	N	N	N
		289	NR 78884 88473	6 m	ALNGLU	N	N	N	N
		290	NR 78881 88462	16 m	-	-	-[e]	-[e]	-[e]

Transect and Loch	Date	Plot tag	Grid reference	Dist. to water*	Dominant species%	Beaver sign# 2010	2011	2012	2013
		291	NR 78885 88451	26 m	BETPUB	N	N	N	N
23. Lilly SSE	4/10	292	NR 78798 88455	0 m	ALNGLU/Salix	N	N	N	N
		293	NR 78798 88450	6 m	BETPUB	N	N	N	N
		294	NR 78803 88441	16 m	BETPUB	N	N	N	N
		295	NR 78809 88430	26 m	BETPUB	N	N	N	N
24. Lochan Buic SW	4/10	296	NR 78747 88723	0 m	BETPUB/Salix	N	Y	Y	Y
		297	NR 78738 88715	6 m	BETPUB	N	N	Y	Y
		298	NR 78730 88719	16 m	BETPUB	N	N	Y	Y
		299	NR 78726 88719	26 m	BETPUB	N	N	N	N
25. Lochan Buic NE	4/10	2101	NR 79040 88975	0 m	BETPUB/ALNGLU/ CORAVE	Y	Y	Y	Y
		2102	NR 79054 88964	6 m	ALNGLU/BETPUB	-	-[c]	-[c]	-[c]
		2103	NR 79067 88965	16 m	CORAVE	N	N	Y	Y
		2104	NR 79063 88977	26 m	BETPUB/CORAVE	N	N	N	N
26. Linne E	4/10	274	NR 79699 90798	0 m	BETPUB	Y	Y	Y	Y
		275	NR 79705 90794	6 m	BETPUB	Y	Y	Y	Y
		300	NR 79710 90785	16 m	BETPUB	Y	Y	Y	Y
		2105	NR 79718 90780	26 m	BETPUB	Y	Y	Y	Y
27. Dubh W	4/10	2705	NR 78346 90062	0 m	BETPUB/SORAUC	-	-[b]	-[b]	-[b]
28. Dubh SW	4/10	2706	NR 78338 90049	0 m	BETPUB/SORAUC	Y	Y	Y	Y
29. Coille Bharr NE	4/10	2894	NR 78665 90445	0 m	ALNGLU/CORAVE	N	Y	Y	Y
		2895	NR 78670 90441	6 m	ALNGLU	N	N	N	N
		2896	NR 78675 90437	16 m	ALNGLU/SORAUC	N	N	N	N
		2897	NR 78703 90399	26 m	BETPUB/SORAUC	N	N	N	N
30. Lochan Buic E	4/10	2921	NR 78914 88790	0 m	BETPUB/Salix	N	N	Y	Y
		2922	NR 78915 88785	6 m	BETPUB/CORAVE	N	N	N	N
31. Lochan Buic W.	11/10	3221	NR 78832 88864	0 m	ANLGLU/BETPUB	N	Y	Y	Y
		3222	NR 78828 88863	6 m	BETPUB	N	Y	Y	Y
		3223	NR 78817 88862	16 m	BETPUB	N	N	N	N

Footnote to Appendix 4: * From nearest edge to water. ‡ Species codes are listed in table 3. # Beaver sign includes any gnawing or felling of woody vegetation up until Nov 2010, Nov 2011, Nov 2012 or Nov 2013 respectively.
Notes: a – Plot now flooded due to beaver activity; tree measurements no longer possible but ground vegetation measurement still possible, b – Plot now flooded due to beaver activity neither tree measurements nor ground vegetation measurement possible, c - Track constructed through plot and neither tree nor ground cover measurements could subsequently be measured, d – Track constructed through plot and ground cover measurements could no longer be taken although trees could still be measured, e - No trees in plot.

APPENDIX 5. PHOTOGRAPHS FROM FIXED POINTS SHOWING CHANGES IN VERTICAL VEGETATION STRUCTURE SINCE INTRODUCTION OF BEAVERS - APPENDIX 5A (A-D) AND DIFFERENCES BETWEEN SUMMER AND WINTER APPENDIX 5B (E-H)

Appendix 5A: Photographs showing vertical vegetation changes since introduction of beavers in plots a) 211 b) 234 c) 300 and d) 272

November 2009

November 2010

November 2011

November 2012

Figure 5a. Plot 211

November 2009 **November 2010**

November 2011 **November 2013**

Figure b. Plot 234

November 2010

November 2011

November 2012

November 2013

Figure c. Plot 300

November 2009

November 2010

November 2011

November 2012

Figure d. Plot 272

Appendix 5B: Photographs showing differences in horizontal vegetation between summer and winter e) 251 f) 256 g) 285 and h) 2895 changes.


July 2012 **November 2012**

Figure e. Plot 251


July 2012 **November 2012**

Figure f. Plot 256

July 2012 **November 2012**

Figure g. Plot 285

July 2012 **November 2012**

Figure h. Plot 2895

APPENDIX 6. RESULTS – SUPPLEMENTARY TABLE. GROUND COVER ESTIMATES

Appendix 6a. Mean percent cover of ten categories estimated in November 2009 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot.

Transect; plot	Percent Cover: Water	Rock	Bare ground	grass/ sedge/ rush	leaf litter	woody litter	ferns	Bryo-phytes	dwarf shrubs	Herb	Seed-lings (count)
1; 0m	2.5	0	0	2.5	70	5	2.5	0	0	0	7.5
1; 6m	0	0	0	0	90	0	15	15	0	0	0
1; 16m	0	0	5	0	30	0	42.5	25	0	0	0
1; 26m	0	0	20	0	30	2.5	40	45	0	0	0
2; 0m	22.5	0	2.5	32.5	5	2.5	2.5	20	20	0	0
2; 6m	5	0	7.5	5	15	12.5	22.5	60	0	0	0.5
2; 18m	10	0	7.5	5	40	7.5	7.5	70	0	0	0
2; 26m	0	0	2.5	5	35	7.5	10	92.5	0	0	0
3; 0m	0	0	0	70	15	0	20	15	0	0	0.5
3; 6m	0	0	0	45	20	5	5	17.5	10	0	0.5
3; 16m	0	0	0	50	15	0	17.5	15	5	0	0.5
3; 26m	0	0	0	5	30	5	5	65	2.5	0	0.5
4; 0m	30	0	0	85	2.5	2.5	0	15	7.5	0	0.5
4; 6m	0	0	0	75	0	2.5	0	15	5	0	2.5
4; 16m	10	0	2.5	5	25	5	0	87.5	2.5	0	0
4; 26m	5	0	2.5	17.5	30	17.5	0	70	0	0	0
5; 0m	0	0	0	100	2.5	2.5	5	5	0	17.5	0
5; 6m	12.5	0	0	90	2.5	2.5	25	0	0	0	0
5; 16m	2.5	0	2.5	12.5	60	2.5	37.5	7.5	0	0.5	1
5; 26m	25	0	2.5	50	22.5	2.5	5	0	0	30.5	0
6; 0m	0	0	0	30	7.5	10	2.5	70	0	0	0
6; 6m	0	0	0	5	25	15	2.5	100	0	7.5	0.5
6; 16m	2.5	0	2.5	25	55	5	2.5	40	0	0	1
6; 26m	5	0	7.5	30	55	5	10	35	0	0	1.5
7; 0m	0	0	0	0	20	12.5	60	17.5	22.5	0	0
7; 7m	0	2.5	0	15	30	12.5	20	40	2.5	0	1
7; 16m	0	17.5	5	0	55	2.5	7.5	15	37.5	0	0
7; 26m	0	7.5	0	0	25	12.5	42.5	30	20	20	1
8; 0m	0	0	2.5	60	65	2.5	0	15	0	2.5	0.5
8; 6m	0	2.5	2.5	30	85	2.5	5	5	0	2.5	0
8; 16m	0	0	2.5	30	80	5	2.5	5	0	5	0
8; 26m	2.5	2.5	5	10	62.5	7.5	5	32.5	0	5	0.5
9; 0m	10	0	37.5	35	10	2.5	2.5	22.5	2.5	5	0
9; 6m	0	0	17.5	55	15	20	5	7.5	2.5	0	0
9; 16m	10	0	15	7.5	50	2.5	10	20	0	5	0
9; 26m	0	0	0	7.5	75	5	5	37.5	2.5	2.5	0
10; 0m	2.5	0	20	7.5	37.5	15	5	20	0	2.5	1.5
10; 6m	0	0	5	50	40	7.5	17.5	30	2.5	2.5	0
10; 16m	0	0	2.5	45	27.5	5	12.5	30	0	0	0.5
10; 26m	2.5	0	7.5	60	22.5	0	12.5	10	2.5	2.5	0
11; 0m	5	25	0	27.5	10	0	5	62.5	15	0	0.5
11; 10m	0	0	0	0	12.5	2.5	52.5	5	50	0	1
11; 20m	0	0	0	25	32.5	0	5	20	32.5	2.5	3.5
12; 0m	55	0	5	75	5	2.5	0	2.5	0	5	0

12; 6m	20	0	2.5	77.5	0	5	5	15	0	5	0
12; 16m	45	0	22.5	10	10	2.5	37.5	5	2.5	0	0
12; 26m	10	0	0	47.5	2.5	0	37.5	2.5	20	0	1
13; 0m	0	0	2.5	55	17.5	2.5	2.5	40	12.5	2.5	0.5
13; 6m	0	0	0	70	12.5	2.5	2.5	22.5	50	0	1.5
13; 16m	0	0	0	5	15	5	55	50	0	0	0.5
13; 26m	0	0	0	17.5	67.5	15	2.5	42.5	0	5	1
14; 0m	2.5	7.5	35	55	55	5	10	20	0	2.5	0
14; 6m	0	17.5	0	17.5	50	5	50	20	2.5	2.5	0
14; 16m	2.5	0	27.5	32.5	37.5	5	40	2.5	0	2.5	0
14; 26m	0	0	0	85	57.5	0	5	17.5	5	0	0
15; 0m	17.5	0	57.5	40	30	5	0	15	2.5	0	2
15; 6m	0	0	2.5	30	42.5	17.5	5	32.5	2.5	0	0
16; 0m	0	0	0	52.5	15	5	5	70	27.5	0	0
16; 6m	0	0	0	5	10	2.5	90	15	2.5	0	0
16; 16m	0	0	0	60	12.5	2.5	37.5	10	2.5	0	0
16; 26m	0	0	0	17.5	32.5	10	12.5	55	0	0	0
17; 0m	65	0	17.5	35	7.5	0	2.5	0	0	5	0
17; 6m	55	0	5	85	5	0	5	2.5	2.5	5	0
17; 16m	47.5	0	17.5	42.5	20	5	7.5	5	0	5	0
17; 26m	0	0	0	25	52.5	15	7.5	25	2.5	2.5	0.5

Appendix 6b. Mean percent ground cover of ten categories estimated in November 2010 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot at plot establishment.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
1; 0m	65	0	20	0	25	0	7.5	15	0	0	0
1; 6m	12.5	0	5	32.5	40	1.25	10	60	10	0	0
1; 16m	0	0	0	0	60	1.25	40	60	1.25	0	0
1; 26m	0	0	2.5	0	65	0	32.5	90	0	1.25	0
2; 0m	0	0	2.5	50	35	26.25	1.25	30	25	0	0
2; 6m	10	0	10	3.75	45	15	2.5	42.5	1.25	3.75	0
2; 18m	0	0	5	5	65	8.75	12.5	85	0	0	0
2; 26m	1.25	0	7.5	7.5	65	3.75	10	90	0	0	0
3; 0m	0	0	0	70	32.5	2.5	3.75	11.25	10	2.5	0
3; 6m	0	0	0	65	17.5	6.25	6.25	27.5	1.25	2.5	0,5
3; 16m	0	0	0	55	65	2.5	3.75	5	2.5	2.5	1
3; 26m	1.25	0	0	30	70	12.5	6.25	27.5	2.5	2.5	0
4; 0m	5	0	0	75	7.5	1.25	0	26.25	6.25	0	0
4; 6m	2.5	0	5	87.5	10	2.5	0	10	0	1.25	0
4; 16m	1.25	0	1.25	5	27.5	12.5	1.25	85	2.5	0	0
4; 26m	1.25	0	0	30	42.5	12.5	1.25	55	0	0	0
5; 0m	0	0	0	97.5	15	2.5	2.5	2.5	30	1.25	0
5; 6m	1.25	0	5	72.5	30	0	1.25	17.5	0	1.25	0
5; 16m	0	0	0	45	45	1.25	7.5	45	7.5	1.25	0
5; 26m	0	0	0	50	30	1.25	1.25	13.75	36.25	2.5	0
6; 0m	100	0	0	25	2.5	2.5	0	2.5	0	0	0
6; 6m	100	0	5	32.5	2.5	2.5	0	3.75	0	0	0
6; 16m	2.5	0	5	47.5	7.5	1.25	1.25	50	0	0	2,5
6; 26m	10	0	37.5	25	35	8.75	3.75	45	1.25	2.5	0
7; 0m	1.25	2.5	2.5	2.5	40	3.75	57.5	20	17.5	2.5	0
7; 7m	0	2.5	1.25	1.25	50	17.5	37.5	27.5	13.75	2.5	0
7; 16m	0	10	1.25	1.25	47.5	2.5	3.75	17.5	42.5	2.5	0
7; 26m	0	10	0	0	45	1.25	26.25	37.5	50	1.25	0
8; 0m	0	0	1.25	55	65	2.5	0	3.75	1.25	2.5	0
8; 6m	0	0	1.25	20	75	3.75	3.75	6.25	0	2.5	0
8; 16m	0	0	1.25	17.5	80	2.5	3.75	8.75	0	2.5	0
8; 26m	0	1.25	1.25	17.5	67.5	2.5	2.5	15	0	2.5	0
9; 0m	27.5	0	0	60	35	0	0	6.25	0	37.5	0
9; 6m	0	0	2.5	77.5	52.5	2.5	0	2.5	1.25	3.75	0
9; 16m	2.5	0	1.25	20	70	3.75	5	42.5	2.5	2.5	0
9; 26m	0	0	1.25	6.25	80	12.5	6.25	35	2.5	3.75	0
10; 0m	2.5	0	2.5	55	25	3.75	7.5	42.5	1.25	0	0
10; 6m	0	0	2.5	25	40	5	22.5	65	2.5	7.5	0,5
10; 16m	0	0	5	60	35	3.75	1.25	32.5	2.5	1.25	0
10; 26m	2.5	0	2.5	30	37.5	1.25	11.25	47.5	0	30	0
11; 0m	25	0	0	45	27.5	0	17.5	32.5	10	0	0
11; 10m	0	0	0	26.25	12.5	3.75	21.25	55	6.25	0	0
11; 20m	0	0	0	15	17.5	7.5	1.25	80	22.5	0	0
12; 0m	12.5	0	3.75	60	3.75	2.5	0	20	0	3.75	0
12; 6m	2.5	0	2.5	50	2.5	2.5	26.25	27.5	0	2.5	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
12; 16m	25	0	1.25	10	37.5	2.5	12.5	45	2.5	6.25	0
12; 26m	0	0	1.25	40	2.5	1.25	11.25	10	33.75	2.5	1
13; 0m	0	0	2.5	40	47.5	3.75	5	32.5	17.5	2.5	0
13; 6m	0	0	0	42.5	42.5	3.75	1.25	15	47.5	1.25	1,5
13; 16m	0	0	0	2.5	75	7.5	17.5	30	1.25	1.25	0,5
13; 26m	0	0	1.25	20	75	2.5	20	37.5	2.5	2.5	0
14; 0m	0	7.5	2.5	85	17.5	15	6.25	30	0	2.5	0
14; 6m	0	5	0	87.5	7.5	3.75	20	12.5	0	2.5	0
14; 16m	0	0	2.5	67.5	32.5	1.25	25	2.5	0	5	0
14; 26m	1.25	0	2.5	97.5	35	3.75	5	5	0	6.25	0
15; 0m	18.75	0	1.25	45	20	1.25	0	47.5	1.25	0	0
15; 6m	5	0	0	60	20	8.75	2.5	20	1.25	1.25	0
16; 0m	0	0	1.25	37.5	40	11.25	6.25	18.75	17.5	1.25	0
16; 6m	0	0	0	27.5	22.5	2.5	40	37.5	17.5	1.25	0
16; 16m	0	0	0	60	15	6.25	12.5	5	0	1.25	0
16; 26m	0	0	0	32.5	35	3.75	12.5	55	0	1.25	0
17; 0m	11.25	0	2.5	67.5	42.5	1.25	1.25	2.5	2.5	2.5	8,5
17; 6m	15	0	1.25	65	27.5	0	3.75	6.25	1.25	2.5	5,5
17; 16m	25	0	15	50	47.5	3.75	2.5	3.75	1.25	3.75	1,5
17; 26m	0	0	0	17.5	72.5	2.5	8.75	20	1.25	2.5	1
18; 0m	85	0	10	35	20	3.75	0	12.5	15	1.25	0
18; 6m	0	0	0	77.5	40	1.25	1.25	32.5	0	2.5	0
18; 16m	5	0	35	17.5	50	0	7.5	35	1.25	22.5	0
19; 0m	0	0	2.5	42.5	12.5	3.75	47.5	12.5	0	0	0
19; 6m	0	0	0	80	15	17.5	2.5	16.25	2.5	0	0
19; 16m	0	0	0	60	45	1.25	10	40	12.5	0	2,5
19; 26m	0	7.5	0	7.5	70	0	10	92.5	45	0	0
20; 0m	100	0	0	65	2.5	0	0	0	0	0	0
20; 6m	75	0	5	47.5	20	0	0	0	0	5	0
20; 16m	5	0	2.5	87.5	40	0	0	15	0	6.25	0
20; 26m	0	0	0	40	50	27.5	1.25	55	0	0	0
21; 0m	2.5	2.5	5	60	40	1.25	7.5	22.5	5	2.5	0
21; 6m	0	0	10	17.5	7.5	0	70	0	0	0	0
21; 16m	0	0	0	37.5	17.5	3.75	50	40	0	2.5	0
21; 26m	0	0	35	15	65	0	35	12.5	0	1.25	0
22; 0m	100	0	0	40	70	2.5	0	0	0	0	0
22; 6m	7.5	0	1.25	72.5	62.5	5	0	5	0	1.25	0
22; 16m	0	0	0	92.5	17.5	0	1.25	7.5	0	3.75	0
22; 26m	12.5	0	5	37.5	45	2.5	1.25	21.25	0	21.25	0
23; 0m	100	0	0	67.5	25	0	0	1.25	0	0	0
23; 7m	37.5	0	0	75	37.5	1.25	0	7.5	0	0	0
23; 16m	0	0	1.25	2.5	75	3.75	2.5	75	0	0	0
23; 26m	0	0	0	20	62.5	6.25	2.5	67.5	0	0	0
24; 0m	2.5	0	2.5	15	10	0	0	92.5	2.5	0	0
24; 6m	0	0	0	65	22.5	1.25	0	32.5	0	0	0
24; 16m	0	0	0	16.25	55	1.25	0	80	0	0	0
24; 26m	0	0	45	7.5	65	5	2.5	45	0	1.25	0
25; 0m	0	10	15	22.5	55	6.25	1.25	35	1.25	1.25	0
25; 6m	0	0	0	0	0	0	0	0	0	0	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
25; 16m	0	0	0	55	50	0	10	45	1.25	1.25	0
25; 26m	0	0	0	65	35	3.75	12.5	22.5	2.5	2.5	0
26; 0m	17.5	0	2.5	25	10	7.5	55	20	1.25	0	0
26; 6m	0	0	0	10	25	7.5	17.5	82.5	2.5	0	0
26; 16m	0	0	2.5	2.5	45	10	7.5	70	16.25	0	0
26; 26m	0	0	0	0	55	22.5	2.5	92.5	0	0	0
27; 0m	100	0	0	0	0	0	0	0	0	0	0
28; 0m	45	0	35	1.25	20	1.25	15	12.5	5	1.25	0
29; 0m	0	2.5	0	25	60	2.5	5	55	2.5	2.5	2
29; 6m	0	0	0	60	40	2.5	17.5	20	0	5	1,5
29; 16m	0	0	0	7.5	20	2.5	35	35	2.5	25	0
29; 26m	17.5	0	7.5	7.5	45	0	25	60	2.5	15	0
30; 0m	2.5	0	25	26.25	30	3.75	15	37.5	1.25	1.25	0
30; 6m	0	0	0	32.5	25	25	1.25	55	1.25	5	0
31; 0m	0	0	0	65	22.5	2.5	17.5	5	1.25	2.5	0
31; 6m	0	0	0	27.5	37.5	2.5	2.5	37.5	0	0	0,5
31; 0m	0	0	2.5	1.25	47.5	3.75	13.75	62.5	2.5	0	0

Appendix 6c. Mean percent ground cover of ten categories estimated in November 2011 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
1; 0m	97.5	0	0	0	0	0	0	2.5	0	0	0
1; 6m	25	0	0	5	17.5	5	7.5	45	5	2.5	0
1; 16m	0	0	0	0	45	5	27.5	80	0	1.275	0
1; 26m	0	0	0	0	37.5	10	17.5	90	0	2.5	0
2; 0m	2.5	0	5	45	22.5	7.5	1.275	40	25	0	0
2; 6m	5	0	5	27.5	22.5	20	2.5	55	0	5	0
2; 18m	0	0	5	17.5	22.5	20	2.5	85	0	1.25	0
2; 26m	2.5	0	5	27.5	40	35	5	80	0	1.25	0
3; 0m	0	0	0	57.5	30	6.25	2.5	35	5	1.25	0
3; 6m	0	0	0	47.5	12.5	3.75	3.75	70	0	0	0
3; 16m	0	0	0	42.5	27.5	7.5	3.75	70	0	1.25	0
3; 26m	0	0	0	47.5	35	12.5	2.75	30	0	1.25	0
4; 0m	5	0	0	65	3.75	1.25	0	40	1.25	0	0
4; 6m	1.25	0	2.5	85	3.75	2.5	0	30	1.25	2.5	0
4; 16m	0	0	0	3.75	17.5	22.5	1.25	92.5	0	0	0
4; 26m	0	0	1.25	20	20	20	1.25	92.5	0	0	0
5; 0m	0	0	0	92.5	2.5	1.25	2.5	15	25	0	0
5; 6m	1.25	0	2.5	72.5	5	3.75	5	32.5	0	0	0
5; 16m	0	0	0	45	15	5	7.5	65	3.75	1.25	0
5; 26m	0	0	2.5	47.5	10	15	2.5	52.5	12.5	3.75	0
6; 0m	100	0	0	77.5	0	0	0	0	0	0	0
6; 6m	100	0	0	42.5	2.5	17.5	0	0	0	0	0
6; 16m	87.5	0	0	40	0	7.5	0	7.5	0	0	0
6; 26m	27.5	0	17.5	32.5	3.75	12.5	1.25	30	0	1.25	0
7; 0m	0	0	2.5	6.25	17.5	5	40	80	7.5	2.5	0
7; 7m	0	2.5	2.5	2.5	50	25	10	65	5	1.25	0
7; 16m	0	7.5	0	0	42.5	3.75	2.5	72.5	37.5	1.25	0
7; 26m	0	17.5	0	0	27.5	2.5	20	55	40	0	0
8; 0m	0	0	2.5	75	30	0	0	25	0	0	0
8; 6m	0	0	22.5	40	50	1.25	1.25	31.25	0	5	0
8; 16m	0	0	0	47.5	45	5	1.25	22.5	0	3.75	0
8; 26m	0	2.5	5	45	40	2.5	3.75	37.5	0	5	0
9; 0m	2.5	0	7.5	62.5	10	5	0	31.25	0	7.5	0
9; 6m	0	0	5	97.5	50	1.25	0	11.25	0	3.75	0
9; 16m	2.5	0	2.5	40	12.5	2.5	1.25	72.5	0	0	0
9; 26m	0	0	0	8.75	30	20	3.75	97.5	0	1.25	0
10; 0m	0	0	12.5	60	7.5	5	2.5	60	0	1.25	0
10; 6m	0	0	0	62.5	15	2.5	8.75	37.5	0	12.5	0
10; 16m	0	0	5	75	7.5	0	2.5	47.5	0	3.75	0
10; 26m	0	0	2.5	35	10	2.5	3.75	40	0	10	0
11; 0m *	10	0	0	20	5	5	0	90	0	0	0
11; 10m	0	0	0	22.5	22.5	5	6.25	65	2.5	0	0
11; 20m	0	0	0	32.5	40	7.5	1.25	85	12.5	0	0
12; 0m	5	0	15	75	1.25	0	0	7.5	0	10	0
12; 6m	1.25	0	2.5	80	5	3.75	12.5	82.5	0	3.75	0
12; 16m	10	0	5	32.5	10	2.5	15	50	5	2.5	0

Transect; plot	Percent Cover										
	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
12; 26m	2.5	0	0	52.5	5	0	10	40	25	2.5	0
13; 0m	0	0	0	55	5	8.75	3.75	75	7.5	3.75	0
13; 6m	0	0	0	72.5	5	7.5	3.75	45	36.25	0	1.5
13; 16m	0	0	0	17.5	25	20	5	80	1.25	1.25	0
13; 26m	*	*	*	*	*	*	*	*	*	*	*
14; 0m	2.5	2.5	2.5	92.5	5	0	2.5	7.5	0	2.5	0
14; 6m	5	0	92.5	3.75	1.25	12.5	15	0	2.5	0	0
14; 16m	0	0	2.5	87.5	10	1.25	7.5	8.75	0	7.5	0
14; 26m	0	0	0	92.5	7.5	2.5	1.25	25	0	2.5	0
15; 0m	0	0	5	50	2.5	2.5	0	55	0	0	0
15; 6m	0	0	2.5	70	5	12.5	0	17.5	0	0	0
16; 0m	0	0	2.5	52.5	5	3.75	5	87.5	11.25	0	0
16; 6m	0	0	2.5	12.5	12.5	10	21.25	60	5	0	0
16; 16m	0	0	0	75	5	30	7.5	12.5	0	0	0
16; 26m	0	0	0	32.5	12.5	1.25	15	67.5	0	0	0
17; 0m	0	0	17.5	77.5	12.5	0	1.25	2.5	0	5	0
17; 6m	50	0	7.5	77.5	7.5	0	2.5	2.5	0	3.75	0
17; 16m	12.5	0	35	52.5	10	3.75	0	3.75	0	7.5	0
17; 26m	0	0	0	60	17.5	20	2.5	55	0	2.5	1
18; 0m	0	0	0	60	40	6.25	1.25	25	20	0	0
18; 6m	0	0	0	77.5	20	5	1.25	42.5	0	3.75	0
18; 16m	1	0	32.5	8.75	55	2.5	2.5	62.5	0	8.75	0
19; 0m	0	0	2.5	47.5	2.5	1.25	47.5	12.5	0	0	0
19; 6m	0	0	0	75	7.5	7.5	5	60	1.25	0	0
19; 16m	0	0	2.5	85	7.5	2.5	17.5	60	2.5	0	0
19; 26m	0	10	0	5	22.5	2.5	12.5	95	22.5	0	0
20; 0m	0	0	5	92.5	5	1.25	0	0	0	8.75	0
20; 6m	0	0	7.5	80	25	0	0	23.75	0	12.5	0
20; 16m	5	0	0	90	17.5	2.5	0	5	0	7.5	0
20; 26m	0	0	25	13.75	50	35	1.25	50	0	5	0
21; 0m	0	0	0	67.5	20	0	8.75	17.5	2.5	3.75	0
21; 6m	0	0	0	15	20	0	82.5	2.5	0	0	0
21; 16m	0	0	0	60	10	2.5	45	22.5	0	2.5	0
21; 26m	0	0	7.5	2.5	77.5	1.25	40	12.5	0	1.25	1.5
22; 0m	0	0	7.5	67.5	60	1.25	0	15	0	1.25	0
22; 6m	0	0	0	85	40	2.5	0	18.75	0	5	0
22; 16m	10	0	0	90	10	0	0	10	0	11.25	0
22; 26m	20	0	10	27.5	30	2.5	0	17.5	0	17.5	0
23; 0m	1.25	0	2.5	92.5	15	1.25	0	7.5	0	0	0
23; 7m	0	0	0	92.5	22.5	0	0	25	0	0	0
23; 16m	0	0	1.25	1.25	30	5	2.5	97.5	0	0	0
23; 26m	0	0	2.5	23.75	25	32.5	0	75	0	0	0
24; 0m	0	0	0	22.5	15	0	0	92.5	0	0	0
24; 6m	0	0	0	87.5	12.5	16.25	0	75	0	1.25	0
24; 16m	0	0	0	8.75	50	50	0	100	0	2.5	0.5
24; 26m	0	0	10	5	50	25	1.25	51.25	0	2.5	0
25; 0m	0	22.5	2.5	30	45	12.5	0	22.5	1.25	2.5	0
25; 6m ***	-	-	-	-	-	-	-	-	-	-	-
25; 16m	0	0	0	57.5	20	0	1.25	60	0	3.75	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
25; 26m	0	0	0	42.5	32.5	22.5	8.75	55	0	2.5	0
26; 0m	15	0	0	16.25	17.5	16.25	40	20	6.25	0	0
26; 6m	0	0	2.5	10	10	17.5	22.5	85	2.5	0	0
26; 16m	0	0	2.5	6.25	22.5	55	2.5	77.5	8.75	0	0
26; 26m	0	0	0	1.25	47.5	50	1.25	95	1.25	0	0
27; 0m****	-	-	-	-	-	-	-	-	-	-	-
28; 0m	97.5	0	0	0	0	0	0	2.5	0	0	0
29; 0m	0	0	0	42.5	60	6.25	2.5	55	0	0	0
29; 6m	0	0	0	82.5	22.5	0	5	20	0	1.25	0
29; 16m	0	0	7.5	32.5	15	2.5	21.25	22.5	0	8.75	0
29; 26m	2.5	0	5	2.5	30	6.25	10	67.5	0	3.75	0
30; 0m	0	0	5	50	12.5	2.5	3.75	72.5	0	3.75	0
30; 6m	0	0	0	55	20	11.25	0	55	0	6.25	0
31; 0m	0	0	0	85	20	6.25	3.75	37.5	2.5	0	0
31; 6m	0	0	0	27.5	10	3.75	0	92.5	0	0	0
31; 0m	0	0	0	1.25	27.5	10	6.25	100	10	0	0

* Only one subplot measured
** Edge of plot bulldozed in 2011
*** Track through centre of plot
**** Plot now underwater and tags cannot be read

Appendix 5d. Mean percent ground cover of ten categories estimated in November 2012 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
1; 0m	70	0	5	5	20	2.5	1.25	15	1.25	2.5	0
1; 6m	20	0	2.5	16.25	45	2.5	13.75	32.5	3.75	1.25	0
1; 16m	0	0	0	1.25	75	6.25	42.5	25	2.5	2.5	0
1; 26m	0	0	0	2.5	80	8.75	17.5	25	1.25	3.75	0
2; 0m	2.5	0	2.5	70	22.5	3.75	2.5	20	15	1.25	0
2; 6m	7.5	0	0	27.5	52.5	5	2.5	40	2.5	2.5	0.5
2; 18m	1.25	0	1.25	31.25	70	3.75	2.5	55	1.25	1.25	0
2; 26m	2.5	5	1.25	21.25	75	6.25	2.5	67.5	0	2.5	0
3; 0m	0	0	0	50	50	2.5	5	15	15	0	1
3; 6m	0	0	0	62.5	35	1.25	7.5	25	2.5	0	0
3; 16m	0	0	0	52.5	52.5	3.75	16.25	25	2.5	2.5	0
3; 26m	7.5	0	0	50	60	3.75	5	40	1.25	6.25	0
4; 0m	10	0	0	80	7.5	1.25	0	17.5	8.75	0	0
4; 6m	2.5	0	0	97.5	2.5	1.25	1.25	11.25	0	1.25	0
4; 16m	0	0	0	11.25	55	3.75	1.25	70	1.25	0	0
4; 26m	1.25	0	0	16.25	60	12.5	1.25	67.5	0	0	0
5; 0m	0	0	0	100	5	1.25	2.5	1.25	15	0	0
5; 6m	2.5	0	0	97.5	12.5	1.25	12.5	2.5	0	0	0
5; 16m	1.25	0	0	45	62.5	1.25	17.5	17.5	2.5	1.25	0.5
5; 26m	1.25	0	0	52.5	37.5	2.5	1.25	16.25	27.5	2.5	0
6; 0m	100	0	0	57.5	2.5	0	0	0	0	2.5	0
6; 6m	100	0	0	57.5	2.5	5	0	1.25	0	5	0
6; 16m	55	0	1.25	55	11.25	1.25	0	22.5	0	5	0
6; 26m	2.5	0	10	40	10	6.25	2.5	35	2.5	7.5	0
7; 0m	0	2.5	1.25	10	50	5	77.5	45	37.5	0	0
7; 7m	0	12.5	2.5	2.5	72.5	11.25	11.25	55	16.25	0	0
7; 16m	0	25	0	1.25	70	3.75	2.5	45	30	0	0
7; 26m	0	37.5	0	1.25	40	2.5	46.25	52.5	62.5	0	0
8; 0m	0	0	0	60	90	1.25	0	2.5	0	0	0
8; 6m	0	0	0	70	87.5	1.25	3.75	2.5	0	0	0
8; 16m	0	0	0	50	75	3.75	2.5	17.5	1.25	3.75	0
8; 26m	0	0	0	40	80	1.25	1.25	17.5	1.25	2.5	0
9; 0m	2.5	0	0	65	40	2.5	1.25	20	3.75	17.5	0
9; 6m	0	0	2.5	77.5	45	2.5	0	2.5	3.75	3.75	0
9; 16m	2.5	0	1.25	45	37.5	1.25	1.25	42.5	2.5	3.75	0
9; 26m	0	0	0	8.75	82.5	3.75	6.25	52.5	2.5	2.5	0
10; 0m	2.5	0	1.25	85	7.5	6.25	3.75	25	0	0	0
10; 6m	0	0	1.25	70	45	2.5	18.75	17.5	2.5	13.75	0
10; 16m	1.25	0	2.5	70	72.5	1.25	1.25	47.5	0	3.75	0
10; 26m	1.25	0	1.25	60	50	0	3.75	26.25	0	16.25	0
11; 0m	1.25	0	7.5	27.5	35	1.25	2.5	50	1.25	1.25	0
11; 10m	0	0	0	31.25	40	2.5	16.25	60	2.5	0	0
11; 20m	0	0	0	36.25	42.5	2.5	1.25	25	12.5	0	3
12; 0m	42.5	0	0	77.5	8.75	1.25	0	2.5	0	5	0
12; 6m	5	0	0	85	2.5	10	20	32.5	1.25	1.25	0
12; 16m	25	0	1.25	31.25	25	3.75	35	45	17.5	2.5	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
12; 26m	5	0	0	47.5	5	2.5	31.25	45	11.25	1.25	0
13; 0m	1.25	0	0	57.5	35	6.25	7.5	50	22.5	2.5	0
13; 6m	0	0	0	62.5	32.5	2.5	1.25	7.5	45	0	0
13; 16m	0	0	0	3.75	77.5	6.25	13.75	50	1.25	2.5	0
13; 26m*	*	*	*	*	*	*	*	*	*	*	*
14; 0m	0	6.25	1.25	72.5	30	1.25	6.25	8.75	0	2.5	0
14; 6m	0	15	0	80	45	2.5	7.5	1.25	0	1.25	0
14; 16m	0	0	0	55	65	2.5	17.5	2.5	0	12.5	0
14; 26m	0	0	0	80	45	2.5	2.5	1.25	0	5	0
15; 0m	5	0	1.25	52.5	15	3.75	0	50	0	0	0
15; 6m	12.5	0	1.25	65	10	8.75	0	40	0	1.25	0
16; 0m	1.25	0	1.25	55	40	3.75	20	52.5	17.5	1.25	0.5
16; 6m	0	0	0	32.5	10	2.5	42.5	32.5	10	1.25	0
16; 16m	0	0	0	85	2.5	11.25	22.5	50	0	0	0
16; 26m	0	0	0	70	6.25	2.5	17.5	52.5	0	0	0
17; 0m	40	0	0	65	35	5	1.25	5	1.25	2.5	1.5
17; 6m	40	0	5	70	10	0	5	3.75	2.5	2.5	5.5
17; 16m	30	0	7.5	67.5	12.5	1.25	1.25	3.75	2.5	2.5	0
17; 26m	0	0	0	32.5	65	2.5	11.25	22.5	3.75	2.5	0.5
18; 0m	30	0	1.25	22.5	75	3.75	1.25	13.75	0	1.25	3
18; 6m	0	0	5	47.5	52.5	2.5	0	33.75	1.25	3.75	1.5
18; 16m	11.25	0	20	25	45	2.5	1.25	16.25	1.25	5	0
19; 0m	2.5	1.25	0	46.25	15	1.25	52.5	6.25	0	0	0
19; 6m	0	0	0	72.5	22.5	3.75	2.5	20	2.5	0	0
19; 16m	0	0	0	70	30	1.25	30	21.25	2.5	0	0
19; 26m	0	10	0	5	55	3.75	10	45	45	0	1
20; 0m	90	0	0	52.5	21.25	1.25	0	1.25	0	5	0
20; 6m	12.5	0	0	52.5	37.5	2.5	0	8.75	0	6.25	0
20; 16m	8.75	0	1.25	67.5	35	2.5	0	1.25	0	7.5	0
20; 26m	1.25	0	15	26.25	35	2.5	1.25	37.5	0	1.25	0
21; 0m	2.5	0	0	72.5	55	2.5	2.25	7.5	3.75	2.5	0
21; 6m	0	0	0	11.25	10	0	77.5	12.5	0	2.5	0
21; 16m	0	0	0	10	87.5	1.25	27.5	7.5	0	2.5	0
21; 26m	0	0	0	6.25	90	1.25	30	3.75	0	2.5	0
22; 0m	5	0	0	25	85	1.25	0	1.25	0	1.25	0
22; 6m	0	0	0	62.5	65	2.5	0	2.5	0	5	0
22; 16m	1.25	0	0	97.5	30	1.25	1.25	3.75	0	17.5	0
22; 26m	5	0	2.5	55	45	2.5	5	8.75	0	30	0
23; 0m	85	0	0	65	3.75	0	0	1.25	0	1.25	1
23; 7m	0	0	0	85	70	1.25	0	20	0	1.25	0
23; 16m	0	0	0	2.5	60	2.5	3.75	87.5	0	0	0
23; 26m	0	0	0	17.5	50	7.5	0	80	0	0	0
24; 0m	0	0	2.5	20	55	1.25	0	90	0	0	0
24; 6m	0	0	0	80	50	2.5	1.25	17.5	1.25	1.25	0
24; 16m	0	0	0	8.75	75	11.25	0	57.5	2.5	0	0
24; 26m	0	0	1.25	5	85	3.75	2.5	15	0	1.25	0
25; 0m	0	32.5	0	27.5	72.5	2.5	1.25	17.5	1.25	1.25	0
25; 6m **	-	-	-	-	-	-	-	-	-	-	-
25; 16m	0	0	0	70	65	1.25	2.5	2.5	1.25	2.5	0

Transect; plot	Percent Cover										
	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
25; 26m	0	0	0	67.5	42.5	2.5	2.5	20	6.25	2.5	1
26; 0m	15	0	1.25	25	20	6.25	41.25	15	3.75	0	0
26; 6m	0	0	0	40	30	2.5	40	55	2.5	0	0
26; 16m	0	0	0	6.25	22.5	22.5	17.5	80	5	0	0
26; 26m	0	0	0	2.5	62.5	12.5	2.5	65	2.5	0	0
27; 0m***	-	-	-	-	-	-	-	-	-	-	-
28; 0m	92.5	1.25	2.5	3.75	2.5	2.5	0	8.75	0	1.25	0
29; 0m	0	10	0	32.5	85	1.25	2.5	12.5	0	1.25	1.5
29; 6m	0	0	0	55	55	1.25	3.75	1.25	2.5	2.5	1.5
29; 16m	0	0	0	50	30	5	22.5	22.5	1.25	16.25	0
29; 26m	3.75	0	2.5	8.75	72.5	2.5	12.5	25	1.25	13.75	0
30; 0m	0	1.25	0	35	60	1.25	8.75	32.5	2.5	3.75	0
30; 6m	0	0	0	27.5	75	5	1.25	36.25	3.75	2.5	1.5
31; 0m	0	0	0	65	35	2.5	25	27.5	2.5	0	0
31; 6m	0	0	0	57.5	50	5	2.5	42.5	0	0	0.5
31; 0m	0	0	0	0	50	6.25	8.75	77.5	16.25	0	0

* Edge of plot bulldozed in 2011
** Track through centre of plot
*** Plot now underwater and tags cannot be read

Appendix 5e. Mean percent ground cover of ten categories estimated in November 2013 in two 2 × 2 m subplots in each plot and mean number of woody seedlings per subplot.

	Percent Cover										
Transect; plot	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
1; 0m	50	0	0	25	25	1.25	1.25	15	1.25	1.25	0
1; 6m	1.25	0	10	11.25	45	3.75	27.5	55	7.5	13.75	0
1; 16m	0	0	0	0	77.5	3.75	45	35	1.25	2.5	0
1; 26m	0	0	0	0	80	2.5	35	30	1.25	3.75	0
2; 0m	2.5	0	1.25	87.5	12.5	3.75	0	2.5	21.25	1.25	1
2; 6m	7.5	0	0	27.5	52.5	7.5	3.75	45	2.5	2.5	0
2; 18m	0	0	0	31.25	80	7.5	3.75	40	1.25	2.5	0
2; 26m	7.5	1.25	1.25	21.25	60	3.75	3.75	55	0	2.5	0
3; 0m	0	0	0	47.5	40	2.5	3.75	16.25	10	2.5	2
3; 6m	0	0	0	65	40	7.5	2.5	27.5	0	1.25	5
3; 16m	0	0	0	60	50	3.75	8.75	3.75	5	2.5	2
3; 26m	1.25	0	0	55	50	6.25	3.75	65	5	2.5	0
4; 0m	10	0	0	87.5	2.5	1.25	0	16.25	6.25	2.5	1
4; 6m	1.25	0	0	100	25	1.25	0	17.5	2.5	2.5	0
4; 16m	0	0	0	16.25	50	6.25	2.5	82.5	1.25	1.25	1
4; 26m	2.5	0	0	31.25	45	8.75	2.5	65	0	0	0
5; 0m	0	0	0	100	30	1.25	1.25	2.5	15	0	0
5; 6m	5	0	0	97.5	45	2.5	15	8.75	0	0	0
5; 16m	1.25	0	0	55	80	2.5	27.5	27.5	1.25	2.5	1
5; 26m	1.25	0	0	60	30	6.25	1.25	40	22.5	3.75	0
6; 0m	100	0	0	95	2.5	7.5	0	5	0	35	0
6; 6m	90	0	7.5	87.5	3.75	11.25	0	2.5	0	36.25	0
6; 16m	1.25	0	0	70	21.25	2.5	0	52.5	0	5	0
6; 26m	2.5	0	2.5	75	6.25	3.75	2.5	25	1.25	35	0
7; 0m	0	2.5	1.25	2.5	65	5	57.5	40	32.5	2.5	0
7; 7m	0	17.5	0	2.5	70	3.75	6.25	55	21.25	1.25	0
7; 16m	0	12.5	0	1.25	70	3.75	6.25	45	47.5	0	0
7; 26m	0	15	0	2.5	45	3.75	40	32.5	55	0	0
8; 0m	0	0	0	47.5	57.5	3.75	0	13.75	1.25	1.25	0
8; 6m	0	0	0	55	75	1.25	2.5	12.5	1.25	11.25	0
8; 16m	0	0	0	65	70	7.5	2.5	20	0	8.75	0
8; 26m	0	0	0	50	70	2.5	1.25	35	1.25	2.5	1
9; 0m	2.5	0	1.25	72.5	22.5	2.5	1.25	7.5	6.25	15	0
9; 6m	2.5	0	1.25	77.5	35	1.25	0	6.25	1.25	16.25	1
9; 16m	1.25	0	1.25	42.5	40	1.25	3.75	41.25	2.5	3.75	0
9; 26m	0	0	0	12.5	75	2.5	3.75	55	2.5	2.5	0
10; 0m	1.25	0	1.25	75	2.5	6.25	5	35	0	2.5	0
10; 6m	1.25	0	1.25	75	30	3.75	26.25	15	6.25	6.25	0
10; 16m	2.5	0	2.5	65	32.5	3.75	1.25	45	2.5	15	0
10; 26m	3.75	0	0	75	50	2.5	3.75	16.25	0	18.75	0
11; 0m	15	15	1.25	40	32.5	1.25	11.25	40	12.5	17.5	0
11; 10m	0	0	0	32.5	32.5	2.5	6.25	70	3.75	0	2
11; 20m	0	0	0	36.25	55	5	2.5	52.5	11.25	0	7
12; 0m	57.5	0	0	80	6.25	5	0	3.75	0	15	0
12; 6m	10	0	0	92.5	2.5	7.5	27.5	30	1.25	2.5	0
12; 16m	5	0	1.25	46.25	40	16.25	31.25	40	2.5	2.5	0

Transect; plot	Percent Cover Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo- phytes	Dwarf shrubs	Herb	Seed- lings
12; 26m	5	0	0	52.5	20	1.25	31.25	45	16.25	3.75	0
13; 0m	0	0	0	52.5	37.5	3.75	3.75	50	45	2.5	2
13; 6m	0	0	0	60	50	2.5	1.25	40	40	1.25	3
13; 16m	0	0	0	32.5	75	10	3.75	45	1.25	2.5	0
13; 26m*	*	*	*	*	*	*	*	*	*	*	*
14; 0m	0	11.25	1.25	82.5	42.5	2.5	6.25	22.5	0	2.5	1
14; 6m	0	1.25	0	100	60	10	25	8.75	0	1.25	0
14; 16m	1.25	0	0	62.5	60	2.5	30	2.5	0	12.5	0
14; 26m	0	0	0	90	65	2.5	3.75	2.5	0	10	0
15; 0m	1.25	0	0	65	6.25	7.5	0	50	1.25	1.25	0
15; 6m	10	0	0	85	15	10	0	30	1.25	0	0
16; 0m	1.25	1.25	5	67.5	20	2.5	36.25	45	20	1.25	1
16; 6m	0	0	0	35	6.25	2.5	62.5	37.5	7.5	1.25	0
16; 16m	0	0	0	100	2.5	17.5	37.5	10	0	0	0
16; 26m	0	0	0	57.5	5	6.25	22.5	60	0	2.5	0
17; 0m	30	0	1.25	55	26.25	5	1.25	1.25	5	27.5	8
17; 6m	20	0	0	85	1.25	0	2.5	1.25	1.25	16.25	2
17; 16m	31.25	0	5	65	25	1.25	1.25	1.25	2.5	15	1
17; 26m	0	0	0	40	65	3.75	5	22.5	2.5	1.25	2
18; 0m	92.5	0	0	10	8.75	3.75	1.25	2.5	7.5	1.25	1
18; 6m	0	0	0	55	55	3.75	2.5	21.25	2.5	2.5	0
18; 16m	11.25	0	3.75	16.25	55	2.5	2.5	40	3.75	6.25	0
19; 0m	1.25	0	0	48.75	15	1.25	51.25	11.25	0	1.25	0
19; 6m	0	0	0	95	15	2.5	1.25	15	2.5	0	0
19; 16m	0	0	0	95	17.5	1.25	32.5	10	12.5	0	0
19; 26m	0	2.5	0	22.5	40	2.5	15	55	37.5	0	0
20; 0m	95	0	0	35	3.75	1.25	0	1.25	1.25	0	0
20; 6m	45	0	1.25	55	26.25	2.5	0	1.25	0	10	0
20; 16m	6.25	0	0	52.5	55	1.25	0	1.25	0	7.5	0
20; 26m	0	0	0	21.25	67.5	3.75	1.25	20	0	11.25	0
21; 0m	1.25	0	0	75	55	2.5	6.25	30	5	2.5	1
21; 6m	0	0	0	11.25	16.25	0	100	11.25	0	2.5	0
21; 16m	0	0	0	22.5	70	2.5	52.5	22.5	0	6.25	0
21; 26m	0	0	1.25	11.25	100	1.25	40	1.25	0	3.75	3
22; 0m	95	0	0	40	45	3.75	0	2.5	0	0	0
22; 6m	0	0	1.25	50	65	2.5	0	7.5	0	2.5	0
22; 16m	5	0	0	80	52.5	1.25	0	3.75	1.25	10	0
22; 26m	15	0	0	30	65	2.5	2.5	13.75	0	30	0
23; 0m	97.5	0	0	67.5	2.5	1.25	0	1.25	0	1.25	0
23; 6m	0	0	0	100	65	1.25	2.5	5	0	2.5	1
23; 16m	0	0	0	2.5	65	2.5	2.5	100	0	0	0
23; 26m	0	0	0	36.25	52.5	2.5	2.5	85	0	0	0
24; 0m	1.25	0	1.25	30	45	2.5	0	90	1.25	0	0
24; 6m	0	0	1.25	60	72.5	6.25	0	15	1.25	0	0
24; 16m	0	0	0	12.5	80	8.75	0	50	1.25	0	1
24; 26m	0	0	1.25	20	87.5	10	2.5	26.25	0	1.25	0
25; 0m	0	32.5	0	27.5	75	2.5	1.25	22.5	0	1.25	4
25; 6m **	*	*	*	*	*	*	*	*	*	*	*
25; 16m	0	0	0	80	65	2.5	2.5	5	2.5	3.75	0

Transect; plot	Percent Cover										
	Water	Rock	Bare ground	Grass/ sedge	Leaf litter	Woody litter	Ferns	Bryo-phytes	Dwarf shrubs	Herb	Seed-lings
25; 26m	0	0	0	62.5	50	3.75	3.75	7.5	3.75	2.5	0
26; 0m	12.5	0	0	38.75	45	6.25	30	12.5	2.5	0	0
26; 6m	0	0	0	42.5	11.25	2.5	82.5	35	3.75	0	0
26; 16m	0	0	2.5	16.25	17.5	13.75	40	57.5	18.75	0	0
26; 26m	0	0	0	8.75	65	37.5	2.5	75	3.75	1.25	3
27; 0m***	*	*	*	*	*	*	*	*	*	*	*
28; 0m	12.5	0	37.5	55	2.5	10	0	12.5	0	22.5	0
29; 0m	0	5	0	50	65	2.5	1.25	27.5	1.25	2.5	0
29; 6m	0	0	0	65	45	1.25	8.75	1.25	1.25	2.5	1
29; 16m	12.5	2.5	0	40	35	1.25	22.5	21.25	2.5	15	0
29; 26m	20	0	1.25	2.5	55	3.75	22.5	47.5	1.25	26.25	0
30; 0m	0	0	1.25	35	52.5	3.75	8.75	45	2.5	7.5	0
30; 6m	0	0	0	41.25	55	6.25	1.25	41.25	2.5	7.5	2
31; 0m	0	0	0	82.5	40	11.25	6.25	13.75	8.75	0	0
31; 6m	0	0	0	52.5	20	22.5	2.5	55	0	0	1
31;16m	0	0	0	1.25	35	2.5	11.25	77.5	16.25	0	0

* Edge of plot bulldozed in 2011
** Track through centre of plot
*** Plot now underwater and tags cannot be read

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