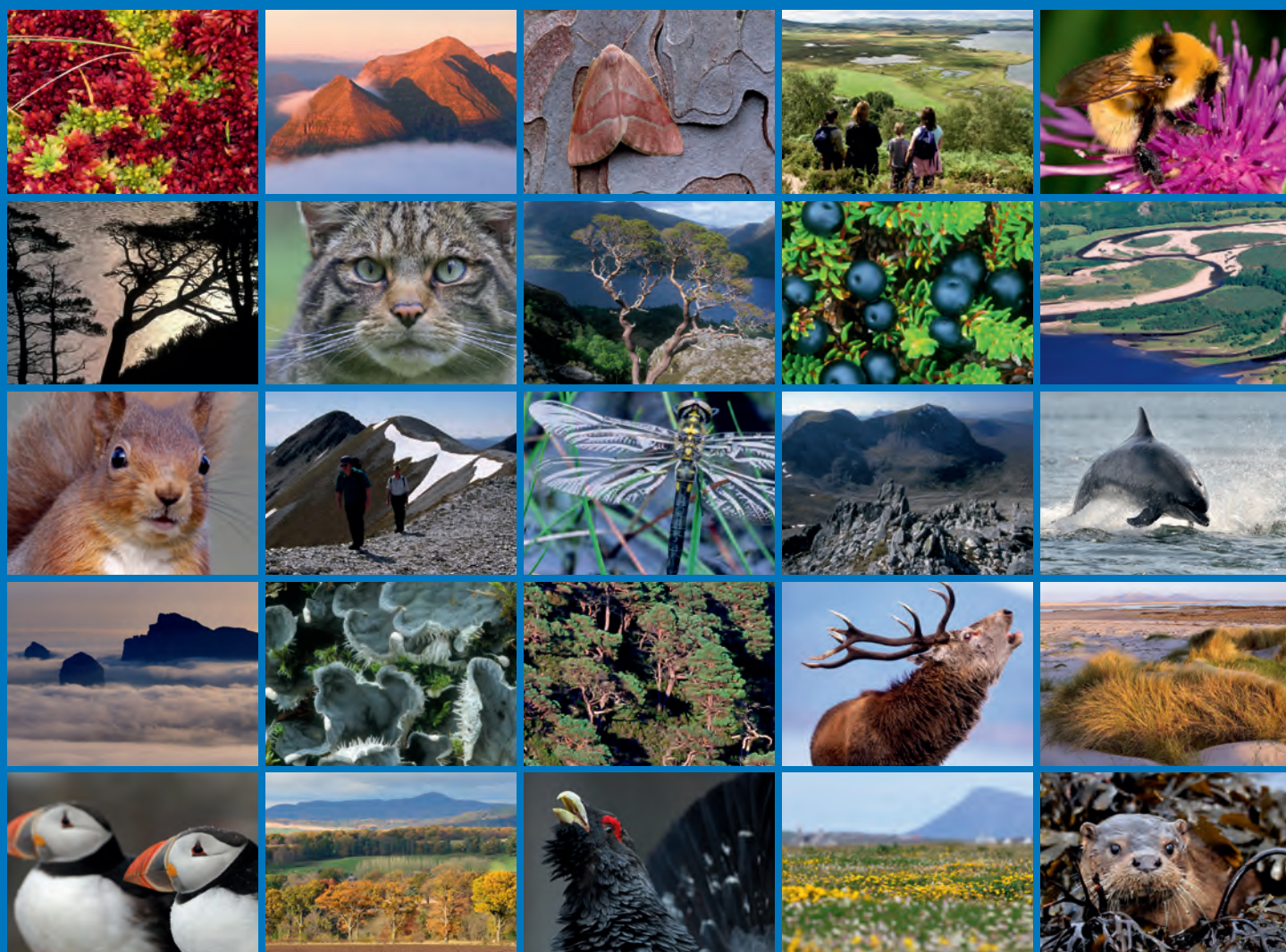# The Scottish Beaver Trial: Monitoring of aquatic vegetation and associated features of the Knapdale lochs 2008-2013, final report

Scottish Natural Heritage
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COMMISSIONED REPORT

The Scottish Beaver Trial: Monitoring of aquatic vegetation and associated features of the Knapdale lochs 2008-2013, final report

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COMMISSIONED REPORT

Summary

The Scottish Beaver Trial: Monitoring of aquatic vegetation and associated features of the Knapdale lochs 2008-2013, final report

Keywords

Aquatic; beaver; macroinvertebrate; Knapdale; loch; macrophyte; plant; trial.

Background

This report provides an overall analysis of aquatic vegetation data collected from 2008 to 2013 as part of a scientific monitoring programme of the Scottish Beaver Trial at Knapdale, Argyll. Surveys of vegetation in lochs across the area of the trial were undertaken in September 2008, providing a baseline data set prior to the release of beavers in spring 2009. Interim monitoring continued over the following five growing seasons, prior to a full resurvey of loch vegetation in September 2013 which followed the same protocol as was used to collect the baseline data. Findings based on interim surveys carried out in 2009, 2011 and 2012, at a subset of the original vegetation transects first sampled in 2008 and 2009, are presented to illustrate temporal variation and the trajectory of change. An assessment of change in plant species richness, composition and cover, across all of the 11 lochs, is followed by an analysis of the extent to which these changes can be related to various aspects of beaver activity. The results of additional monitoring at Dubh Loch, undertaken to quantify changes in habitat, vegetation and aquatic invertebrates associated with dam building by beavers, are also presented.

Main findings

- Beaver activity has had a clear and measurable impact on the aquatic plant communities present in some of the Knapdale Lochs. The evidence for this comes from fixed-point photography, repeated surveys of fixed quadrats and re-mapping of vegetation polygons at a whole-loch scale.

- The greatest effects of beaver were on plant cover, with richness being little affected. These effects are most evident on lochs with lodges that have been occupied for several successive growing seasons by multiple animals. Intermittent occupancy by one or two individuals produced weak effects.

- Four species, common club-rush *Schoenoplectus lacustris,* great fen-sedge *Cladium mariscus,* white water-lily *Nymphaea alba* and water horsetail *Equisetum fluviatile*, were affected by direct herbivory. Impacts on *N. alba* and *E. fluviatile* were small and rather variable between territories or between years and these effects are probably transient. Selective grazing of *S. lacustris* and *C. mariscus* by beavers caused significant reductions

in the standing stock of these species in beaver-occupied lochs, averaging 39% and 81% respectively. Given the low productivity of the Knapdale lochs, recovery of populations of these species in the absence of beaver may prove to be slow.

- There were no apparent adverse effects on the submerged plant assemblages that form part of the basis for designation of the Taynish and Knapdale Woods Special Area of Conservation.

- One site, Dubh Loch, experienced a marked and sustained water level rise due to dam building. Changes in the loch bathymetry were partly offset by the buoyancy of peat and associated vegetation. Whilst much of the original aquatic vegetation was lost through submersion or herbivory, newly inundated areas were rapidly colonised between 2011 and 2013, thus greatly reducing the net effect of the water level rise. The rapidity with which aquatic vegetation established suggests the pre-existence of a long-lasting seedbank of wetland species. Both the overall species richness and the heterogeneity of vegetation increased. Invertebrate colonisation of newly-created habitat was also rapid, with chironomid larvae and corixids dominating. Water beetle diversity increased relative to independent baseline surveys. Dam-building is likely to have long-lasting effects at this site and, in the event of abandonment by beavers, return to baseline conditions is likely to take several decades.

- Three other sites (Un-named Loch (North) and Lochs Linne and Fidhle) experienced a small or temporary rise in water level due to dam building. Vegetation at these sites did not show any directional change that would indicate increased tolerance of soil saturation. Monitoring over longer periods may be required to detect such trends.

- Beavers alter aquatic vegetation in standing waters principally through the mechanisms of herbivory and water level rise, although the timing, scale and severity of the resulting effects are difficult to predict. Whether effects are considered positive, neutral or negative is likely to vary between systems according to their productivity, and over time, and in relation to the *status quo*. Positive effects are most likely against a baseline of degraded habitat, whereas in an environment of high quality, such as Knapdale, widespread positive effects will be more difficult to demonstrate.

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Acknowledgements

1. INTRODUCTION

The European beaver *Castor fiber* became extinct in Scotland in the 16th century mainly as a result of over-exploitation (Kitchener 2001). Under the Habitats Directive, EU Member States have a duty to consider the desirability of reintroducing this and other animal species listed under Annex IV of the Directive. Various investigations have been undertaken since 1995 to consider the feasibility and desirability of restoring beavers to Scotland (Conroy and Kitchener 1996; Daniels *et al.*, 2000; MacDonald *et al.*, 1997; Webb *et al.*, 1997). In 2007, Scottish Natural Heritage (SNH) launched the Species Action Framework, setting out a strategic and partnership-based approach to species management in Scotland.

A five-year scientific trial reintroduction of the European beaver to Knapdale Forest in Argyll commenced in May 2009, following the granting of a licence by the Scottish Government in May 2008, to the Scottish Wildlife Trust (SWT) and the Royal Zoological Society of Scotland (RZSS). Monitoring of the beavers indicates they have been resident on or regularly utilising seven of the 11 primary lochs located within the survey area (Harrington, Feber and MacDonald 2012). This remained the case when the 2013 macrophyte survey was undertaken (SBT (pers. com.), 2013). The licence application lists a number of aims of the trial that are pertinent to the present study:

- *"Study the ecology and biology of the European beaver in the Scottish environment*
- *Assess the effects of beaver activities on the natural [….] environment*
- *Generate information during the proposed trial release that will inform a potential further release of beavers at other sites with different habitat characteristics."*

The licence also sets out a number of specific criteria for success and failure, which include the following:

"Criteria for success:

- *The beaver population demonstrates a positive contribution to ecosystem function*
- *Beaver re-introduction is integrated with habitat management/restoration."*

"Criteria for failure:

- *Significant and unsustainable damage is incurred by the ecosystem within the study site."*

The use of a scientific trial has allowed monitoring data to be collected from lochs that are subject to varying degrees of influence by beavers, as well as lochs that are unaffected, and for these data to be compared with the pre-introduction baseline, thereby allowing a test of the relevant criteria for success and failure. Project partners, including the University of Stirling, independent from the licence-holders, were appointed by SNH to collect monitoring data on the Scottish Beaver Trial (SBT). Independent monitoring of the SBT is essential, as it allows for a fair and balanced evaluation of the effects of five years of beaver occupancy. Thus, data on a range of ecosystem attributes have been collected by the project partners to allow assessment of the ecological effects of beaver activity in a near-natural environment within the Scottish landscape.

Aquatic vegetation is of particular significance in the context of the SBT because the beaver release sites were located within or adjacent to the Taynish and Knapdale Woods Special Area of Conservation (SAC). Aquatic vegetation is a qualifying feature of the SAC, specifically oligotrophic to mesotrophic standing waters featuring plant communities of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea*, i.e. clear water lochs with aquatic vegetation and low to moderate nutrient levels. The aquatic vegetation of oligotrophic and

mesotrophic standing waters is a qualifying feature of five lochs within the SAC (see Table 1; Page 7). The underpinning SSSIs of the SAC, Taynish Woods SSSI and Knapdale Woods SSSI, are also designated for their standing water features. Consequently, assessment of the response of aquatic vegetation to the reintroduction of beavers is a key element of the trial. In this report, the terms 'aquatic plant' and 'aquatic vegetation' are used in a generic sense, to refer to all plant species that complete part or all of their life cycle rooted with at least their basal parts permanently submerged. When referring to strictly aquatic species (sometimes referred to as hydrophytes), the term 'floating-leaved and submerged species' is used to discriminate these from emergent species (sometimes referred to as helophytes or semi-aquatic species), in which most of the photosynthetic structures are aerial (i.e. borne above the water surface).

This report presents an analysis of data collected during the aquatic vegetation surveys undertaken from September 2008 to September 2013, as part of a wider programme of monitoring for the five-year trial reintroduction. Where appropriate, results have been compared to pre-introduction baseline data collected by the same surveyors during either September 2008 or September 2009. Comparisons have also been made with reference to background patterns of inter-annual variability in vegetation observed at lochs in the absence of beavers. Discussions of general trends at the loch level and in relation to the level of beaver activity are provided based on these data. Previous reports (Willby and Casas-Mulet 2010; Willby, *et al.,* 2011; Willby and Perfect 2014) detail the results of baseline surveys of the Knapdale lochs and interim monitoring of aquatic vegetation during the period of the SBT. Willby and Casas-Mulet (2010) also make comparisons between the latest baseline data and previous surveys of some of the Knapdale lochs. The present report provides an overall assessment of the data collected over the last five years and offers a critical evaluation of the effects of beavers (positive, negative or neutral) on aquatic vegetation. It represents the final analysis of the results of monitoring over the entire period of the trial. As would be expected in a project of several years' duration, there may be differences in methods of analyses and presentation of results between this report and earlier, interim reports. The data analyses in the present report supersede those presented in interim reports.

Collection of aquatic vegetation data serves three purposes. First, it will help in the evaluation of the success of the trial reintroduction against established criteria. Second, it allows any impacts of beavers on the integrity of the Taynish and Knapdale Woods SAC to be identified. Third, it provides an evidence base from which to make predictions about the potential effects of future changes in the beaver population at Knapdale and in Scotland as a whole.

The primary focus of this report is on aquatic vegetation, because of its importance in defining habitat for higher trophic levels, its well-known role in the diet of beavers and because it forms a qualifying feature of the SAC. However, in the course of this study, additional opportunities arose to assess the response of aquatic invertebrates to the creation of novel habitats formed as a result of dam building by beavers. Associated geospatial surveys were also put in place to quantify changes in water body area and shape complexity caused by dam building. This monitoring was unplanned and opportunistic, and in contrast to the surveys of aquatic vegetation, was not supported by the collection of baseline data, since this would have been excessively costly and its value post-release would largely have depended on where beavers established territories and what, if any, ecosystem engineering behaviour occurred. This report therefore includes results of surveys of aquatic invertebrate colonisation of Dubh Loch, a water body that experienced significant water level rise as a result of dam building. Based on these results, published evidence and our experience of beaver formed habitats on Tayside and in Sweden, some predictions are made in the discussion of the implications for wider aquatic biota of an increased and more generally distributed beaver population in Scotland.

2. OBJECTIVES

The objectives of the aquatic vegetation surveys and additional monitoring were as presented below.

1. At the beginning and end of the 5-year trial, collect data from a full set of fixed transects and undertake polygon-scale mapping of vegetation on each of the primary lochs within the Knapdale survey area using the approaches documented by Willby and Casas-Mulet (2010).
2. Analyse and review the data collected over the five-year period of the trial relative to baseline data.
3. Comment on whether beaver activity has had any impact on the SAC qualifying macrophyte species or assemblage, including the distribution of invasive non-native species, such as Canadian waterweed *Elodea canadensis*.
4. Evaluate the effectiveness of the monitoring approaches employed.
5. Predict the short- to medium-term effects of continued presence of beavers at Knapdale for aquatic vegetation and associated biota.
6. Provide an expert and evidence-based assessment of potential impacts of beavers in Scotland on aquatic vegetation and associated biota in the event of a wider scale reintroduction.

3. BACKGROUND

3.1 Effects of beavers on aquatic vegetation

Beavers have the potential to affect aquatic vegetation through a variety of direct and indirect mechanisms that operate over a range of spatial and temporal scales (Rosell *et al.*, 2005). Scales range from rapid but localised reductions in vegetation cover, resulting from preferential grazing of individual species (e.g. Fryxell and Doucet 1993; Parker *et al.,* 2007; Law *et al.*, 2014b), or changes in light regime or physical habitat structure, occurring as a result of felling or caching activity (Naiman *et al.,* 1988; Jones *et al.,* 2009), through to larger scale changes in the type and distribution of vegetation, caused by changes in water level regime associated with damming (Pollock *et al.,* 2003).   In relation to the major environmental influences on loch vegetation, a number of direct or indirect, established or potential effects of beavers can be identified (Figure 1).
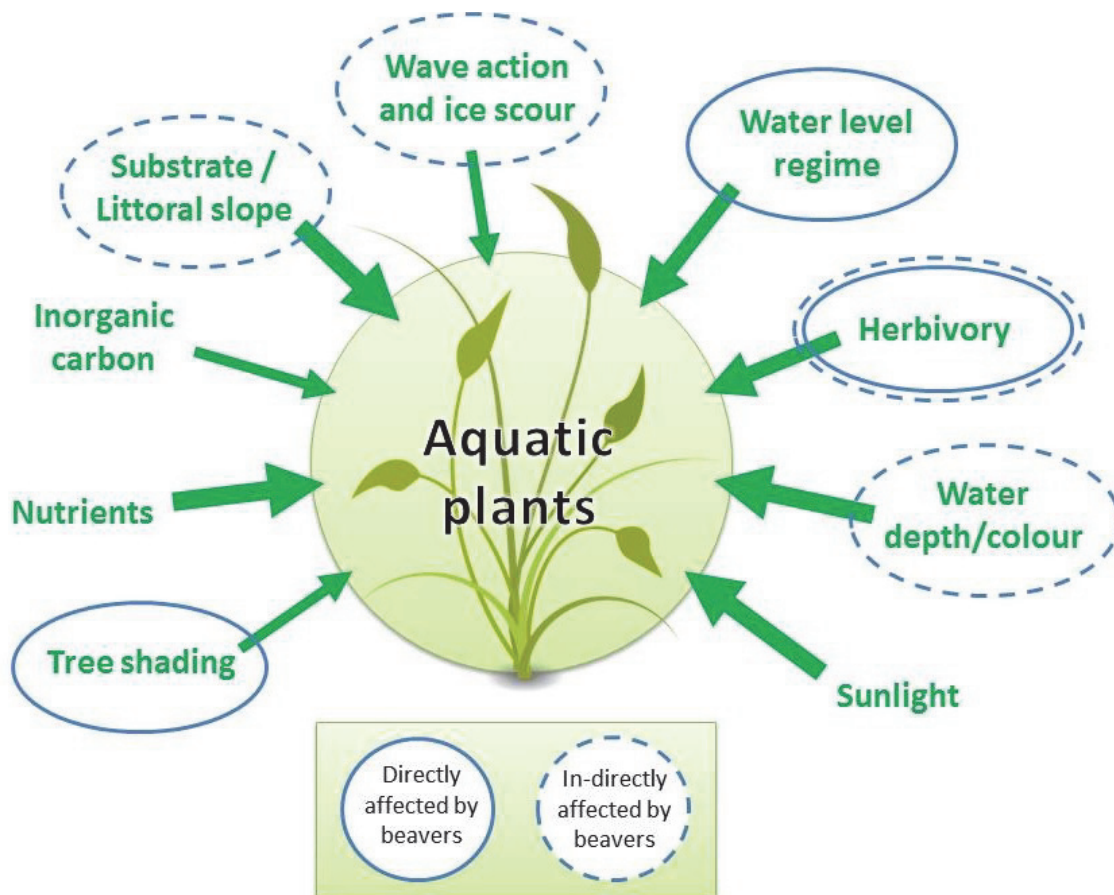
Figure 1. Diagram indicating the major environmental factors influencing loch vegetation

Note: circles indicate those factors likely to be directly (solid) or indirectly (dashed) affected by beavers. Other factors are likely to be unaffected or only weakly influenced by beavers.

3.1.1 *Herbivory*

Aquatic plants have been demonstrated through observation and stable isotope analysis to form a major constituent of beaver diet, the contribution varying seasonally and between habitats (Milligan and Humphries 2010). Although it is evident that beavers can have impacts on the composition and biomass of herbaceous vegetation by direct herbivory (Law *et al.*, 2014a,b) and can alter competitive interactions (Parker *et al.*, 2007), such effects are relatively poorly researched; impacts of beavers on herbaceous vegetation are typically

attributed to the indirect effects of habitat modification (Parker *et al.,* 2007), whilst other aquatic rodents, such as muskrat (*Ondatra zibethicus*), are a more typical subject of studies of aquatic plant-grazer interactions (e.g. Danell 1997).

3.1.2 Water level change

Hydrological alterations by beavers have been extensively studied, often in the context of successional changes in vegetation that occur in beaver-generated wetlands over decadal cycles of creation and abandonment (Ray *et al.*, 2001; Little *et al.*, 2012). The presence of these engineered habitats and the coexistence of beaver wetlands spanning a range of ages has been demonstrated to increase plant diversity at the landscape scale (Wright *et al.*, 2002; Bonner *et al.*, 2009). Hence, the importance of beaver wetlands in providing habitat for a wide range of biota including invertebrates (Rolauffs *et al.*, 2001), fish (Kemp *et al.*, 2011), amphibians (Dalbeck *et al.*, 2007) and bats (Nummi *et al.*, 2011) is well-recognised.

There are other less well-documented potential effects of elevated water levels on aquatic vegetation including, for example, increase in water colour associated with the accumulation of organic matter derived from microbial decomposition of inundated terrestrial vegetation (Peczula and Szczurowska 2013). Coupled with an increase in water depth, increased humic content could have important impacts on the submerged light climate.

3.1.3 Water level regime

Impoundment by beavers increases water storage and tends to stabilise water level regime, with associated effects on water chemistry (Fuller and Peckarsky 2011). However, water level rise often results in the shallow inundation of terrestrial habitat. The temporary exposure of such areas during dry summers, coupled with their high microtopographic variation, should favour enhanced plant species richness. Several studies suggest that the water level regime itself is at least as important as water depth *per se* in driving patterns of colonisation by aquatic vegetation (e.g. Pollock *et al.*, 1998). Effects of impoundment specifically on water chemistry do not appear to be systematic, but are rather a function of context, pond morphology and flow regime (Fuller and Peckarsky 2011; Little *et al.*, 2012).

3.1.4 Wave action

Beavers may indirectly increase the effects of wave action in larger bodies of water through raising water levels, as recently inundated areas may be more vulnerable to wave erosion and ice scour. Beavers are central place foragers i.e. they bring trees to a certain location, the 'central place' (Orians and Pearson 1979) and hence habitually remove trees from the adjacent woodland and transport entire cut stems to the safety of shallow water for caching or processing. An increase in the accumulation of woody debris in shallow littoral areas may increase loss of aquatic vegetation through the traction of woody material over the bed, especially in more exposed sites, or, at sufficiently high densities, may shade out smaller submerged plants.

3.1.5 Tree shading

There are extensively documented effects of beavers on woody species associated with selective felling and removal of mainly smaller diameter trees of preferred species such as willows. Tree loss and decreased regeneration in riparian zones will also occur without felling, as a direct result of water level rise caused by beaver dam construction (Townsend and Butler 1996). Reduced canopy cover and selective felling by beavers are known to alter tree composition (Rosell *et al.*, 2005), but studies of effects on the herbaceous under-storey are surprisingly rare and somewhat inconclusive (Brzyski and Schulte 2009). The specific effects of reduced shading of the littoral zone associated with tree felling at pond or loch margins have not been quantified. In areas with extensive overhanging trees, canopy

removal may be expected to stimulate growth of aquatic species if habitat conditions are favourable.

3.2 Location of lochs

The lochs included in the monitoring programme are located in and around the Taynish and Knapdale Woods SAC. Locations are shown in Figure 2, whilst grid references and the unique Water Body Identifier Codes (WBIDs) from the GB Lakes Inventory are presented in Table 1. At the outset of the SBT, water bodies were classified as primary or secondary for the purposes of the aquatic macrophyte monitoring. Primary lochs included the beaver release sites and closely adjacent lochs. The secondary lochs were a series of canal reservoirs situated on the edge of the release area that could potentially have been utilised by wider-ranging beavers. Baseline surveys of both primary and secondary lochs were undertaken in 2008. The geographical reach of the trial was extended in 2009, and baseline data were collected from an additional three primary lochs. Primary lochs were selected for annual survey throughout the trial, whereas secondary lochs would only be resurveyed in the event of beavers moving into the vicinity.

Four secondary lochs were surveyed in 2008. Surveys of these sites followed the methods described by Lassiere (1998) and Murphy *et al.* (2002), and the results are provided in Willby and Casas-Mulet (2010). All but one of the canal reservoirs (Lochan Duin) had steep rocky shores with extensive exposure, because of draw-down of water levels for operating the Crinan Canal. The habitat was highly unsuitable for beavers and there is no evidence from either a repeat visit in 2012 or searches undertaken independently by SBT staff (R. Campbell-Palmer pers. comm.) that beavers ever used any of the canal reservoirs. No further mention is therefore made of these water bodies in this report.

Table 1. Geographical and baseline survey information for the primary and secondary lochs at Knapdale

Loch name	British National Grid reference	WBID[1]	Baseline survey year	Status	Altitude (m)	Area (ha)	Perimeter (km)	Max depth (m)[3]
Primary Lochs								
Dubh Loch	NR784902	25202	2008	SAC[2]	38	0.4	0.3	<5
Creagmhor Loch[4]	NR803910	25160	2008	SAC	68	5.2	1.1	10-15
Loch Barnluasgan	NR792912	25144	2008	SAC	43	5.3	1.2	10-15
Loch Coille-Bharr	NR782901	25179	2008	SAC	32	33.4	4.4	28
Loch Fidhle[5]	NR799909			SAC				10-15
Loch Linne	NR797910	25145	2008	SAC	39	16.5	3.1	27
Loch Losgunn	NR791898	25209	2008		68	2.1	0.7	5-10
Un-named loch (N)[6]	NR801910	25168	2008	SAC[2]	68	1.1	0.5	<5
Additional primary lochs								
Lochan Buic	NR789889	25242	2009		49	3.9	1.1	5-10
Loch McKay	NR798886	25264	2009		142	1.9	0.6	5-10
Un-named loch (S)	NR788885	25268	2009		47	1.6	0.5	5-10
Secondary Lochs								
Daill Loch	NR813899	25199			151	11.7	3.1	10-15
Loch an Add	NR804887	25228			154	24.2	4.6	10-15
Loch na Bric	NR803892	25229			152	5.2	1.1	10-15
Lochan Duin	NR804898	25210			148	3.1	0.7	5-10

1   WBID - unique water body identifier code from the GB Lakes Inventory.
2   Water body lies within the SAC, but does not support the aquatic plant communities for which the SAC was partly designated.
3   The maximum depths are based on modelled maxima, as given in the GB Lakes Inventory, or estimated during field surveys. The depths of the two largest water bodies were confirmed from bathymetric mapping in 2012 commissioned by SNH.
4   There are various derivations of this name used on different Ordnance Survey sheets.
5   Loch Fidhle is contiguous with Loch Linne and as such, it is not considered as a discrete water body by the GB Lakes Inventory. However, for the purposes of the SBT these are treated as distinct sites.
6   In the GB Lakes Inventory, Un-named Loch (North) is erroneously labelled as Loch Fidhle, which is located to the south-west. Larger scale maps refer to this water body as Lochan Beag.

3.3 General views of the primary lochs

Figure 3 gives an indication of the character of each of the lochs encompassed by this survey and their overall setting. In general terms, these are well-vegetated water bodies with extensive emergent and floating-leaved vegetation characterised by species that are typical of minimally impacted, low to moderate alkalinity lowland lochs in Scotland. The surrounding topography is undulating and land cover is dominated by either coniferous plantation forestry or native broad-leaved woodland.
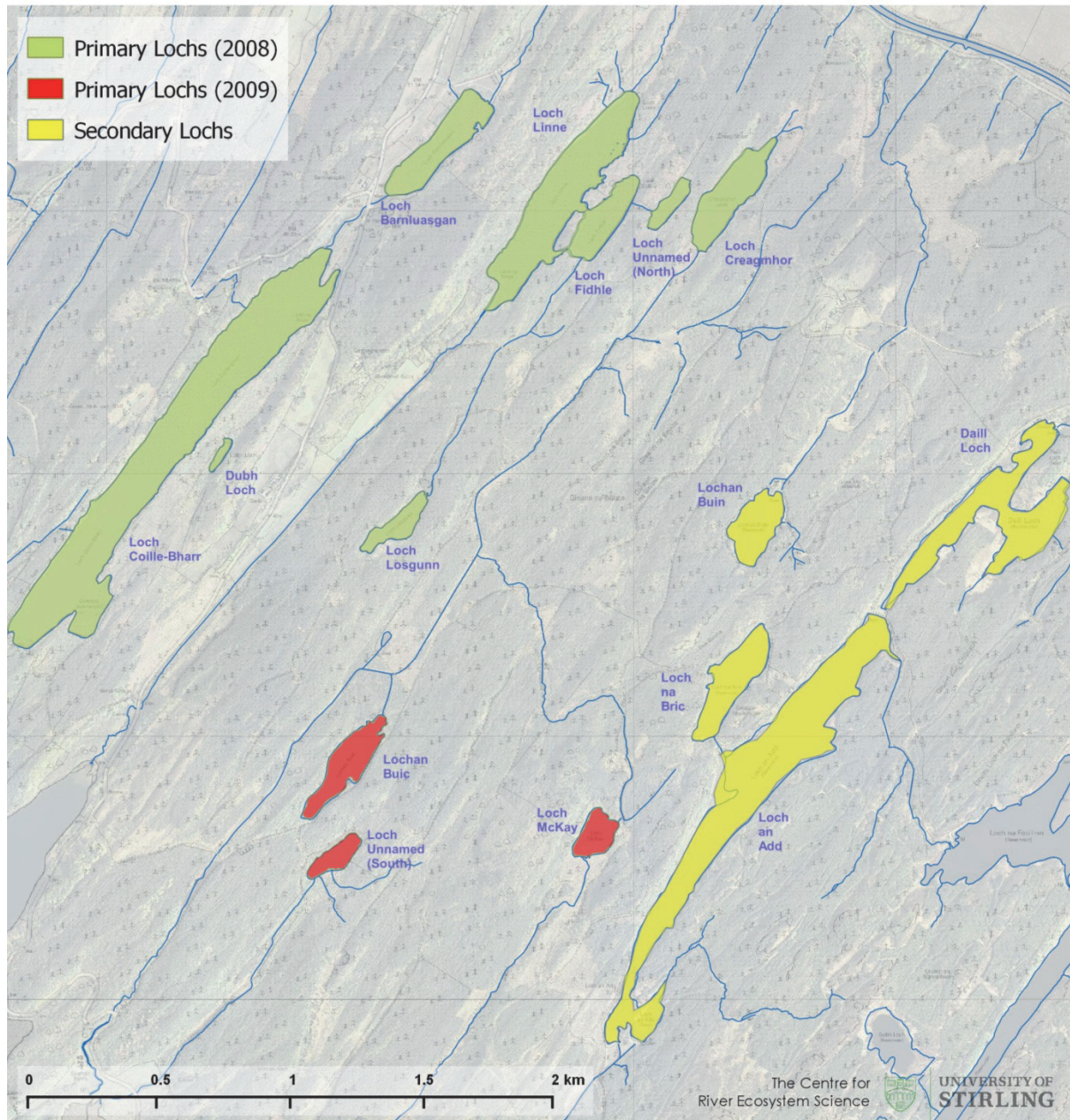
Figure 2. Locations of the primary lochs surveyed in 2008 and 2009 and the secondary lochs surveyed in 2008

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Loch Losgunn   Loch Fidhle   Loch Linne

Un-named south   Dubh Loch   Loch McKay

Creagmhor Loch   Un-named North   Loch Barnluasgan

Loch Coille-Bharr   Lochan Buic

Figure 3. Photographs illustrating the character of each of the primary lochs covered by the aquatic macrophyte surveys

3.4 Environmental character of the Knapdale lochs

Knapdale sits on strongly-folded, ancient, metamorphosed rocks interrupted by base-rich igneous intrusions. This creates an undulating topography of parallel ridges following a south west to north east axis (Stephenson and Merritt 2010). The Knapdale lochs are enclosed between these ridges (Figure 2) and therefore tend to be elongate in shape, with relatively low shoreline complexity. This also means that water body areas are generally large relative to their catchments. Coupled with the extensively wooded nature of the landscape, loch water levels are therefore rather stable, typically fluctuating by less than 0.5m annually. Although the local drainage network has been modified as a result of forestry and agricultural activity, historical OS maps suggest that the lochs themselves have not been substantially altered since at least 1870.

The primary lochs covered by the survey differ with regard to both their physical character and water chemistry. In general, these are small to medium-sized water bodies (from less than 1 to 34 ha) of mostly shallow depth (less than 5 m), moderately to strongly coloured, low to moderate alkalinity (5 to 28 mg L^{-1} $CaCO_3$) waters. Relevant physical data for the lochs are summarised in Table 1 and key aspects of water chemistry are shown in Figure 4. Water chemistry was monitored by SEPA approximately monthly during the period from 2003 to 2005 and for the duration of the trial (2008 to 2014). Dubh Loch was added to the monitoring network in 2010. The features of these data that are of most relevance to macrophytes are described below and are considered later in this report to support interpretations of any recorded changes in vegetation.

In terms of their water chemistry, the Knapdale lochs are typically circum-neutral and nutrient-poor. Nutrient levels have been compared using the geometric mean of recorded concentrations, which calculates the exponential of the mean logged concentrations. This is a better measure of 'central tendency' when data fit a log-normal distribution as is the case with the Knapdale water chemistry data which cannot fall below zero, yet have occasionally very high readings. It gives a better indication of the general chemical conditions to which the macrophytes are subjected within the lochs, as well as being an effective method for reducing the influence of potentially erroneous outlying values. It is a commonly used approach in the analysis of water chemistry data. Geometric means for nitrate-nitrogen (nitrate-N) are mostly in the range 55 to 68 µg N L^{-1}, ammonia-N concentrations are typically around 25 µg N L^{-1} and orthophosphate phosphorus (P) concentrations are mostly in the range 2 to 4 µg P L^{-1}. Geometric annual mean chlorophyll-a (chl-a) concentrations rarely exceed 2 µg chl-a L^{-1}. At face value, the mean total phosphorus (TP) concentrations are somewhat higher than might be expected (7 to 13 µg P L^{-1}). However, given the very low chlorophyll-a and inorganic P levels (as indicated by measured concentrations for orthophosphate-P), the elevated water column TP concentrations may be a reflection of organic P sources, as these lochs have a moderate to high dissolved organic carbon (DOC) content (6 to 20 mg C L^{-1}). This reflects the strongly organic soils of their catchment areas. TP concentrations of this magnitude are typical of pristine, humic lakes in Scandinavia (Hellsten *et al*., 2014). DOC concentrations of 6 to 7 mg C L^{-1} approximately equate to a colour threshold value of 30 mg Pt L^{-1} which is typically used to separate clear water and humic lakes in Europe (Hellsten *et al*., 2014).[1] It is apparent that the Knapdale lochs are close to or above this threshold. Electrical conductivity (typically 90 to 150 µS cm^{-1}) and major ion concentrations reflect a weak maritime influence.

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[1] Pt is the standardised unit of measurement of colour on the platinum-cobalt (or Hazen) scale
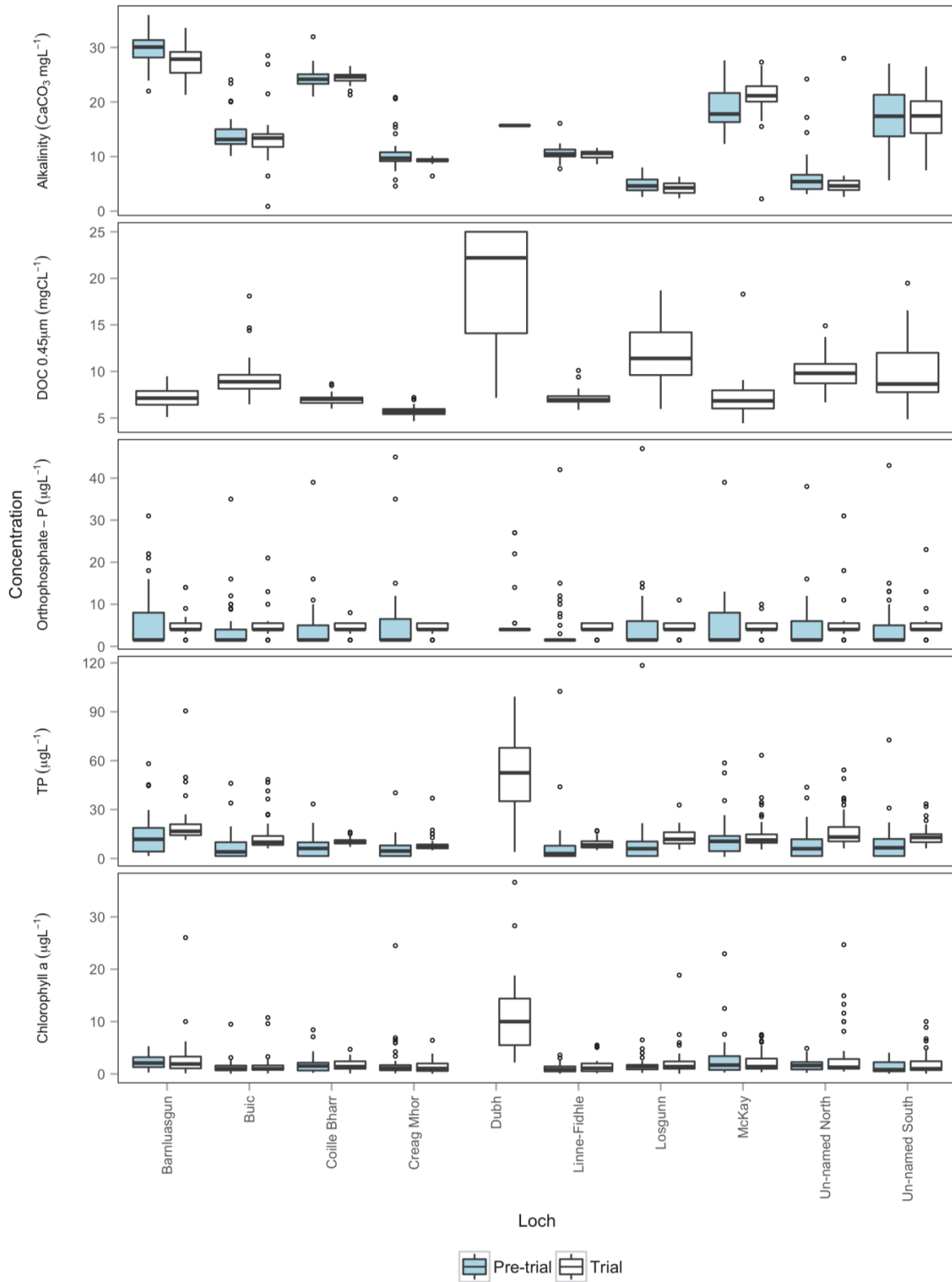
Figure 4. Chemical characteristics of the primary lochs: alkalinity, orthophosphate-P, TP, chlorophyll-a and DOC

Note: coloured bars refer to data collected from 2003 to 2005. Open bars indicate data collected during the trial years (2009 to 2013). DOC was only monitored during the trial years. Dubh Loch was added to the monitoring network in 2010. Lochs Linne and Fidhle are treated as a contiguous water body for water chemistry sampling. Contains SEPA data © Scottish Environment Protection Agency and database right [2014]. All rights reserved.

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3.5   Rationale for methods

In developing a survey protocol for the assessment of aquatic vegetation in the 11 lochs at Knapdale in 2008, Willby and Casas-Mulet (2010) considered the survey methods that had previously been applied to some of these lochs, for a variety of different purposes. These included the Scottish Loch Survey Project method (Lassiere 1998), the Site Condition Monitoring method (Gunn *et al.,* 2004) and the method adopted by Murphy *et al.* (2002) for a previous baseline survey of the Knapdale Lochs in 2002. The latter was intended to form a baseline survey to support an earlier application by SNH for a licence to release beavers at Knapdale. Criteria were established to ensure that the output of monitoring provided for a fully informed outcome to the trial. To address specific criteria regarding the degree and nature of damage or enhancement to natural ecosystem features, the primary requirements for the survey design were the ability to:

1. detect change at different spatial scales;
2. discriminate between changes due to external factors and those attributable to beavers, and
3. capture the trajectory of any change in vegetation at individual sites through repeat sampling.

Following discussions with the project partners, the survey methods discussed above were refined to meet these requirements. These refinements can be summarised as follows:

1. increase the number of fixed transects per loch;
2. quantify the submerged aquatic zone beyond the limits of beds of floating-leaved vegetation by increasing the number of quadrats per transect;
3. ensure that quadrats include stands of preferred food species, especially where these are of limited extent within a loch;
4. map vegetation polygons at higher spatial resolution by circumnavigating polygons in a boat and taking regular GPS readings to define the boundaries of each polygon;
5. record maximum depths of colonisation by macrophytes in each loch;
6. consider other attributes besides species composition (e.g. flower density); and
7. examine localised areas used for feeding by beavers to establish dietary preferences.

The agreed method relied on a combination of mapping discrete polygons of vegetation at a whole loch scale, coupled with surveys of vegetation in 2m x 2m fixed quadrats on multiple transects distributed around each loch. This method was first implemented in the surveys of eight primary lochs in 2008 (Willby and Casas-Mulet 2010) and three additional primary lochs in 2009 (Willby *et a*l., 2011). Although these latter three sites were surveyed a few months after beavers had been released at Knapdale, they were outwith the release area and had never been used by beavers at the time of survey and are therefore considered as part of the baseline data collection phase.

3.6   Adaptive monitoring activities

Given that both the location of beaver territories and the level of damming activity could not be known for certain at the outset of the trial, an adaptive element was incorporated into the monitoring plans. The significant modifications to the monitoring plan were focused at Dubh Loch, where the construction of a relatively large dam altered the water levels and water chemistry and provided an unprecedented opportunity to assess how aquatic vegetation and associated biota would respond to a major physical change in habitat. Thus a number of additional monitoring activities were initiated in 2011 and continued annually. These included:

- geospatial surveys to map changes in the position of the shoreline associated with inundation of new areas caused by damming and canal construction by beavers;
- macroinvertebrate sampling to assess colonisation of new habitat and to compare the assemblage at this site with that associated with beaver-generated wetlands elsewhere in Scotland or other parts of Europe; and
- extended vegetation sampling to incorporate formerly terrestrial areas which were not included in the baseline survey of this site in 2008, but which are now inundated.

Geospatial surveys were also initiated at Un-named Loch (North) to quantify the effects of water level rise associated with a small dam.

In 2013, following observations of the scale of decline of the emergent plant great fen-sedge *Cladium mariscus* in several lochs, a greenhouse-based germination experiment was established at Stirling University, using sediment from the affected lochs to determine whether re-establishment of this species was possible in the absence of beavers.

4. METHODS

4.1 Survey approaches and timing

The majority of macrophyte survey data were collected through the use of two approaches: (i) polygon mapping of stands of vegetation by boat using a GPS and (ii) repeat survey of fixed quadrats. These approaches are illustrated in the example in Figure 5 and described in detail in sections 4.2 and 4.3.
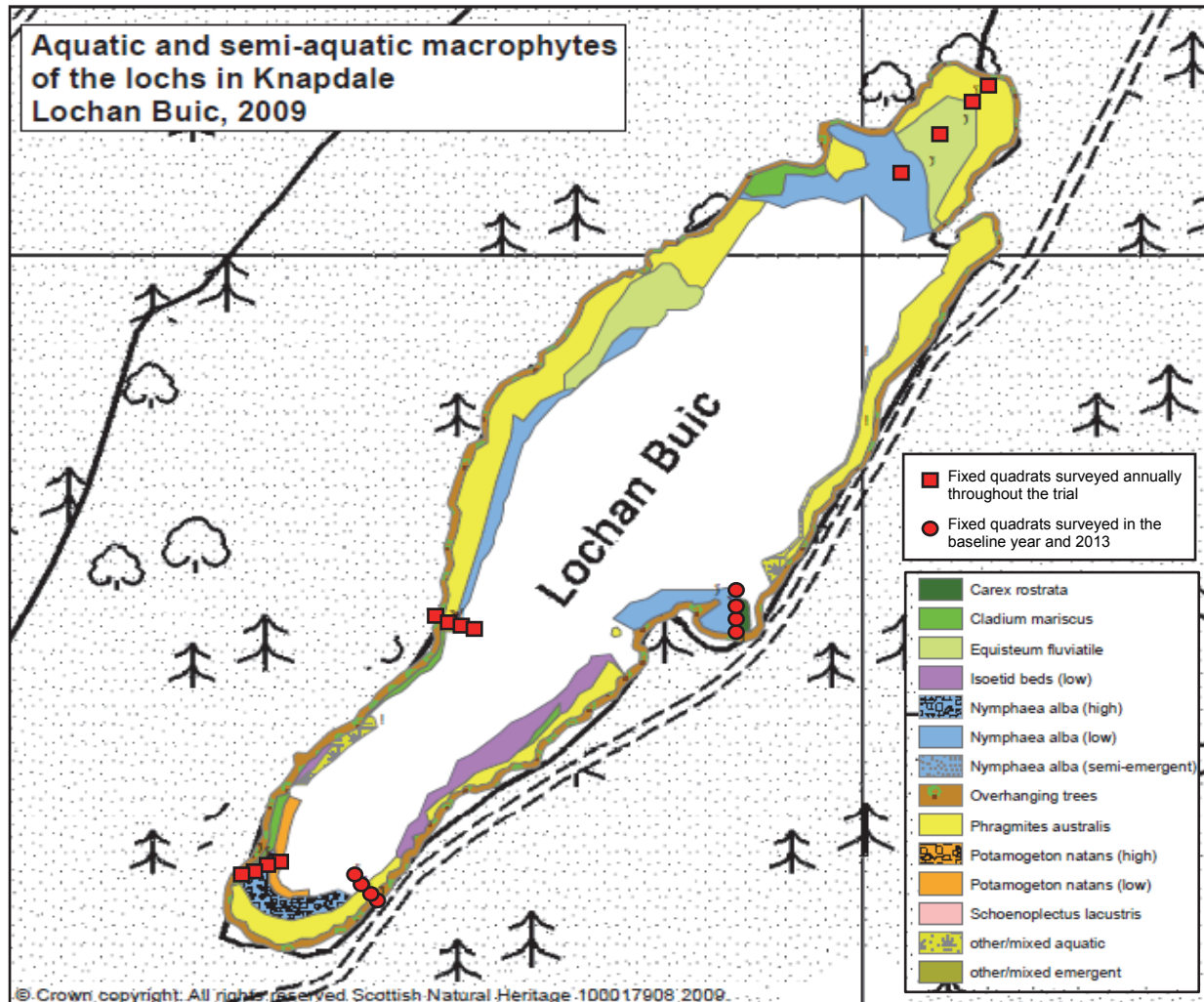
Figure 5. Illustration of the range of aquatic vegetation survey methods employed, using the baseline survey of Lochan Buic as an example.

Note: coloured polygons represent different stands of dominant species and their density (high or low) if variable, as identified and mapped in the field by circumnavigating each polygon in a canoe and taking GPS readings at 5-10 m intervals. Base map reproduced by permission of Ordnance Survey on behalf of HMSO. © Crown copyright and database right 2014. All rights reserved. Ordnance Survey Licence number 100017908.

Following the baseline surveys of the original eight primary lochs in 2008 that included up to five transects per loch, monitoring data for a fixed subset of the vegetation transects (three per loch) were collected in September 2009, May and September 2011 and September 2012. In the same way, baseline data were collected in additional primary lochs in September 2009 and a subset of the transects on these lochs was resurveyed in May and September of 2011, and September 2012. In September 2013, the full population of 50 baseline transects on all 11 lochs was resurveyed.

Macrophyte surveys were mostly undertaken in early to mid-September, near the end of the macrophyte growing season. In Scotland, non-evergreen macrophytes senesce fairly rapidly after this time and any impacts of beavers on macrophytes would be expected to be most apparent following a full growing season in which to manifest. In 2011, macrophyte surveys were also undertaken in late May, at the beginning of the macrophyte growing season. These surveys were designed to establish whether any effects of feeding by beavers specifically on evergreen species over the winter period would be more evident in spring, in line with observations at a site on Tayside (Law *et al.* 2014b). A comparison of May and September surveys in 2011 is provided in Willby and Perfect (2014). This analysis revealed that May was generally too early in the growing season to register significant effects of herbivory at Knapdale, though this finding may have been influenced by the hard winter of 2010/11. Given the lack of comparable data for May in 2012 or 2013, all the data presented in this report refer to late summer (September) sampling unless stated otherwise.

Table 2 summarises the schedule for survey activity throughout the trial project that is covered in this report. When the transect surveys were undertaken, all lochs lying within beaver territories were circumnavigated and specific evidence of beaver feeding on aquatic vegetation was recorded based on field signs (spot sampling). On these occasions, lochs lying outside known territories were also checked for any evidence of use by beavers.

Table 2. Timing of application of different survey methods 2008-2013

	2008		2009		2010		2011		2012		2013	
	May	Sept	May	Sept	May	Sept	May	Sept	May	Sept	May	Sept
Polygon mapping		■		▨								■
Transect surveys		■		▨			▨	▨		▨		■
Spot sampling				■			■	■	■	■	■	
Geospatial surveys							▨		▨		▨	
Invertebrate sampling							▨		▨		▨	

Note: black filling refers to surveys of all transects in all primary lochs. Shaded cells refer to surveys of a subset of lochs or a subset of transects.

Data collected in 2008, 2009 and 2011 together with partial analysis and interpretation, have been reported in Willby and Casas-Mulet (2010); Willby *et al*. (2011) and Willby and Perfect (2014) respectively. The present report integrates all these data with the final phase of data collection in 2012 and 2013 that has not been previously reported. Dates, sampling methods and conditions during macrophyte surveys over the full period of monitoring are detailed in Table 3.

Table 3. Details of survey methods and conditions during all surveys

Loch name	Methods[1]	Autumn 2008 survey conditions[2]	Autumn 2009 survey conditions[2]	Spring 2011 survey conditions[2]	Autumn 2011 survey conditions[2]	Autumn 2012 survey conditions[2]	Autumn 2013 survey conditions[2]
Creagmhor Loch	B,R,U	Good-Moderate	Moderate	Poor	Moderate	Good	Moderate
Dubh Loch	R,U	Good	Good	Moderate	Moderate	Moderate	Moderate
Loch Barnluasgan	B,R,U,S	Poor	Moderate	Moderate	Moderate	Poor	Good
Loch Coille-Bharr	B,R,U,S	Good	Good-Moderate	Poor	Moderate	Moderate	Moderate
Loch Fidhle	B,R,U,S	Moderate	Moderate-Poor	Moderate	Moderate	Good	Good
Loch Linne	B,R,U,S	Moderate-Poor	Moderate-Poor	Moderate	Moderate	Good	Good
Loch Losgunn	B,R,U	Good-Moderate	Moderate	Good	Moderate	Poor	Moderate
Loch McKay	B,R,U	-	Good-Moderate	Moderate	Moderate	Good	Good
Lochan Buic	B,R,U,S	-	Poor	Moderate	Good	Moderate	Good
Un-named (North)	B,R	Good	Moderate	Good	Good	Good	Good
Un-named (South)	B,R,U	-	Moderate	Moderate	Moderate	Good	Moderate

Loch name	Methods[1]	Autumn 2008 survey dates	Autumn 2009 survey dates	Spring 2011 survey dates	Autumn 2011 survey dates	Autumn 2012 survey dates	Autumn 2013 survey dates
Creagmhor Loch	B,R,U	11/09/2008	22/09/2009	18/05/2011	01/09/2011	05/09/2012	18/09/2013
Dubh Loch	R,U	11/09/2008	24/09/2009	19/05/2011	01/09/2011	06/09/2012	06/09/2013
Loch Barnluasgan	B,R,U,S	09/09/2008	23/09/2009	19/05/2011	01/09/2011	06/09/2012	19/09/2013
Loch Coille-Bharr	B,R,U,S	12/09/2008	24/09/2009	24/05/2011	01/09/2011	06/09/2012	05/09/2013
Loch Fidhle	B,R,U,S	10/09/2008	23/09/2009	19/05/2011	31/08/2011	05/09/2012	04/09/2013
Loch Linne	B,R,U,S	10/09/2008	23/09/2009	19/05/2011	31/08/2011	05/09/2012	04/09/2013
Loch Losgunn	B,R,U	01/10/2008	24/09/2009	24/05/2011	31/08/2011	06/09/2012	18/09/2013
Loch McKay	B,R,U	-	22/09/2009	24/05/2011	02/09/2011	04/09/2012	17/09/2013
Lochan Buic	B,R,U,S	-	21/09/2009	24/05/2011	02/09/2011	04/09/2012	03/09/2013
Un-named (North)	B,R	11/09/2008	22/09/2009	18/05/2011	01/09/2011	05/09/2012	05/09/2013
Un-named (South)	B,R,U	-	22/09/2009	24/05/2011	02/09/2011	04/09/2012	19/09/2013

1. Survey methods employed, where B - boat; R - rake; U - underwater viewing *in situ*; S - snorkelling
2. Good - still, strong incident overhead light; Moderate - light wind, cloud and angled light, occasional light showers; Poor - moderate wind, full cloud cover, intermittent heavy rain

4.2 Polygon surveys

The process of mapping vegetation at each site involved the identification of macrophyte beds. These were recorded as polygons, each characterised by the dominance of a particular species or combinations of species. The tendency for aquatic macrophytes to form large, relatively discrete and near mono-dominant beds enabled polygons to be defined

and mapped with relatively minimal subjectivity. The number of polygons in each loch depended on the diversity and complexity of the vegetation, the number ranging from nine to 30. Each polygon was mapped by circumnavigating the macrophyte bed in a canoe, taking GPS readings every 5-10 m depending on the size and shape of the polygon. The hand-held Garmin GPS72 receiver provided location information. The geographic accuracy (i.e. uncertainty in position relative to the OS grid) reported by the device at the time of survey was typically 4-8 m (8-13 m in shade) but ground-truthing indicated that relative accuracy (i.e. position of one mapped point relative to another) was much higher (less than 3 m). Plant composition (percentage cover for each species), water depth and substrate were recorded for each polygon. A total of 234 polygons were described and mapped across the primary lochs during baseline surveys in 2008 and 2009. Subsequently, all polygons were digitised using QGIS and were classified according to the dominant species in each polygon. When overlain on digital aerial photographs taken in 2005, it was evident that this provided a robust approach to vegetation mapping, there being a close match between polygons and coarse scale vegetation features on the aerial photographs. During visits to these sites in 2011, a small number of errors in the GIS mapping of specific polygons were noted and corrected. These involved closure of polygons at incorrect positions due to an incomplete set of polygon co-ordinates.

All 11 primary lochs were resurveyed in September 2013 by the same personnel following the same polygon mapping approach as was used during the baseline surveys. The availability of improved GPS technology in 2013 allowed an increase in the mapping precision, thus reducing survey error. Polygons were mapped using a Garmin Glo GPS/GLONASS receiver blue-toothed to field computer. This provided a method of real time mapping, making it possible to validate the positioning and size of polygons directly in the field. The sensor was regularly ground-truthed and consistently provided a relative accuracy of less than 2m. Reference sections of shoreline were also walked and marked to verify the underlying OS base map, which had proved to be inaccurate at some sites in 2008. No attempt was made to directly replicate the positions of polygons mapped in 2008 or 2009, although the classification of major polygon types was largely the same. In 2013, a total of 224 polygons was defined and mapped.

For both baseline and 2013 surveys, the digitised polygon data were used to calculate the shape area for the individual polygons. By multiplying these by the percentage cover scores of the species present within each polygon, an individual cover-weighted area was calculated for each macrophyte species. This effectively provided an estimate for the standing stock (as square metres occupied) of each species recorded in each loch on each date. Spatial change in polygon locations was not considered between survey dates, as this is too prone to the effects of GPS resolution at the time of the survey and was not the purpose of the exercise. Moreover, the results of these surveys indicated that the basic positioning of polygons was largely stable between the 2008/09 and 2013 surveys.

Measurement error was estimated for the polygon areas and the individual macrophyte areas using the following approach.

A selection of polygons covering a range of sizes was mapped using multiple GPS devices. These polygons were mapped twice several hours apart using three individual devices, providing an element of temporal as well as spatial variation in mapping error. This provided six separate measurements of polygon area for each of the polygon sizes. A model was then built for the relationship between polygon area and the standard deviation in measured area, as shown in Figure 6. This model was used to predict the standard deviation in area for each of the individual polygons mapped during the surveys.

The estimated error for the assessments of percentage cover has been based on repeat assessments of cover from a randomised assortment of photos showing the Knapdale

polygons. As with polygon area, data were then used to model the relationship, in this case between percentage cover and the standard deviation of assessed cover (Figure 6). Standard deviation for each of the species cover scores was then predicted using the model.
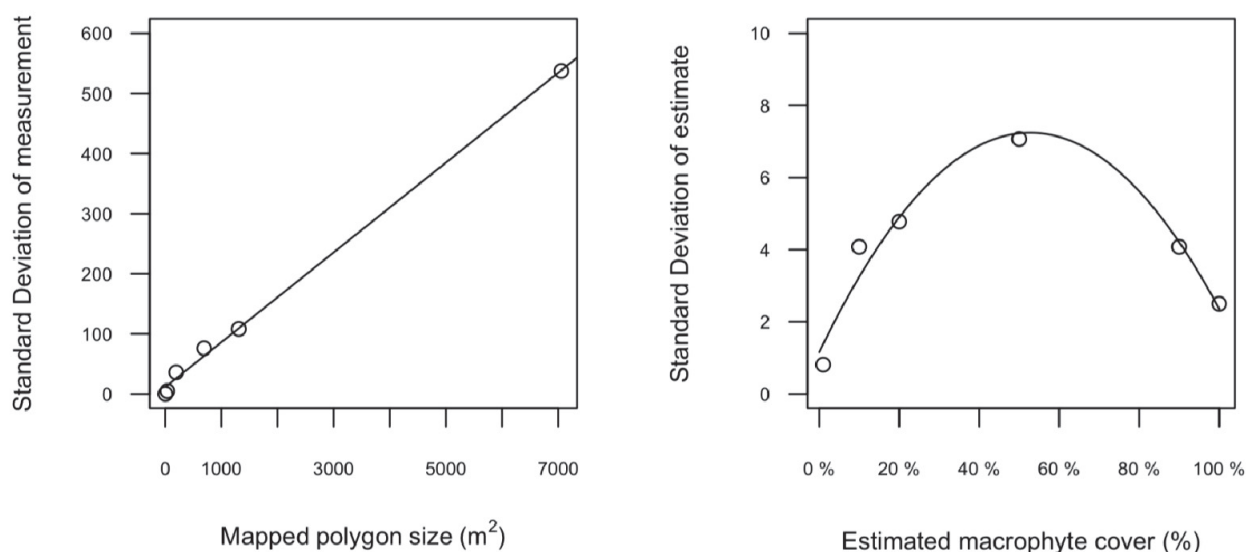
Figure 6. Graphs showing the relationship between measured values and standard deviation for both mapped polygon area and estimated macrophyte cover

Error was then calculated for species area at the loch and polygon scales using theoretical equations for the propagation of error as shown in Equation 1 and Equation 2 where a, b, and c are the measured areas and/or assessed cover scores; and σ_a, σ_b, and σ_c are the predicted standard deviations of those variables.

Equation 1 – Arithmetic calculation for the propagation of error during addition or subtraction

$$\sigma_x = \sqrt{\sigma_a{}^2 + \sigma_b{}^2 + \sigma_c{}^2}$$

Equation 2 – Arithmetic calculation for the propagation of error during multiplication or division

$$\frac{\sigma_x}{x} = \sqrt{\left(\frac{\sigma_a}{a}\right)^2 + \left(\frac{\sigma_b}{b}\right)^2 + \left(\frac{\sigma_c}{c}\right)^2}$$

Propagation of error for total polygon area in m² (loch scale) and total species percentage cover (polygon scale) were both calculated using Equation 1. Propagation of error for macrophyte area of individual species m² (polygon scale) made use of Equation 2. Propagation of error for total community cover m² (polygon scale), total community cover m² (loch scale) and individual species cover m² (loch scale) required a combination of both equations.

To estimate the uncertainty in species richness at a loch level, the number of species apparently lost and the number of species apparently gained between the baseline and 2013

surveys was derived for each of the four lochs with low or zero beaver occupancy. These lochs were used as they indicate the likely repeatability of surveys carried out by the same observers at different times, but without any potential additional influence of beavers. It is assumed in these repeat surveys that no species were truly lost or gained (true species turnover at the whole loch scale over such a short time interval would be very unlikely), but were merely not detected. The mean of the numbers gained and lost was then expressed as a proportion of the mean number of species recorded in each of the two surveys. This suggested an average error of approximately ±10% in the number of species recorded per survey. This error was then assumed to apply to surveys of those lochs occupied by beavers.

4.3   Transect surveys

In the course of polygon mapping, sites were identified within each loch to establish fixed transects. Transects were intended to facilitate high-resolution replicate sampling of fixed points in a loch because annual whole loch polygon surveys would have been prohibitively costly and may have been too coarse-grained to capture local changes in vegetation. The number of transects per water body (four or five) depended on loch surface area and the extent and complexity of aquatic vegetation. Transects were located to ensure good separation (with a minimum distance between transects of about 50 m shoreline perimeter) and their locations were designed to capture the range of growing conditions present. Given the specific focus on the effects of beavers on aquatic vegetation, transects were not positioned in sparsely or un-vegetated locations (e.g. associated with heavy tree shade, steeply shelving or rocky margins). At each location, a transect was established running perpendicular to the shore, from a point 2 m inland to a water depth of 3-5 m, or the maximum depth of macrophyte colonisation if less. On each transect a 2 m x 2 m quadrat was located on the shore, typically 1-2 m from the water's edge. The mid-point of the landward edge of this quadrat was marked with a length of angled steel railing driven into the soil, to a depth of approximately 0.5 m, leaving approximately 1 m projecting above the surface. The markers were conspicuous and allowed transect lines to be visually located from a distance and ensured that they were avoided by other fieldworkers. Three further quadrats of the same size were positioned along each transect, one at the water's edge in the marginal zone, a second at a water depth of between 0.5 m and 1 m, and the third at the end of the transect, near the limit of the vegetated zone. The mid-point of each of the four 2 m x 2 m quadrats was recorded with a hand-held GPS. The back edge of these quadrats was also marked using a wooden or plastic stake, which ensured ease of relocation. Outermost quadrats, i.e. those furthest from the shore, could only be marked where water depth or substrate type permitted.

In total, 50 transects were established around the perimeter of the 11 primary lochs, each transect line initially containing four fixed quadrats. Subsequently, in Dubh Loch in 2011, the transect lines were extended landward to encompass newly inundated areas by adding extra quadrats. An additional transect line was also added at the south end of Dubh Loch at this time. Following baseline surveys in 2008 or 2009, in which the fixed quadrats were established, a fixed subset of three transects on each loch was surveyed in 2011 and 2012. In 2013, the full set of transects on each loch was resurveyed. A standard survey protocol was adopted, as described in Willby and Casas-Mulet (2010) and all data were collected by the same team of surveyors. Data were collected from a total of 760 unique quadrat x survey x date combinations.

On each visit, the water depth and substrate were noted for each 2 m x 2 m quadrat. The percentage cover of all plants present in each 2 m x 2 m quadrat was estimated visually to the nearest 5% if more than 5% cover and the nearest 1% if less than 5% cover, and recorded on waterproof paper. Quadrats located on the bank or in shallow water (of less than 0.5 m) were clearly viewable from a standing position. In deeper water, quadrats were

generally viewed from a canoe or using a snorkel-mask, as required. To avoid disturbing the vegetation along transects, a rake was not used. At several sites, where water was deeper than 1.5 m and the bed of the loch was not clearly visible from the surface, snorkelling along transects was used to confirm the cover of individual species. Snorkelling was also used as the most appropriate survey method when *in situ* viewing of submerged vegetation revealed a high density or complexity of vegetation structure. In some cases, quadrat markers had detached or were not visible due to high macrophyte cover or growth of epiphytic algae. For unmarked quadrats and those with missing markers, a combination of GPS, alignment with other quadrats on the same transect, measured water depths and photographic records were used to find the correct position, although exact overlap of quadrats at the outer end of the transects proved impossible to achieve. Spatial overlap of these quadrats was 50-70%, based on blind relocation of those outermost quadrats that could be physically marked. However, such quadrats were always located in large, relatively homogeneous beds of vegetation, so the consequences of reduced relocation accuracy are likely to be small. Across all quadrats on all transects mean spatial overlap of sampling areas was estimated to be 90%.

Several dependent variables were considered to describe the transect vegetation data: (i) species richness (i.e. number of species per quadrat); (ii) summed cover (i.e. the sum of the individual species percentage cover values of all species recorded in a quadrat); (iii) indicator species score to reflect composition. In the latter case, the composition was synthesised into a cover-weighted mean indicator score for light and moisture (Equation 3) using the Ellenberg scores for British plants (Hill *et al.*, 1999). Ellenberg scores are an empirically validated, expert-based system that ranks species according to their strength of association with different environmental conditions (e.g. dense shade or standing water).

A simple calculation of the mean Ellenberg score for all species present within a quadrat would not allow for the fact that although a range of species are present, those species best suited to the environmental conditions may dominate the quadrat. By 'weighting' the Ellenberg score for each species by their respective cover values, a score is produced that should give an indication of the general light or moisture preferences of the community present, and as such gives an indication of the environmental conditions to which the community is exposed.

*Equation 3 - Calculation of the cover-weighted mean indicator score where c^a is the percentage cover for species **a** and E^a is the Ellenberg score (either light or moisture) for species **a***

$$Indicator\ score = \frac{(C^a \times E^a) + (C^b \times E^b) + (C^c \times E^c) + \cdots}{Summed\ cover\ of\ all\ species}$$

4.4   General abundance surveys

At the conclusion of the polygon mapping and transect surveys, an overall assessment of the abundance of all taxa recorded in each water body was made and agreed by two observers. The DAFOR scoring system (as described by Lassiere 1998) was the basis for describing abundance[2]. In line with previous surveys, DAFOR values were prefixed with 'L' for 'locally' to signify a concentration of a taxon at a particular abundance level, rather than a general distribution throughout the water body. Plants that could not be identified directly in

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[2] The DAFOR scale is used for classifying species into categories of abundance at a site. It takes its name from the first letters of the five levels recorded: D (dominant), A (abundant), F (frequent), O (occasional) and R (rare).

the field were retained and identified subsequently using Preston (1995), Stewart and Church (1992), or Rich and Jermy (1998).

4.5   Geospatial surveys of selected lochs

The perimeters of Dubh Loch and Un-named Loch (North) were documented using differential GPS (DGPS) (Leica GPS1200) capable of providing a spatial accuracy of approximately 5 cm. These lochs were identified for survey as they were subject to the greatest change in area and depth as a result of damming of the outflows by beavers. Positions along the water's edge were recorded every 3-5 m around the perimeter of the loch. These surveys were carried out annually in May from 2011 to 2013.

The Shoreline Development Index (SDI) (Hutchinson 1957) was used to quantify changes in loch shoreline complexity. The SDI is designed to account for the influence of loch size on the perimeter to area ratio. A higher score indicates a more irregular shape or a greater number of inlets and bays. As such it reflects the potential for development of littoral communities. The following equation (from Hutchinson 1957) was used to calculate the SDI for the primary lochs and evaluate change in the SDI as a result of dam building:

$$Shoreline\ Development\ Index = \frac{Shoreline\ Length}{2 * \sqrt{\pi} * Loch\ Area}$$

Area and SDI values for new outlines calculated using the DGPS data were compared with pre-change data from Ordnance Survey.

4.6   Macroinvertebrate sampling

Macroinvertebrate assemblages within the zone of Dubh Loch that was inundated as a result of dam building were surveyed annually from May 2011 to 2013. Samples were collected using a D-frame sweep net (1 mm mesh) by sweeping vegetation and disturbing benthic surfaces over an area of approximately 2 m^2 for 1 minute. Samples were collected from seven discrete locations that reflected the diversity of habitats present (Figure 26; page 52). Collected material was partially sorted on a large white tray in the field with adult beetles identified and returned to the site, bar a few voucher specimens. Retained material was preserved in 70% methylated spirits (industrial) and stored at 4°C prior to sorting. All individuals were identified to the highest taxonomic level possible. For the purposes of numerical analyses, those individuals that could only be identified to family or genus were assigned to the closest determined species to ensure that no abundance data were lost. Annual changes in community composition were explored and overall composition relative to similar sampling undertaken at other beaver sites in the UK and Sweden was assessed. Reference was also made to records of water beetles collected from Dubh Loch in May 2009 by Dr Garth Foster (pers. comm., 2011), shortly before beavers were released.

An individual-based rarefaction curve (Colwell *et al.*, 2004) was used to observe species accumulation for (i) all taxa and (ii) water beetles, due to differences in the number of individuals found per sample and per year. Rarefaction allows the calculation of species richness for a given number of individuals, based on the construction of so-called rarefaction curves. In this case, rarefaction was determined based on 1000 resampling events from the total population of individuals collected each year to estimate the mean number of species that would be associated with a given number of individuals. Species composition and turnover between samples per year were compared using non-metric multidimensional scaling (NMDS) based on the Bray-Curtis dissimilarity Index (BCI) matrix which assesses pairwise similarity amongst samples. Richness was assessed as numbers of species per sample and as Shannon's Diversity Index (H'). The significance of differences in BCI, richness and H' between years was tested using a Kruskal Wallis test with a Tukey's test

then used to determine differences between pairs of years. All statistical analyses and graphics were produced using R Studio version 2.15.0 (R Development Core Team, 2012) with the additional packages; Vegan (Oksanen *et al.* 2012), BiodiversityR (Kindt and Coe 2005) and ecodist (Goslee and Urban 2007).

4.7 Greenhouse experiment on seedling regeneration

In view of significant declines in the cover of *C. mariscus* in several lochs as a result of foraging and herbivory by beavers, a greenhouse-based experiment was set up to simulate the effects of beaver removal and thus determine the potential for re-establishment of this plant species. In May 2013, submerged sediment was collected from the littoral zone of two water bodies, Loch Creagmhor and Loch Fidhle, from areas that had formerly supported stands of *C. mariscus,* plus control areas of the same lochs (i.e. where *C. mariscus* had not previously been observed growing). Stem and leaf litter of *C. mariscus* was also collected from the same lochs. A germination trial was set up in a polytunnel by placing this sediment in shallow trays to determine whether regrowth of *C. mariscus* from seed or stem fragments could occur in the absence of continued foraging by beavers. This experimental approach was adopted as an alternative to field exclosures, which would have been difficult and costly to assemble and monitor, and carried a risk of entrapment of beaver kits.

The following four treatments were applied to the sediment from each loch: (i) *C. mariscus* sediment, (ii) *C. mariscus* sediment + litter, (iii) control sediment and (iv) control sediment + litter. Four replicate trays were established for each loch-treatment combination. Trays were arranged in a fully randomised design in an unheated, ventilated polytunnel (Figure 7), with a natural light and temperature regime (day time maximum of $25^{o}C$). Trays were suspended in a larger reservoir tray that ensured full soil saturation and which was replenished three times per week with local un-chlorinated tap water. Based on published field observation and research on germination requirements of *C. mariscus* and other closely related species, the conditions provided would have been expected to be favourable for germination, if viable seed or other propagules were present (Ponzio *et al*., 1995; Lorenzen *et al*., 2000). Germination of all species was monitored monthly over the subsequent 13 months, after which no new germination was observed. The effect of these treatments on germination was analysed using a Generalised Linear Model with a Poisson log-link function (for number of species) or a General Linear Model (for square root transformed numbers of individuals).

Figure 7. Layout of polytunnel experiment for germination trial

4.8 Analysis of beaver effects

To assess the potential effects of beaver activity on vegetation, several indices were used to quantify beaver occupancy of individual lochs. Lochs were considered 'occupied' when they supported an active lodge. The number and age of animals and occupancy of individual lochs were derived from data provided by SBT staff. Occupancy was determined from direct observations of animals, radio-tracking, or use of camera traps, rather than indirectly from field signs. In constructing the indices, the rationale was that the impact on vegetation would increase with the number of animals present at a site and their duration of habitation, and would be greater during the plant growth season than at other times of year. Various candidate terms were considered to reflect beaver occupancy. (A beaver month equates to one animal for one month. For example, if a single animal occupied a site continuously for the whole trial period relevant to this report (May 2009 to September 2013) by the final macrophyte sample date (September 2013) that site would have experienced 53 beaver months. If there were two animals the value would be 106 beaver months):

(i)   total cumulative beaver months
(ii)   juvenile-weighted cumulative beaver months: as for (i) but with juveniles (animals less than 12 months old) carrying half the weight of adults in the calculation of beaver months. If one adult and one juvenile occupied a site continuously for 53 months, this would equate to 79.5 juvenile weighted-cumulative beaver months.
(iii)   total beaver months in the current growing season (occupancy in the months outwith the May to September growing season are excluded from the calculation)
(iv)   juvenile-weighted total beaver months in the current growing season
(v)   total beaver months across the current and preceding growing seasons (total beaver months in the year up to the date of survey, together with those in the preceding year, excluding any that are outwith the May-September growing season)
(vi)   juvenile-weighted total beaver months across the current and preceding growing seasons
(vii)   cumulative months of occupancy independent of the number of animals present
(viii) cumulative growing season months of occupancy independent of the number of animals present.

Exploratory analyses of the relationship between these variables and different vegetation metrics suggested that the fifth term in the above list; 'total beaver months across the current and preceding growing seasons' was the optimal continuous term to reflect the effects of beaver occupancy on vegetation, based on changes recorded across the duration of the trial. This supports the expectation that impacts would increase with the number of animals present and be greater during the plant growing season. It also implies that if there are several intervening seasons with low occupancy effects will begin to diminish. Furthermore, the use of a term that does not down-weight the impact of juveniles is consistent with the findings of other studies that indicate that aquatic plant herbivory by beaver kits, despite their smaller body size, can be as significant as that of adults, because kits do not supplement their diet with woody material during summer to the same extent as adults (Milligan and Humphries 2010). However, in practice all the beaver occupancy terms are highly intercorrelated. The disadvantage of terms based on cumulative occupancy is that by incorporating a temporal dimension, it is difficult to test the effect of any year x occupancy interaction term independently and the significance of this interaction is potentially as important as the occupancy main effect, as the effects of a given level of occupancy may vary by year. The 11 lochs were therefore stratified according to three main classes of occupancy: low (i.e. never, or only very briefly occupied lochs); medium (intermittently occupied by small numbers of non-breeding animals); high (prolonged occupancy by breeding adults and young). Each occupancy class contained three or four different lochs

(Table 4). Although two beavers were originally released at Un-named Loch (South) in May 2010, they spent only two months there and there is no evidence that this site was regularly occupied after June 2010. Consequently this site was included in the Low occupancy category.

Table 4. Assignment of lochs to different levels of beaver occupancy based on the number of beaver months in different growing seasons

Loch	2008	2009	2010	2011	2012	2013	Class
Barnluasgan	BL	0	0	0	0	0	
Losgunn	BL	0	0	0	0	0	
McKay	-	BL	0	0	0	0	Low
Un-named (South)	-	BL	3	0	0	0	
Coille-Bharr	BL	12	0	0	0	4	
Creagmhor	BL	2	8	6	0	0	Medium
Un-named (North)	BL	0	0	6	10	5	
Buic	-	BL	5	10	11	21	
Dubh	BL	3	17	22	24	16	
Fidhle	BL	16	17	18	21	18	High
Linne	BL	16	17	18	21	18	

Note: values refer to total beaver months during the growing season (May – September inclusive) of the year in question. If three beavers (adult or juvenile) are present for one entire growing season (5 months) this equates to 15 beaver months. BL indicates the year of baseline data collection. Data on numbers of animals per month provided by SBT.

Linear mixed effects modelling was applied to the quadrat data using R version 2.15.0 and the package lme4 (Bates *et al*., 2013). Quadrat-level richness was modelled via a Generalised Linear mixed model with a Poisson family distribution using a log-link function and fit by Maximum Likelihood. To ensure a log-normal form to the Poisson distribution (qualitatively equivalent to a negative binomial), which represented the observed distribution of quadrat level richness values (Figure 8), an observational level random effect was included in the model. For summed cover, values commonly exceeded 100 due to multi-layering of vegetation. Cover data were used in their raw form following inspection of regression diagnostics based on raw and variously transformed data. This confirmed normality, independence and homogeneity in the model residuals using untransformed data. A General Linear Model with Gaussian distribution using an identity-link function and fit by REML was used in the modelling of the cover data.

Loch, transect, quadrat position and their interaction terms with year of sampling were nested within the model as random effects to account for the nested structure of data points. Two random effects terms were considered during model evaluation, one containing both random slope and random intercepts (year | loch/transect/quadrat), and one based only on random intercepts (1 | loch/transect/quadrat). Inspection of model AIC values confirmed the superiority of models using only the random intercept term. Year of sampling was treated as a fixed factor to take account of non-linear effects in the repeated measures sampling design. Occupancy (as a factor) was considered both in terms of a main effect (thus assessing whether high or medium occupancy differ intrinsically from low occupancy lochs) and as an interaction with year (thus assessing whether high or medium occupancy lochs differ from low occupancy lochs on a year by year basis). Final models were therefore of the form:

Richness ~ occupancy * year + (1 | loch/transect/quadrat) + (1 | obs)
Summed Cover ~ occupancy * year + (1 | loch/transect/quadrat)

Ellenberg indicator value ~ occupancy * year + (1 | loch/transect)

where '1 |' is used to indicate the random intercepts and '/' is used to indicate the nested effects, (i.e. transects are nested within loch and quadrats are nested within transects). Occupancy comprises three levels, High, Medium or Low and year comprises baseline, 2009, 2011, 2012 or 2013.

In subsequent analyses, the effect of adding and removing various sub-components of the quadrat dataset, on the analyses, were considered.

- Data were excluded for the first quadrat from each transect to provide a stricter focus on aquatic vegetation.
- Dubh Loch experienced a pronounced rise in water level associated with damming by beavers which was unique amongst the beaver-occupied sites. Thus, by excluding this site from the dataset, it was possible to test whether effects associated with other aspects of beaver activity (e.g. foraging, tree felling) were significant in their own right.
- Several trial analyses were undertaken in which different components of the submerged vegetation community were excluded. These are subject to significant weather-related variation in detectability, potentially increasing the noise in the dataset. However, exclusion of data for submerged species tended to weaken rather strengthen the statistical models and for this reason submerged species were retained in the dataset throughout the analyses.
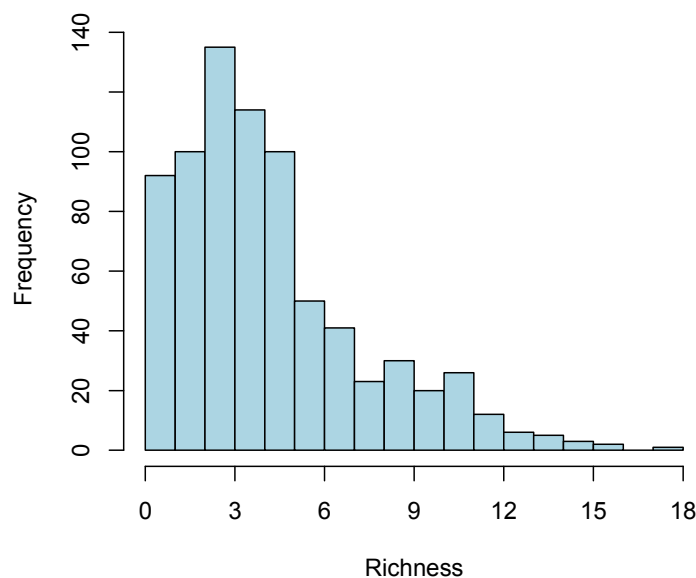
Figure 8. Frequency distribution of observed quadrat level richness

5. RESULTS

5.1 Analysis of polygon data

The scale at which it is possible to reproduce polygon maps for the purposes of this report is of insufficient sensitivity to illustrate the differences in the results of the baseline surveys of 2008 and 2009, and those of the final surveys carried out in 2013. However, the baseline maps of the polygons outlined in 2008 and 2009 are presented in the Appendix, and the polygon data are analysed and presented in a number of ways below.

5.1.1 Loch level species richness

Figure 9 compares the species richness of aquatic vegetation in different lochs between the baseline and 2013 polygon surveys. The general pattern is for the number of species recorded to have increased. This probably reflects a combination of increased familiarity of the surveyors with all sites over the duration of the trial (i.e. not simply in the baseline survey year and 2013) and superior conditions for detectability of aquatic plants in 2013 due to good light conditions and lower water levels. The increase in richness is typically higher in those lochs with high beaver occupancy (median increase of richness of 23%) compared to those lochs with low occupancy (median increase of 6%), but there are insufficient data at this scale of sampling to test whether this result might be an effect of beavers.
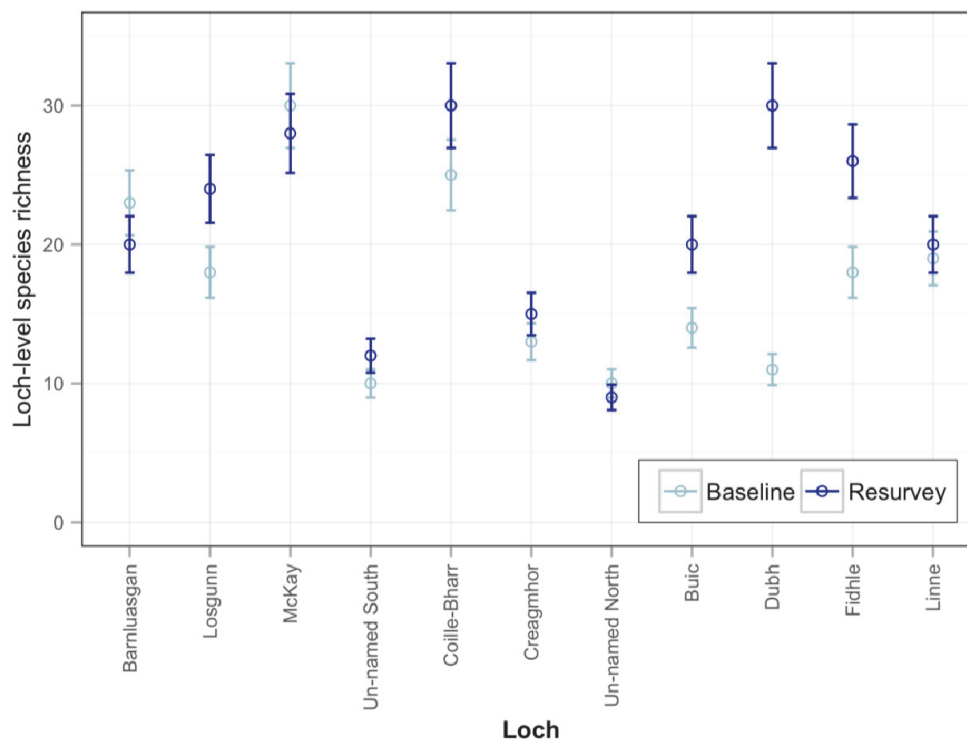
Figure 9. Richness of aquatic plant species in baseline and 2013 polygon surveys

Note: lochs are listed from left to right in order of increasing beaver occupancy. Bars around the points show the estimated standard deviation in richness.

5.1.2 Loch level plant cover

Figure 10 presents firstly the total area of mapped polygons in each loch in the baseline and 2013 surveys, and secondly the total extent of vegetation across these polygons (total community cover). If vegetation is highly dispersed across a polygon, but with low cover, there will be a significant contrast between the mapped area of a polygon and the amount of

cover with which this polygon equates. This presentation of the data is restricted to emergent and floating-leaved species, as these species account for the majority of cover and can be mapped with the highest precision. This is because ease of recording is not vulnerable to weather, disturbance of the water surface, and clarity problems that influence detectability of fully submerged species. This analysis demonstrates two points: (i) in general there was an increase in both total polygon area and vegetated area across the full range of lochs between the baseline and 2013 survey; (ii) the average increase in vegetated area is proportionally greater than the increase in polygon area demonstrating that cover of different species increased mostly through consolidation of cover within existing polygons rather than through expansion of these polygons.
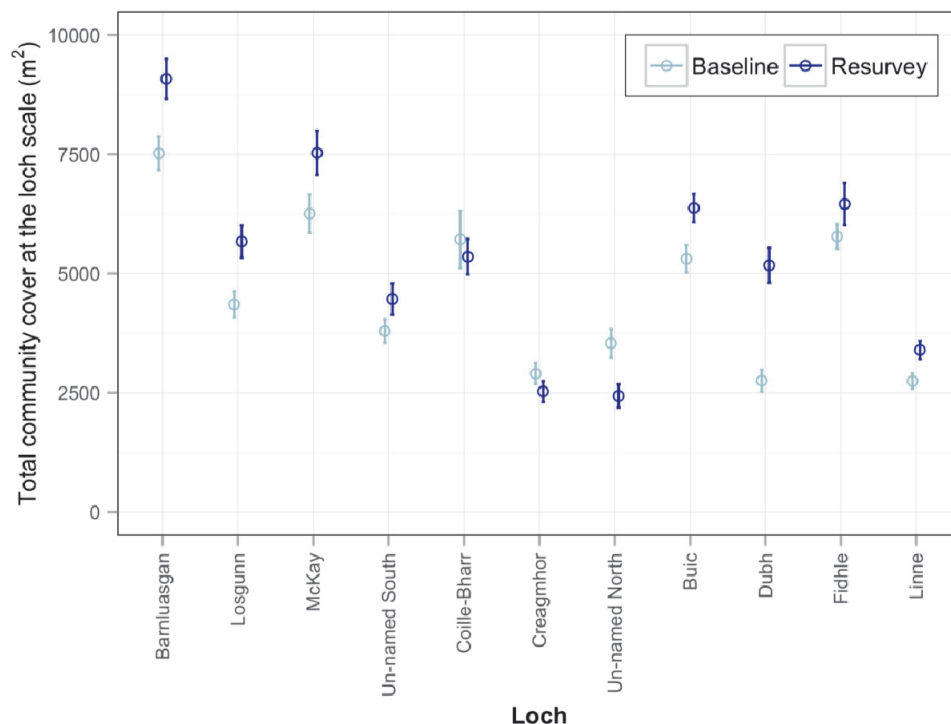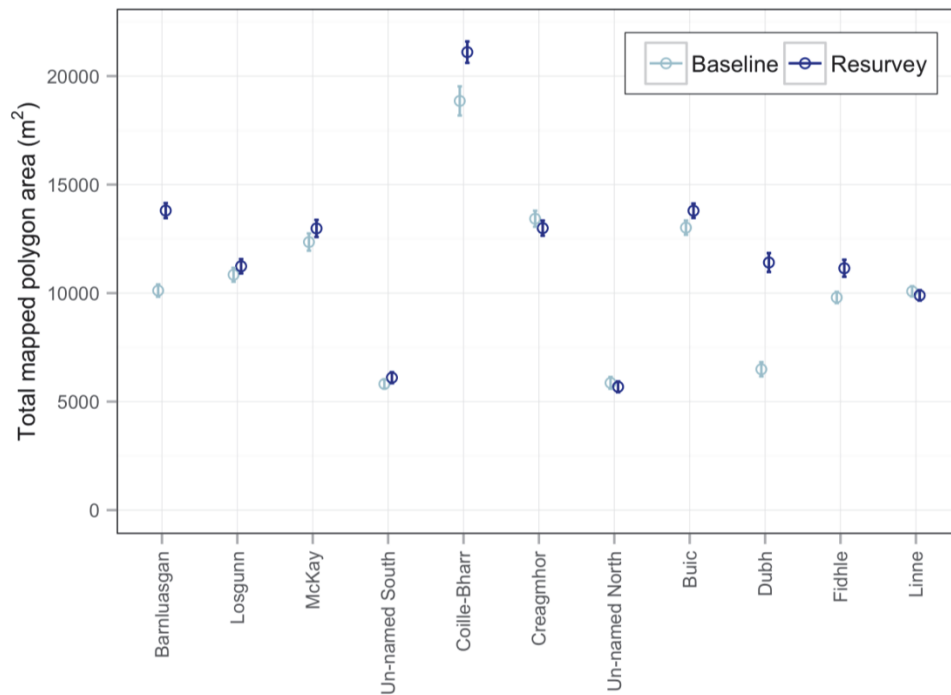
Figure 10. Total polygon area (upper) and total cover (lower) of emergent and floating-leaved species in baseline and 2013 polygon surveys

Note: lochs are listed from left to right in order of increasing beaver occupancy. Bars around the points show the estimated standard deviation.

5.1.3 Species level changes in cover

Figure 11 presents the standing stock (as square metres of cover) of the nine commonest, palatable, species across the Knapdale lochs in the baseline and 2013 surveys based on their contribution to overall cover. The relative change in cover between baseline and 2013 surveys of all the major species found in the lochs (i.e. those that account for the bulk of the recorded cover) is summarised in Table 5. Figure 12 provides an assessment of the change in the global resource of each of these species in the 11 lochs in relation to increasing levels of beaver occupancy. Changes are presented in the context of the percentile distribution of the recorded percentage change across all species in all lochs. Thus, changes that lie within the global interquartile range have low scope for critical interpretation. The further an observed change lies towards the extremities of the distribution of the global population of changes, the less likely it is that such a change can be attributed to operator error and inter-annual variation.

Table 5. Percentage change in cover recorded between baseline and 2013 polygon surveys, for major macrophyte species in the Knapdale lochs. Results are grouped according to levels of beaver occupancy.

	Low				Medium			High			
	Barnluasgan	Losgunn	McKay	Un-named South	Coille-Bharr	Creagmhor	Un-named North	Buic	Dubh	Fidhle	Linne
Carex rostrata	64	24	11	-25	-9		26	-11	**2394**	-13	29
Cladium mariscus						**-96**		**-87**	-58	**-100**	-66
Elodea canadensis	-62				45			-83			
Equisetum fluviatile	114		-2	68	21	-13	-25*	-22	9	**212***	207*
Littorella uniflora	-18	-2	112*		32	45		670*			-8
Lobelia dortmanna	7	11	16		-16	31		204*			21
Nymphaea alba	-10	85	60	36	-33	-26	-28	104	-65	57	94
Potamogeton natans	58	-9	35	17	85	323*	-34	6	-22	-19	4
Schoenoplectus lacustris	66		5	88	39	-24				-76	**-95**

Percentages in **bold** indicate values falling below the 10th or above the 90th percentiles of change for all species across all lochs between 2013 and 2008.
* Indicates a species that had a low absolute cover **(less than 200 m^2)** in both surveys.

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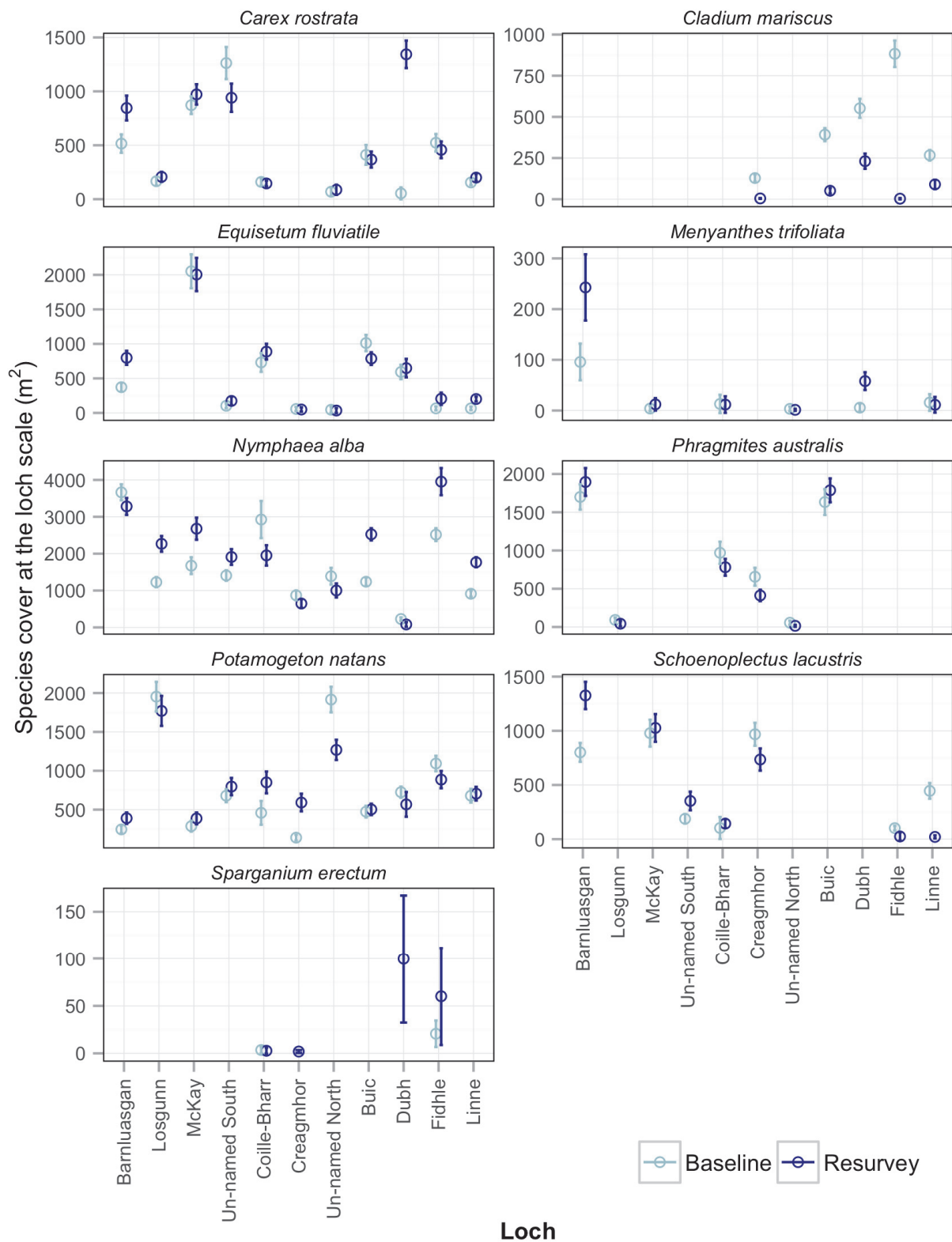
Figure 11. Species cover in square metres summed across polygons, within each of the surveyed lochs for baseline and 2013 polygon surveys

Note: results are presented for a range of species known to be palatable to beavers based on observations at Knapdale or published data. Bars indicate the estimated standard deviation in species coverage. Lochs are listed from left to right in order of increasing beaver occupancy. Note differences in y axis scales.
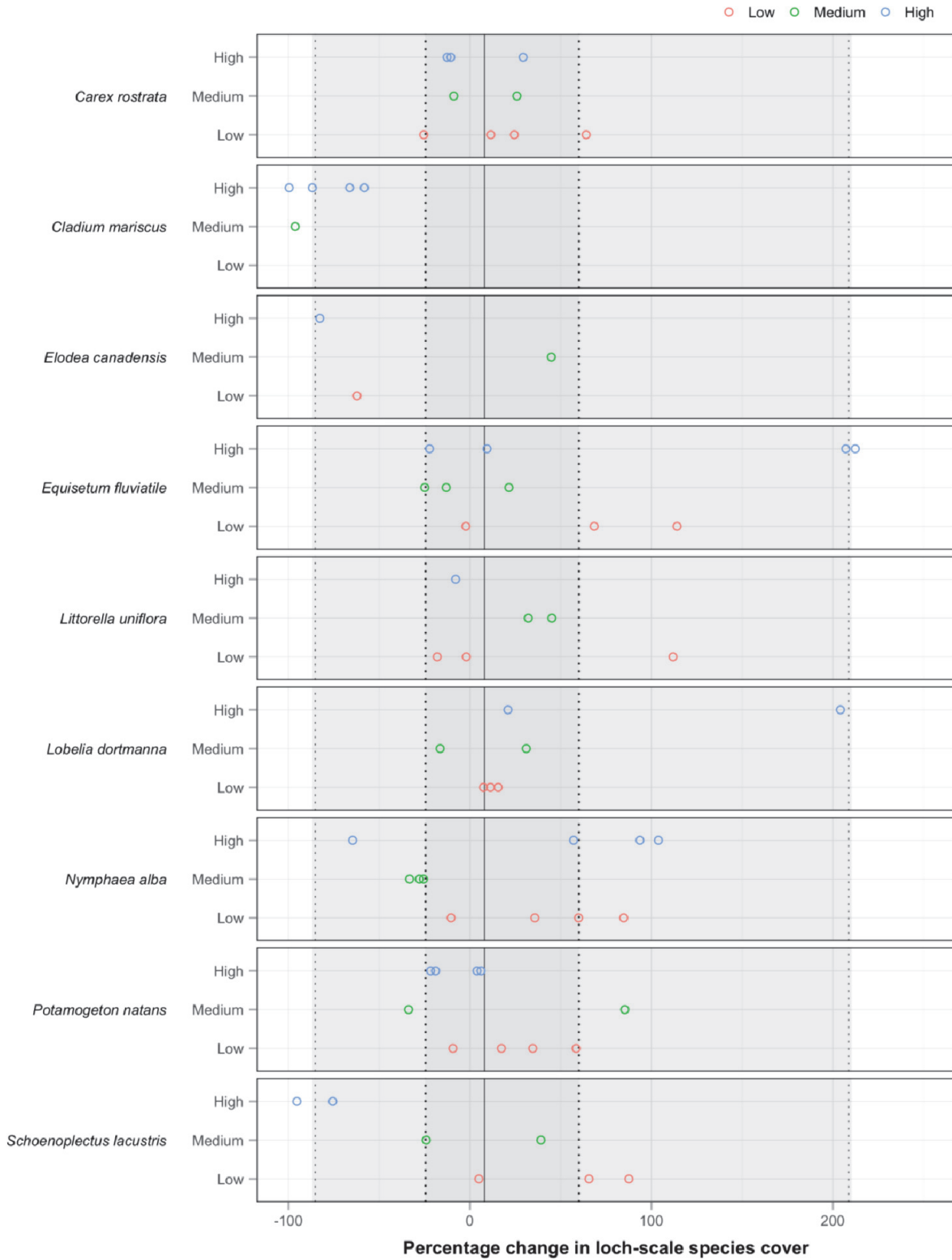
Figure 12. Change in observed percentage cover between 2008 and 2013 for different levels of beaver occupancy

Note: data are presented for major species recorded in the Knapdale Lochs. The dashed vertical lines indicate the 10th, 25th, 75th, and 90th percentiles (from left to right, consecutively). For ease of display, three points exceeding a 250% increase are not plotted (see Table 5 and species accounts on pages 33-35), but contributed to calculation of the percentiles of change.

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Nymphaea alba (white water-lily) (*Figure 11*, Figure 12) showed a high average level of increase in the unoccupied lochs consistent with the quality of the growing conditions in 2013 compared to the baseline year but remained the dominant component of the vegetation in almost all sites. In one of the unoccupied lochs, Loch Losgunn, it is possible that the increase observed was partly influenced by the removal of tree shade associated with clear-felling part of the adjacent catchment during spring 2012. Against a backdrop of general increase in cover in the low occupancy lochs, *N. alba* in the medium occupancy lochs (Coille-Bharr, Un-named North and Creagmhor) declined, typically by about 30%. In Coille-Bharr, signs of active feeding on *N. alba* rhizomes by beavers were observed during 2013 in the sheltered bay in the south west corner of the loch, and it is possible that this also occurred over the winter of 2012-13. Three of the high occupancy lochs (Buic, Linne and Fidhle) also exhibited a strong increase in *N. alba*, probably due at least in part to its expansion into areas formerly occupied by *C. mariscus*. The increase in cover of *N. alba* in Lochan Buic occurred despite active feeding by beavers on this species during 2011.   In the remaining high occupancy loch (Dubh Loch) the decline of 65% was probably largely attributable to a water level rise of over 1m. *N. alba* in Dubh Loch was already growing close to the limits of its ecological tolerance in deep water with poor light penetration, which is probably why it had a low cover in the baseline survey.

Potamogeton natans (broad-leaved pondweed) (*Figure 11*) showed relatively minor changes in overall terms (Figure 12). Creagmhor exhibited the most pronounced increase, which could not be easily accounted for, although one possibility is that *P. natans* benefits from a shift in the competitive equilibrium with *N. alba*. Where the latter performed well, as observed in Losgunn, Linne and Fidhle, increases were achieved by expansion into habitat occupied by *P. natans*, or consolidation of low-density beds where it coexisted with *P. natans*. Decreases in *N. alba* as a result of herbivory by beaver, as in Coille-Bharr, may have favoured the expansion of *P. natans.* The declines in *P. natans* in Un-named Loch (North) and Dubh Loch are almost certainly driven by either increased water depth or disturbance and an associated potential increase in water colour intensity as no direct herbivory of *P. natans* by beaver was noted in these sites.

Schoenoplectus lacustris (common club-rush) (*Figure 11*, Figure 12) increased in cover in most of the low and medium occupancy lochs but not the highly occupied ones. In the case of Creagmhor, the decline was modest and consistent with intermittent feeding on this species by a small number of animals and is probably within the range of inter-annual variability in cover. In both Linne and to a lesser extent Fidhle, beavers fed heavily on *S. lacustris* from the outset of the trial and the scale of the reductions observed (95% and 76% respectively) are entirely consistent with general observations of beaver feeding behaviour and feeding remains.

Cladium mariscus (great fen-sedge) (Figure 11, Figure 12) was only found in five lochs, all of which were occupied by beavers. Given the general pattern of increased cover across most species in those lochs with low or zero beaver occupancy (Figure 12), a similar scale of increase (about 5-25%) in the cover of *C. mariscus* might have been expected. However, this species was heavily grazed by beavers wherever it occurred, especially in Loch Fidhle, Lochan Buic and Creagmhor Loch (Table 5). In Loch Linne and Dubh Loch, the decrease in cover was less severe and may have been partly caused by a temporary or permanent increase in water level rather than direct grazing. In overall terms the standing stock of *C. mariscus* in the Knapdale lochs decreased by 83%. Only one other species, *S. lacustris* in Loch Linne, experienced beaver-induced declines on a similar scale. It is unclear whether beavers would actively select lochs containing *C. mariscus* and in most cases they only began to utilise this species after occupying a loch for several years. At the outset of the trial, two families were released onto water bodies containing *C. mariscus* (Linne/Fidhle, Creagmhor). The Creagmhor family abandoned this site only to return in 2013 when feeding on *C. mariscus* was then intense. The Linne/Fidhle family have never left this site. Of the

remaining release sites, Coille-Bharr, which does not contain *C. mariscus*, was quickly abandoned in favour of Dubh Loch where *C. mariscus* is present, whilst Un-named Loch South was also abandoned in favour of Lochan Buic which supported *C. mariscus*. In such cases it is unclear whether the motivation for movement is behavioural, reflects a specific preference for *C. mariscus*, or is driven more by a preference for the conditions under which *C. mariscus* occurs. A larger sample size would be required to resolve this question.

Equisetum fluviatile (water horsetail) (*Figure 11*, Figure 12) cover was stable or increased in most lochs, even Loch Coille-Bharr where signs of this species being fed upon were commonly observed. In Dubh Loch, despite the loss of a large bed of *E. fluviatile* due to water level rise, the overall population remained stable. This was mainly as a result of a mire at the south end of the site becoming inundated, but also due to recolonisation of the newly formed wetland area. Of the occupied lochs only Lochan Buic experienced a noticeable decline (22%) in cover of this species. This was consistent with moderate feeding on *E. fluviatile* by beavers at this site, although some losses may have been incurred indirectly through feeding on other species, such as *C. mariscus* and *N. alba*.

Carex rostrata (bottle sedge) (*Figure 11*, Figure 12*) showed little overall change across ten of the 11 lochs. The only marked change was in Dubh Loch. Here, in the baseline survey, there was a large area of mire dominated by *C. rostrata* that had been deemed to lie outwith the loch area. In 2013, this had become inundated and connected via beaver dug canals to the expanded Dubh Loch. Since *C. rostrata* is tolerant of a wide range of water depths up to 1m and readily forms floating mire, the expansion in cover of this species at Dubh Loch was considered to be different from the primary colonisation of new wetland areas.

Littorella uniflora (shoreweed) (Table 5, Figure 12) showed little change in all but two sites (lochs McKay and Buic). In these water bodies, the initial extent was relatively small (less than 200 m^2) and may have been underestimated due to the conditions at the time of survey. Based on the distribution of percentage change values, there is no evidence that this species was affected by beaver occupancy. As an understorey species, *L. uniflora* might be expected to respond to changes in the cover of the dominant floating-leaved species, but such a response may require sampling over longer time scales to detect.

Lobelia dortmanna (water lobelia) (Table 5, Figure 12), like *L. uniflora,* showed comparatively little variation in cover (except in Loch Buic). There is no obvious explanation for the disproportionally large increase in *L. dortmanna* in Lochan Buic, other than improved detectability, but the starting cover of *L. dortmanna* in this site was initially small which will inflate the effect of a small absolute increase in cover.

Elodea canadensis (Canadian waterweed) (Table 5, Figure 12) was restricted to three sites at the outset of the trial. This species showed some pronounced fluctuations in cover that are consistent with its 'boom and bust' behaviour elsewhere in the UK and Europe ever since the time of its invasion in the early 1800s, and thus appear to be independent of beaver activity.

5.1.4   Changes in loch-level plant composition based on polygon data

Figures 13 and 14 use an ordination (Detrended Correspondence Analysis) of polygon scale data to explore whether and how the vegetation of different lochs has changed between baseline survey and 2013. In Figure 13, the data are presented so that the ellipses contain the centroid of the polygon data for a loch for a given level of occupancy in a given year. At this scale of analysis it is apparent that the composition of vegetation of high occupancy lochs has shifted whereas that of low and medium occupancy lochs has remained stable. In DCA the axes scores are scaled in units of the average standard deviation of species turnover.
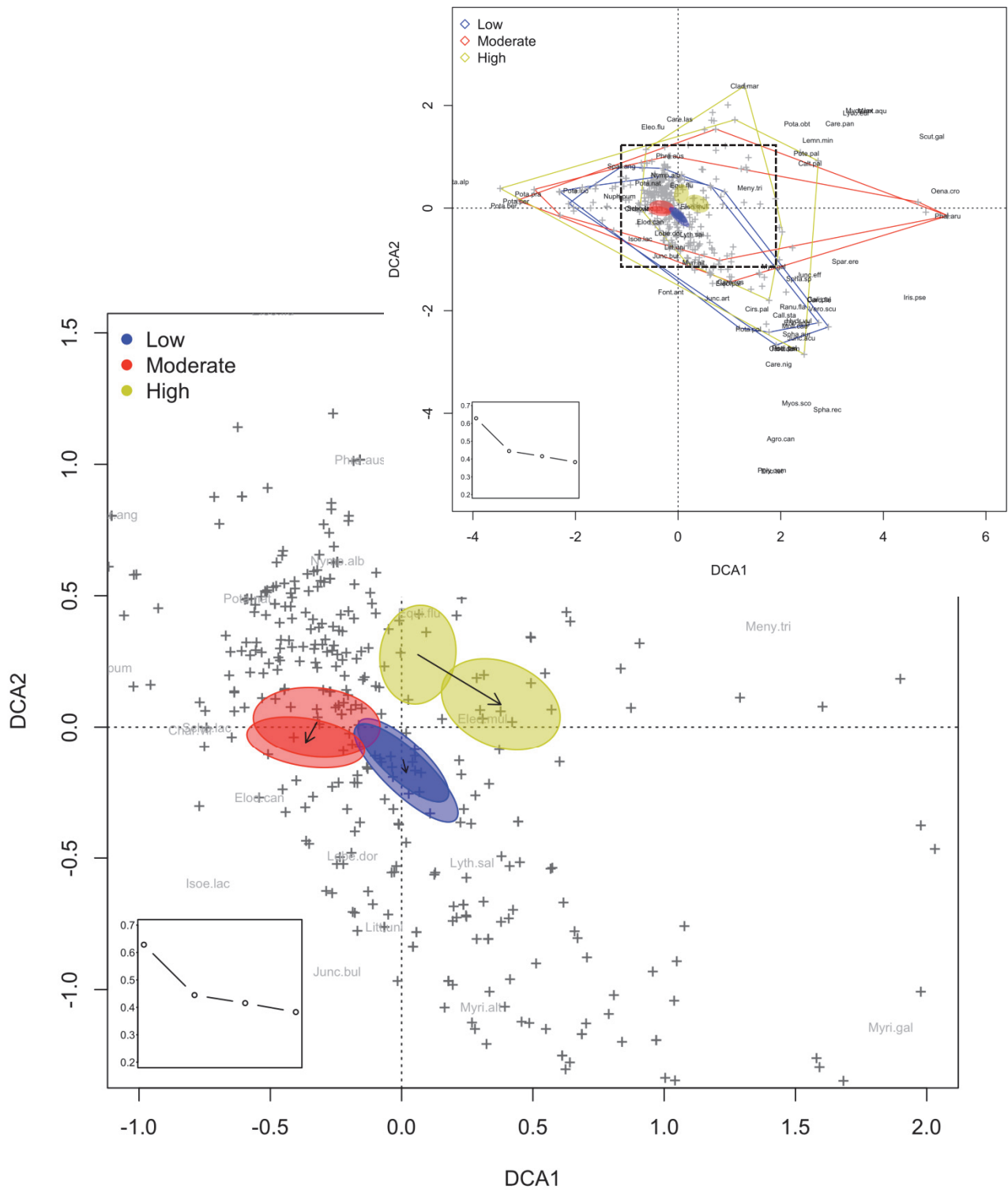
Figure 13. Detrended Correspondence Analysis of polygon data indicating the relative changes in polygon composition between 2008 and 2013 for lochs grouped by occupancy

Note: each cross represents a polygon. Ellipses contain 90% of the year x occupancy centroids. Black dashed lines in upper right inset show area of expanded detail in main figure to lower left.

This means that on average two sites separated by 4 axis units will have no species in common, whilst sites 1 to 1.4 units apart will have about 50% of their species in common. It can thus be seen that in the present analysis the DCA axes lengths are short and the shifts

in composition over time, even in the high occupancy group of lochs, are on average rather small. An analysis of the data where the focus is on site rather than occupancy (Figure 14), however, demonstrates the strong influence of Dubh Loch on the apparent shift in composition of lochs in the high occupancy category. Thus, while Dubh Loch has experienced transformational changes that are clearly translated into changes in polygon data composition, the other three lochs in the high occupancy category, Linne, Fidhle and Buic, have deviated much less from their starting position. Inspection of the species scores confirms that the shift in Dubh Loch is consistent with a decline in aquatic species, such as *N. alba* and *P. natans*, and an increase in the relative importance of mire forming species or those of disturbed wet margins. Four lochs, Fidhle, Buic (High occupancy), Creagmhor (Medium occupancy) and Losgunn (Low occupancy), show an intermediate shift in composition, mostly on the weaker second (vertical) axis. This shift appears to be most closely related with a decline in the relative importance of *C. mariscus* in the occupied lochs, but the basis for the shift in Loch Losgunn (where *C. mariscus* is absent) is less clear and may be related to the expansion of mire vegetation.
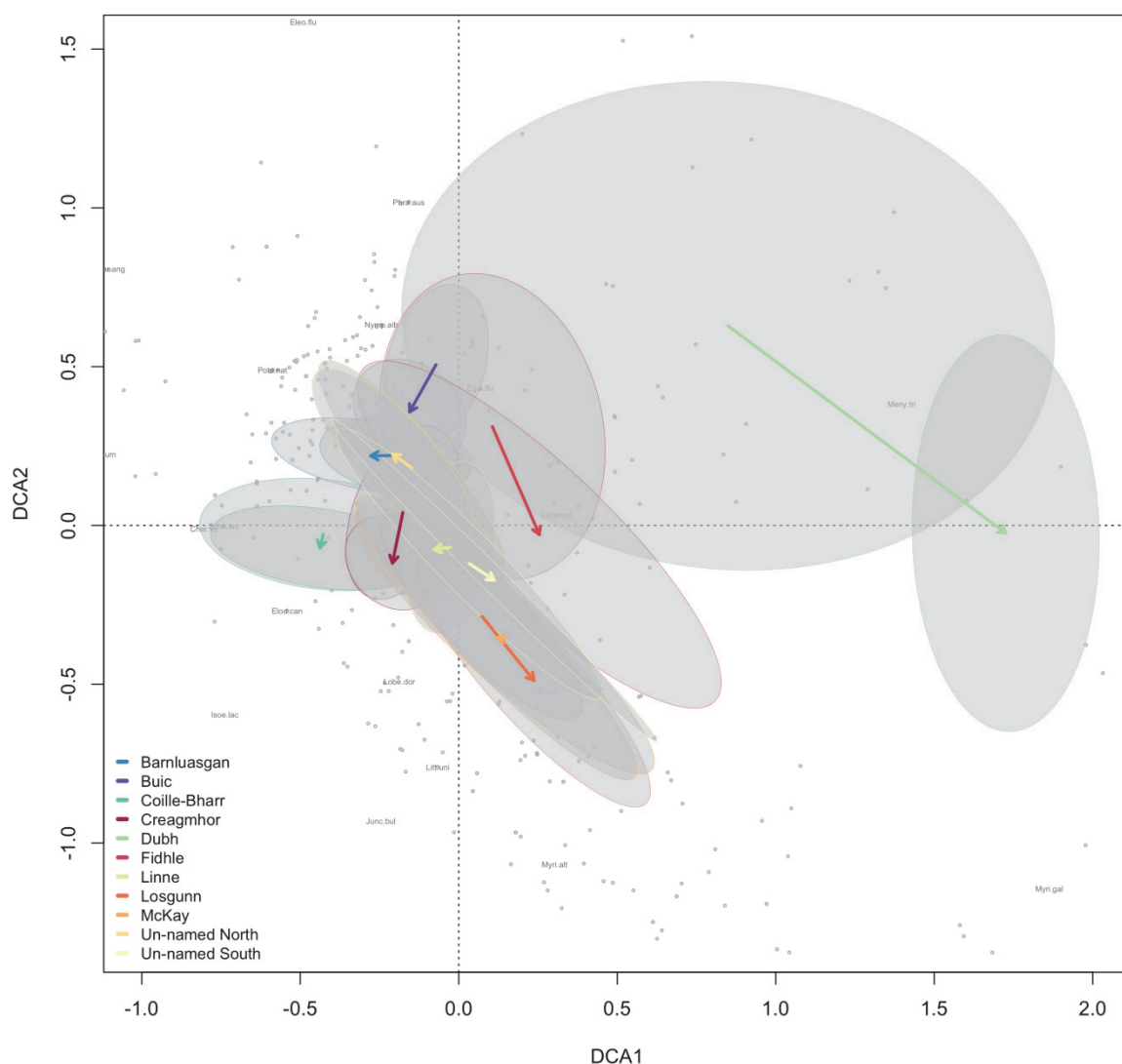
Figure 14. Ellipsoids indicating the plant composition of individual lochs in 2008 and 2013 plotted on the same DCA axes as Figure 13 and highlighting the influence of Dubh Loch

Note: each ellipse contains 90% of the site x year polygon data. The head and tail of each arrow correspond to the loch centroid in 2013 and 2008 respectively.

5.2 Analysis of beaver effects using transect data

5.2.1 Species richness

The application of mixed effects modelling techniques allowed us to test the proportion of variability in richness that could be attributed to changes resulting from beaver occupancy, relative to the influence of other factors. Parameter estimates and their significance are summarised in Table 6. The parameter estimates quantify the direction and magnitude of the effect, and the model predicts the natural log of species richness.

Changes in richness in individual lochs over time and classification by level of beaver occupancy are shown in Figure 15 and the overall effect of beaver occupancy is summarised in Figure 16.

Table 6. Parameter estimates and their associated significance indicated by a linear mixed effects model of species richness in quadrats

Fixed effects	Estimate	Std.Error	z value	Pr(>|z|)
(Intercept)	1.39440	0.15415	9.046	<2e-16 ***
Medium occupancy (main effect)	-0.24927	0.22808	-1.093	0.2744
High occupancy (main effect)	-0.16439	0.21719	-0.757	0.4491
2009 (main effect)	0.05365	0.09673	0.555	0.5791
2011 (main effect)	0.16764	0.10000	1.676	0.0936 .
2012 (main effect)	0.16745	0.10000	1.674	0.0940 .
2013 (main effect)	0.11498	0.09162	1.255	0.2095
Medium occupancy * 2009 (interaction)	-0.06993	0.14729	-0.475	0.6349
High occupancy * 2009 (interaction)	-0.03445	0.14002	-0.246	0.8057
Medium occupancy * 2011 (interaction)	-0.02717	0.14591	-0.186	0.8523
High occupancy * 2011 (interaction)	0.05286	0.14076	0.376	0.7073
Medium occupancy * 2012 (interaction)	-0.01411	0.14564	-0.097	0.9228
High occupancy * 2012 (interaction)	-0.03115	0.14200	-0.219	0.8264
Medium occupancy * 2013 (interaction)	0.04747	0.12952	0.367	0.7140
High occupancy * 2013 (interaction)	-0.13452	0.13247	-1.015	0.3099

Different levels of statistical significance attributed to each factor by the model are indicated by the following codes: *** = p<0.001; ** = p<0.01; * = p<0.05; . = P<0.1.
Values indicate the probability that the estimate associated with a given effect differs from zero due to chance alone.

The model for richness indicates that beaver occupancy does not have a significant effect on quadrat level plant species richness, whether as a main effect or through an interaction with year, regardless of the subset of data used. The 'year' term is only significant in models at a threshold of p = 0.1 in 2011 and 2012, being slightly more species-rich on average in these years than in the baseline year (Figure 15). The most likely explanation for this year effect is a sampling artefact caused by repeat sampling by the same surveyors resulting in increases the rate of species detection. This is an inevitable artefact of surveys being conducted by the same surveyors and being repeated at relatively high frequency, and might apply to almost any biological survey dataset. This feature is most pronounced in 2011 when quadrats were sampled in both May and September (although only September data are illustrated and used in the present analysis). Retention of vernal species might also have been prolonged in 2011 due to the exceptionally hard winter of 2010/11. Thereafter the number of species stabilises. Figure 17 indicates that this effect is most apparent at the landward end of transects (Quadrat 1) where richness is generally highest and the chance of under-detection is increased due to the structural complexity of the vegetation. The same pattern does not apply to open water quadrats because there are intrinsically fewer species,

lower cover, and the species concerned are larger and generally more easily detectable, even when their cover is low.

Table 7 summarises the contribution of different factors to variation in quadrat level species richness. Clearly, as might be expected, the dominant factor is position on transect. This is consistent with the typical hydroseral pattern of declining richness from shore (seven to nine species in Quadrat 1) to open water (three to five species in Quadrats 2 to 4), as summarised in Figure 17. The second most important factor is loch identity. This reflects the level to which richness varies between lochs on a given position on a transect, as illustrated in Figure 17, and is partly a reflection of intrinsic differences between lochs in their size, depth, exposure and fertility. The other factors together account for a small proportion of the total variation in richness, suggesting that variation between transects within a loch is small and that variation in richness between years is also fairly minor.

Table 7. ANOVA table showing the variance apportioned to the different factors by a Generalised Linear Model of richness with all factors included as main effects

Independent variables	Deviance	Df
Occupancy	34.72	2
Year	16.87	4
Loch	127.78	8
Position on transect	712.78	3
Position around loch	15.25	5
Occupancy*Year interaction	7.07	8
Residual	670.06	729

The very limited variation in richness associated with beaver occupancy is consistent with Figures 16 and 17. The small amount of variation attributable to year implies that it is unlikely that any potential beaver effect is being masked by inter-annual fluctuations in richness and there is no suggestion from the occupancy*year interaction terms in Table 6 that any beaver effect on richness is starting to emerge. In principle, through a combination of reducing tree shade, selective reductions in the cover of palatable dominant species, or fluctuating water levels, it might be expected that beavers would increase recruitment of smaller species, thus elevating patch scale richness. The failure to observe this in the quadrat scale data suggests that (i) beavers will rarely cause the complete loss of a species from a quadrat, or, if they do, new species colonise sufficiently quickly to mask this loss and, (ii) there is little evidence for localised increases in richness that might occur as a consequence of lowering the cover of a dominant species. Hence, any possible loch-scale increased richness in high beaver occupancy lochs noted in 5.1.1 is probably not a function of increased local richness.
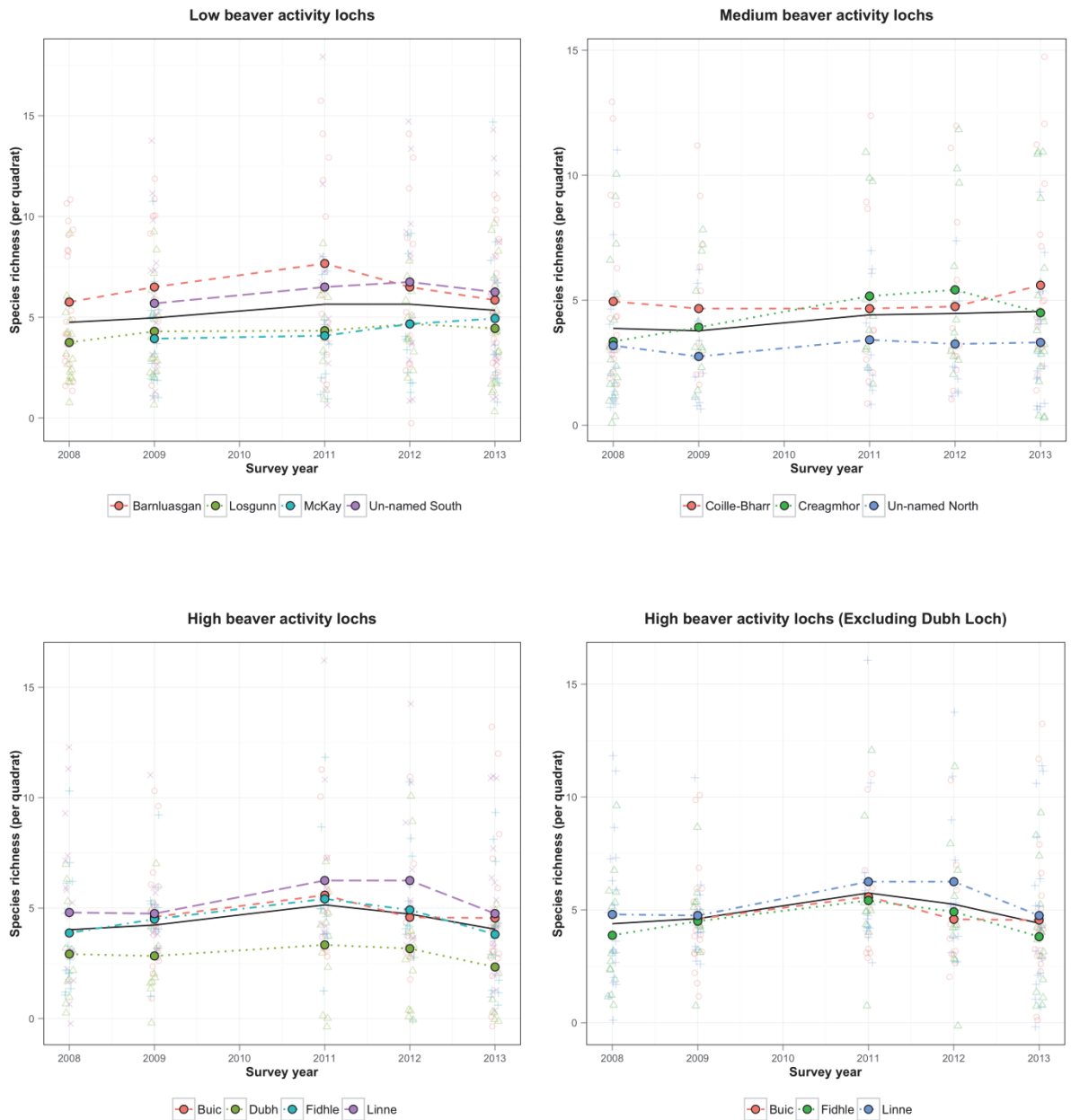
Figure 15. Comparison of mean quadrat-level species richness presented across years for individual survey lochs

Note: only September data are included, to allow a fair comparison across years. Individual graphs are presented for each level of beaver occupancy, with the black lines indicating the mean richness at each level. The group containing the high-occupancy lochs has been presented with and without Dubh Loch included, due to the unique pronounced water level change at this site.
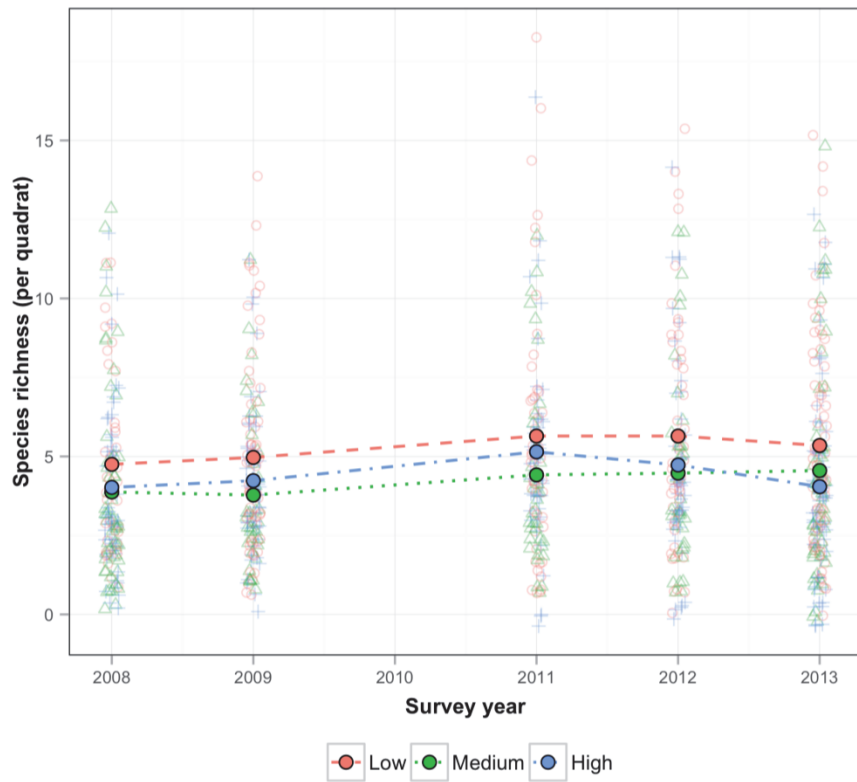
Figure 16. Comparison of mean quadrat species richness presented according to level of beaver occupancy (patterned lines)

Note: only September data are presented, to allow a fair comparison across years. Lochs had the potential to become occupied from 2009 onwards.
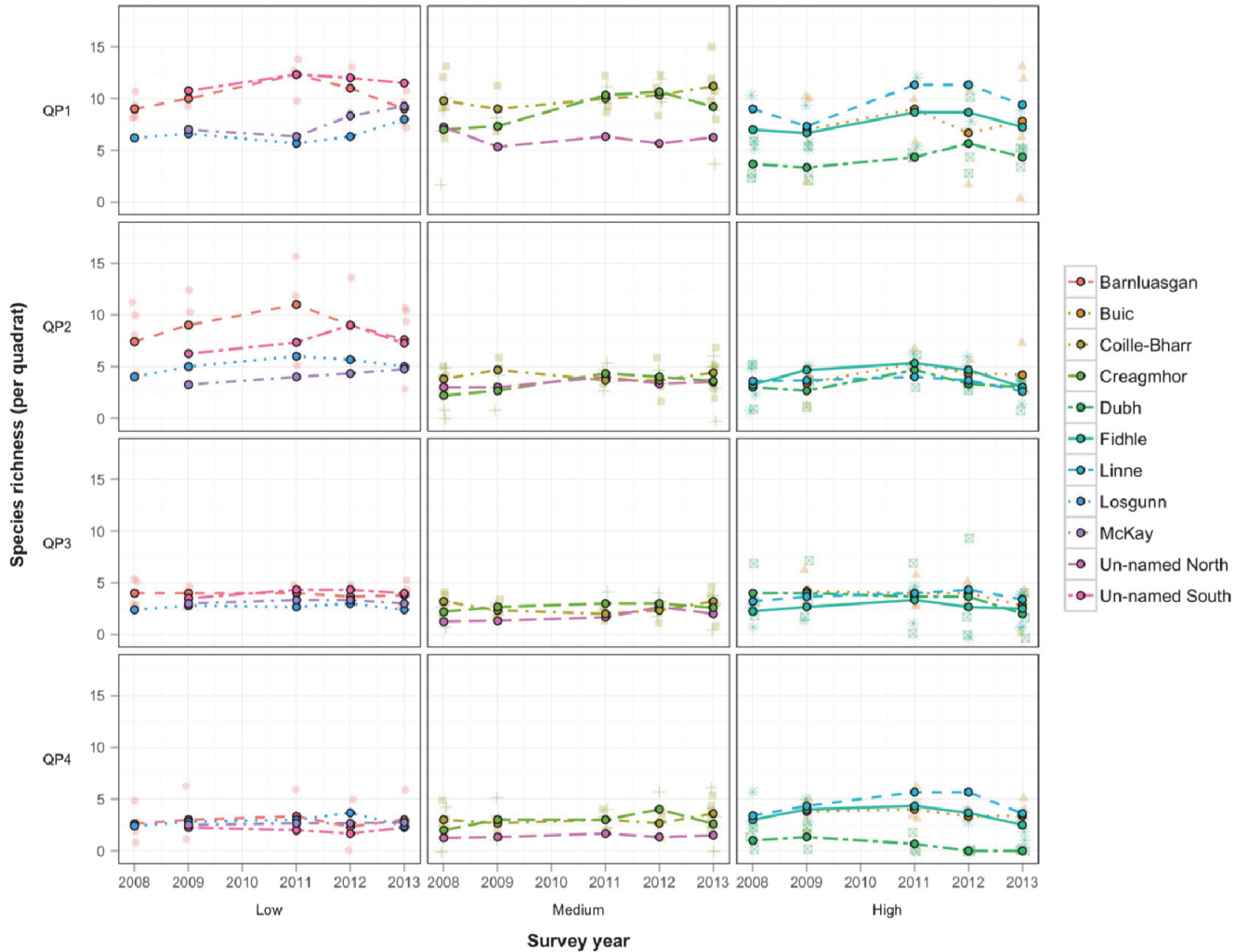
Figure 17. Comparison of mean quadrat species richness presented across years in relation to quadrat position on transect (QP1 (most landward) to QP4 (open water) from top to bottom) and beaver occupancy (Low to High)

5.2.2 Vegetation cover

The application of mixed effects modelling techniques allowed testing of the proportion of variability in total cover that could be attributed to differences in beaver occupancy. Parameter estimates and their significance are summarised in Table 8. The parameter estimates indicate the magnitude and direction of change in cover relative to low occupancy lochs in the baseline year, expressed in units of summed cover. For example, the 'medium occupancy (main effect)' is the difference between the medium occupancy lochs in 2008 and the low occupancy lochs in 2008, and the '2009 (main effect)' is the difference between the low occupancy lochs in 2009 and the low occupancy lochs in 2008. The interaction terms are a measure of the difference between the differences. For example, the difference in cover between 2008 and 2013 for the high occupancy lochs is 26.48 percentage points lower than the difference between 2008 and 2013 for the low occupancy lochs.

Changes in quadrat total cover in individual lochs over time are shown in Figure 18 and the beaver effect is summarised in Figure 19. These figures reveal a reduction in cover over time in those lochs in the High occupancy group that is not replicated in lochs in the Low and Medium occupancy categories. In Dubh Loch, the vegetation cover at individual quadrats decreased by an average of 65% between 2008 and 2013, with the outer quadrats originally

dominated by floating-leaved species losing their entire cover (Figure 20). In Fidhle, the average reduction in cover over the same period was 45% and this was mostly associated with high losses of *C. mariscus* from several transects. In the other High occupancy lochs, Buic and Linne, losses based on transect level data were more modest. In the Medium occupancy category there was also a noticeable decline in total cover of Un-named Loch (North) but this was offset by an apparent increase in cover in Loch Creagmhor, such that there was no discernible beaver effect for the Medium occupancy lochs (Table 8). Other than this there are no clear trends in cover on any of the other lochs – either with or without beavers.

Table 8. Parameter estimates and their associated significance in linear mixed effects models of summed cover with (upper) and without (lower) Dubh Loch

Fixed effects	Estimate	Std.Error	df	t-value	Pr(>|t|)	
All data						
(Intercept)	75.98297	7.72552	53.00	9.835	1.50e-13	***
Medium occupancy (main effect)	-23.00227	11.52132	48.30	-1.996	0.05154	.
High occupancy (main effect)	-4.31920	10.86570	51.90	-0.398	0.69262	
2009 (main effect)	-0.04363	3.64993	562.70	-0.012	0.99047	
2011 (main effect)	-0.20523	3.90374	567.80	-0.053	0.95809	
2012 (main effect)	-0.93439	3.90374	567.80	-0.239	0.81091	
2013 (main effect)	-1.51963	3.48311	555.00	-0.436	0.66280	
Medium occupancy * 2009 (interaction)	0.50780	5.23773	566.80	0.097	0.92280	
High occupancy * 2009 (interaction)	-10.07145	5.07752	563.60	-1.984	0.04779	*
Medium occupancy * 2011 (interaction)	0.44717	5.41766	569.20	0.083	0.93425	
High occupancy * 2011 (interaction)	-15.52902	5.31346	566.30	-2.923	0.00361	**
Medium occupancy * 2012 (interaction)	5.64856	5.41766	569.20	1.043	0.29757	
High occupancy * 2012 (interaction)	-24.90402	5.31346	566.30	-4.687	3.48e-06	***
Medium occupancy * 2013 (interaction)	2.69820	4.72145	552.90	0.571	0.56791	
High occupancy * 2013 (interaction)	-26.48060	4.78007	554.30	-5.540	4.68e-08	***
Excluding Dubh Loch						
(Intercept)	75.94663	7.79650	46.10	9.741	9.15e-13	***
Medium occupancy (main effect)	-22.96430	11.67186	42.60	-1.967	0.05566	.
High occupancy (main effect)	-8.25374	11.80727	44.60	-0.699	0.48815	
2009 (main effect)	0.03407	3.35864	512.10	0.010	0.99191	
2011 (main effect)	-0.08382	3.59356	516.10	-0.023	0.98140	
2012 (main effect)	-0.81298	3.59356	516.10	-0.226	0.82111	
2013 (main effect)	-1.48673	3.20323	506.20	-0.464	0.64275	
Medium occupancy * 2009 (interaction)	0.36011	4.82117	515.40	0.075	0.94049	
High occupancy * 2009 (interaction)	-10.05776	5.06629	515.40	-1.985	0.04765	*
Medium occupancy * 2011 (interaction)	0.25577	4.98767	517.20	0.051	0.95912	
High occupancy * 2011 (interaction)	-7.73389	5.30319	517.40	-1.458	0.14535	
Medium occupancy * 2012 (interaction)	5.45716	4.98767	517.20	1.094	0.27441	
High occupancy * 2012 (interaction)	-16.22695	5.30319	517.40	-3.060	0.00233	**
Medium occupancy * 2013 (interaction)	2.66530	4.34129	504.60	0.614	0.53953	
High occupancy * 2013 (interaction)	-18.12061	4.70274	506.10	-3.853	0.00013	***

Different levels of statistical significance attributed to each factor by the model are indicated by the following codes:
*** = p<0.001; ** = p<0.01; * = p<0.05; . = P<0.1.
Values indicate the probability that the estimate associated with a given effect differs from zero due to chance alone.

Based on an analysis of the global dataset using a linear mixed model (Table 8) it may be concluded that there is a significant negative effect of beavers on plant cover at the highest level of occupancy and that this effect increases with time (Figure 19). However, this effect is only distinguishable from inter-annual fluctuations in cover after several years of high-level occupancy by beavers. Thus, in 2009 the high occupancy effect was notable, but of

borderline significance (p = 0.048). In subsequent years, the differences in quadrat level cover from the baseline were highly significant in high beaver occupancy lochs, but there was not enough evidence to say that there was a beaver effect in lochs in the medium occupancy class (Table 8; Figure 19).
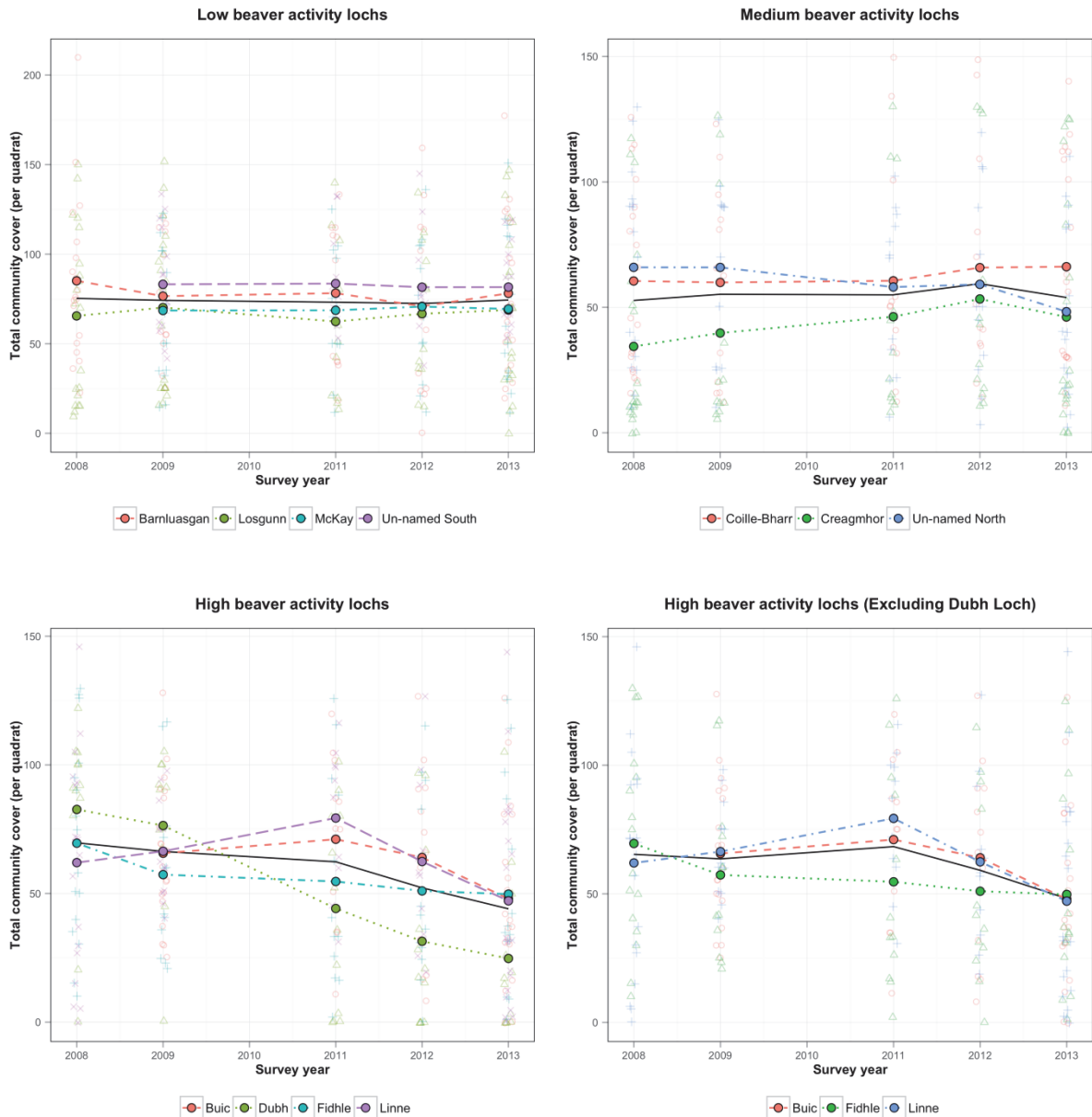
Figure 18. Comparison of quadrat level sum cover (total of the species cover values) across survey years for each of the lochs

Note: only September data are included to allow comparison with baseline data. Individual graphs are presented for each level of beaver occupancy with the black lines indicating the mean richness for each level. The group containing the high-occupancy lochs has been presented with and without Dubh Loch included, due to the pronounced water level change unique to this site.
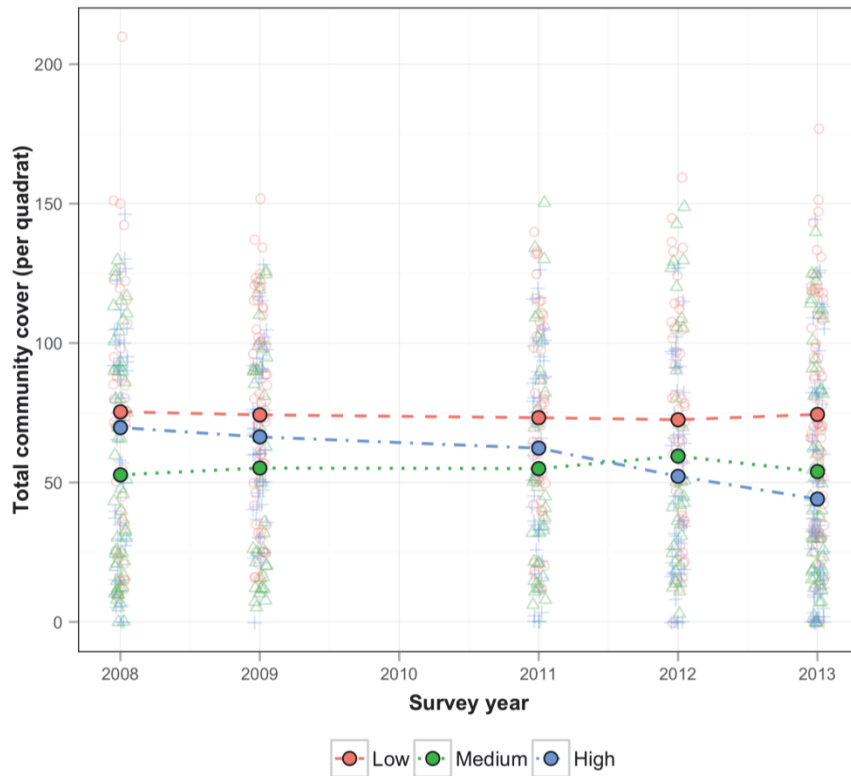
Figure 19. Comparison of quadrat-level total community cover presented across years

Note: patterned lines indicate the mean value at each level of beaver occupancy (Low to High). Only September data are presented to allow a fair comparison across years. Lochs had the potential to become occupied from 2009 onwards.

Given that one of the of high occupancy lochs, Dubh Loch, was unique in terms of the water level increase that it experienced due to damming, it is possible that the effects of high levels of occupancy by beavers cannot be generalised. However, an analysis of the data from which Dubh Loch was excluded (Table 8) clearly refutes this. Although the size of effect is lowered relative to an analysis of the full dataset (shown by less negative parameter estimates for high occupancy x year interactions, i.e. -18.1 compared to -26.5 for high-level occupancy lochs in 2013), and the high occupancy x year effect is no longer significant in 2011, the effects of high-level occupancy in 2012 and 2013 are still significant. Therefore beavers can significantly affect plant cover directly and independently of major water level rise, although the effects observed in some of the other high-level occupancy lochs (Lochs Linne and Fidhle) may still have been influenced by more modest, temporary water level rise. Even in the case of Dubh Loch itself, the effects of water level rise are not applied in a simple and uniform manner in all quadrats, due to bed instability, as described in 5.6.1, and it would be inappropriate to ascribe all of the reduction in vegetation cover on Dubh Loch transects to increased water depth.

Table 8 and Figure 19 offer some interesting additional evidence that beavers might actively select those lochs with higher initial cover (in this context more productive lochs) over lochs with lower cover. The model outputs in Table 8 show that the parameter estimate for the Medium occupancy lochs in 2008 is lower than that for low occupancy lochs in 2008 (although the difference is only significant at a threshold of p = 0.1). This finding should not be over-interpreted, since beavers were deliberately introduced to specific lochs, meaning that their probability of relocating would vary. Creagmhor Loch had lower cover than all of the other water bodies and beavers had an intermittent presence at this site, eventually

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moving to the adjacent well-vegetated Loch Un-named North. Animals that were originally released in Loch Coille-Bharr also moved to the more densely vegetated Dubh Loch. On the other hand animals released at Loch Un-named South soon vacated that site in preference for the less well-vegetated Lochan Buic. A larger sample size, greater variation in cover between water bodies and a lack of intervention in the distribution of animals would be required to fully assess any possible relationship between occupancy and plant cover.

Table 9 summarises the contribution of different factors to variation in quadrat level summed cover. As with species richness, the dominant factor is position on transect. This is consistent with the typical hydroseral pattern of declining cover from shore (about 120% summed cover in Quadrat 1) to open water (50% summed cover in Quadrats 2 to 4), as summarised in Figure 20. The second most important factor is occupancy. After occupancy, loch identity is the most important factor, although it is a proportionally less important source of variation in cover than in richness. This analysis indicates that variation in cover between positions within a loch and between years is minor compared to other sources of variation. The interaction between occupancy and year is a proportionally more important source of variation in summed cover (3.2% of explained variation) than it is for species richness (0.8% of explained variation). This is consistent with the finding of a reduction in cover through herbivory or inundation but not a complete loss of individual species.

Table 9. ANOVA table showing the variance apportioned to the different factors by a General Linear Model of quadrat cover with all factors included as main effects

Independent variables	Deviance	Df
Occupancy	53702	2
Year	8593	4
Loch	32120	8
Position on transect	461603	3
Position around loch	7876	5
Occupancy*Year interaction	18976	8
Residual	613372	729

Figure 20 illustrates the trend in quadrat level cover stratified by quadrat position, occupancy and loch. This suggests a change in the cover at all quadrats in the high occupancy group of lochs, although these changes tend to be more subdued in the outermost quadrats, perhaps because the species most affected by herbivory or water level changes tend to be more associated with the landward end of transects.
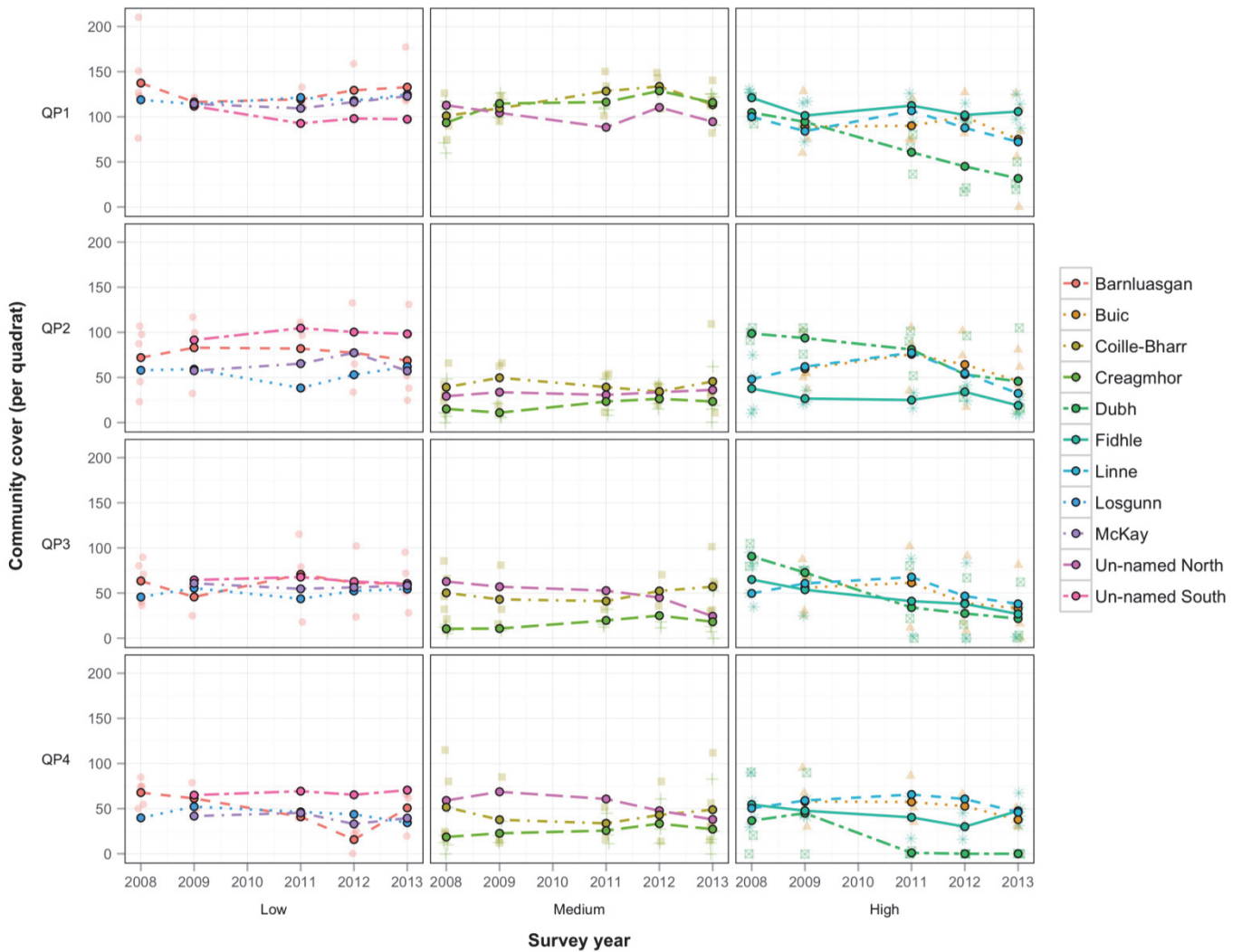
Figure 20. Comparison of mean quadrat summed cover presented across years in relation to quadrat position on transect (QP1 (most landward) to QP4 (open water) from top to bottom). Lochs are graphed individually but grouped into levels of beaver occupancy (Low to High).

5.2.3 Compositional changes in fixed quadrats

To evaluate potential environmental drivers of change in plant species composition associated with beaver occupancy, the Ellenberg indicator scores for moisture (F) and light (L) derived by Hill *et al.* (1999) were used. Increases in the values of these indices at a community level would suggest a shift in composition towards species associated with elevated moisture conditions or greater light availability, respectively. These are both potential scenarios associated with water level rise caused by dams, or a reduction in shade caused either by tree felling or tree death as a result of inundation. F values of lochs grouped by occupancy level and the pattern of change in values over time are shown in Figure 21. This graph suggests that there is little change in F score with time in different groups of lochs, which is contrary to expectations of floristic adjustment to inundation. No difference in L scores between sites or over time was observed.
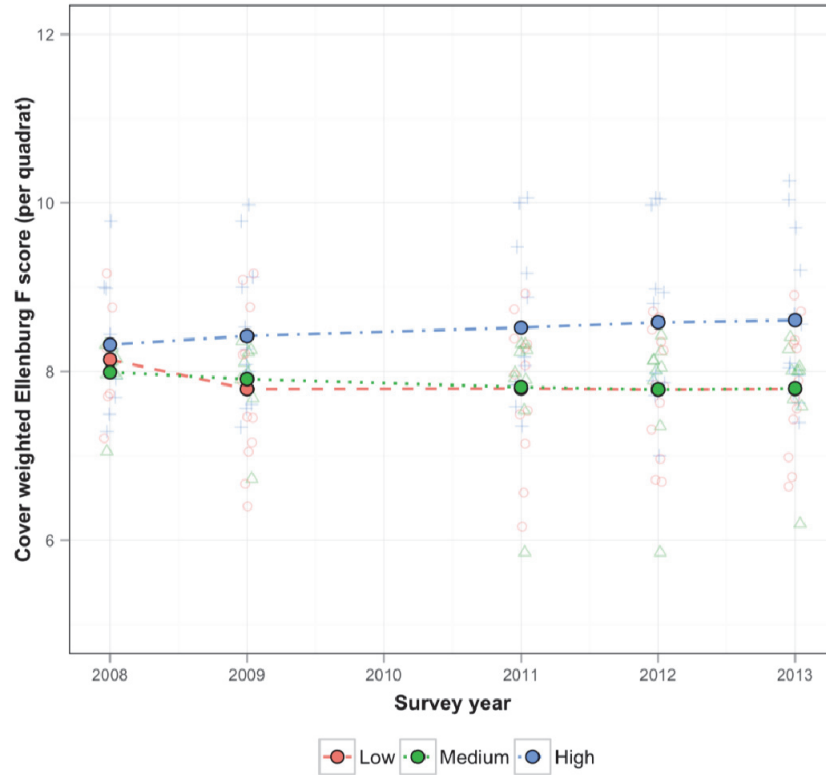
Figure 21. Change in cover-weighted Ellenberg F-score in relation to level of beaver occupancy

Note: patterned lines indicate the mean value at each level of beaver occupancy (Low to High). Only September data are presented to allow a fair comparison across years. Lochs had the potential to become occupied from 2009 onwards.

Changes in quadrat composition in relation to soil moisture or periodic inundation are likely to be most evident in the landward quadrats since the outermost quadrats are already naturally dominated by aquatic species with high F scores. Data from Quadrat 1 only, stratified by occupancy level, are presented in Figure 22. This suggests a very weak increase in F values of the shoreline vegetation with time at the highest level of beaver occupancy, although this change appears to be mainly driven by changes in Dubh Loch and is not statistically significant (Table 10).
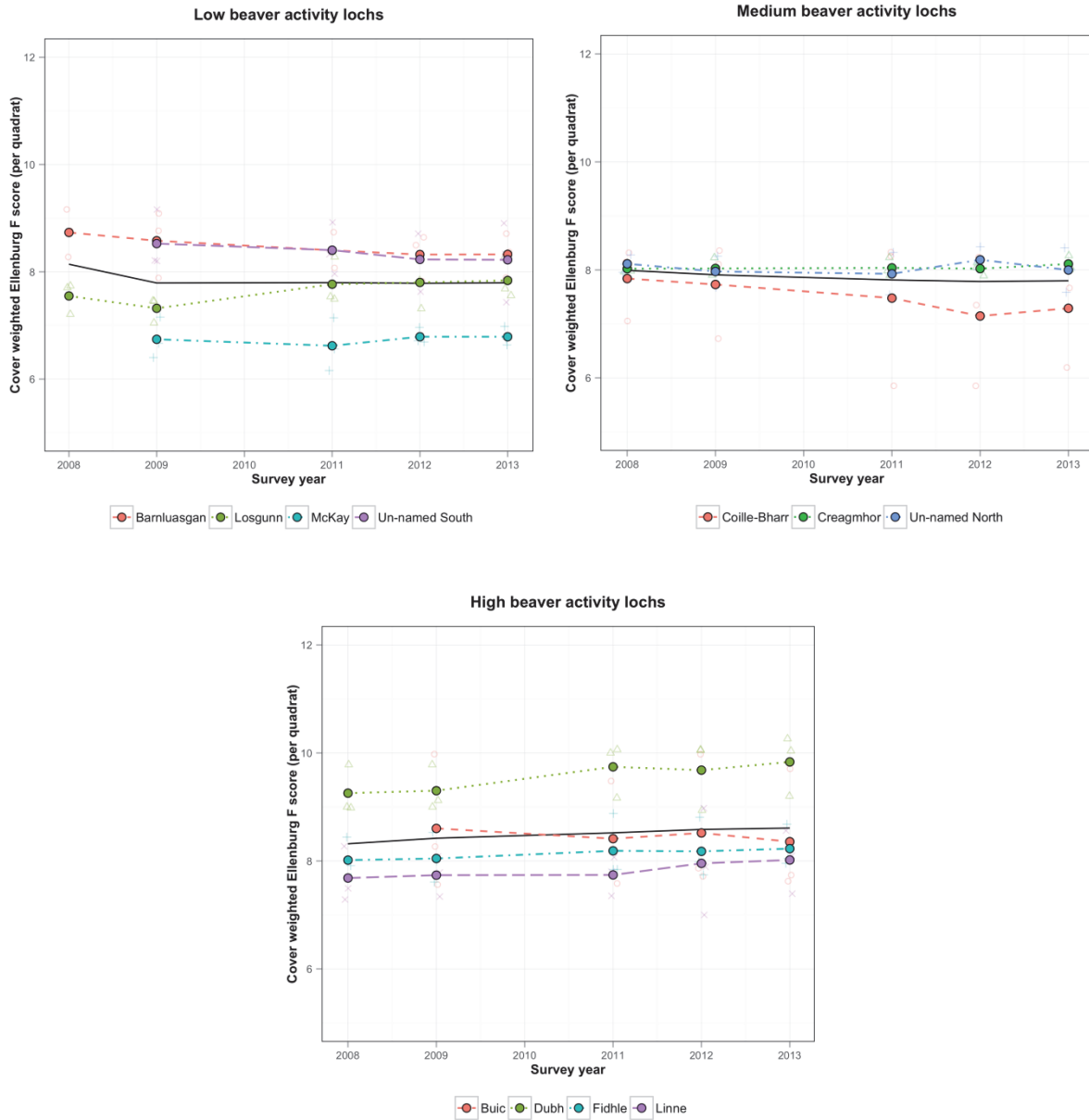
Figure 22. Comparison of cover weighted mean Ellenberg moisture (F) scores in Quadrat 1 on each fixed transect

Note: patterned lines indicate trends in mean score at the individual loch level. The mean of the cover-weighted F-score across lochs within each occupancy level is indicated by a solid line.

Table 10. Summary of model outputs of tests of the effect of year and beaver occupancy on Ellenberg F values applied to Quadrat 1 data

Fixed effects	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	7.82490	0.43209	17.68	18.109	7.41e-13 ***
Medium occupancy (main effect)	-0.40302	0.61932	13.91	-0.651	0.526
High occupancy (main effect)	0.31549	0.59728	16.26	0.528	0.604
2009 (main effect)	-0.03463	0.33539	168.60	-0.103	0.918
2011 (main effect)	-0.02633	0.35389	168.27	-0.074	0.941
2012 (main effect)	-0.03920	0.35389	168.27	-0.111	0.912
2013 (main effect)	-0.04531	0.32509	168.13	-0.139	0.889
Medium occupancy * 2009 (interaction)	0.52212	0.47685	167.32	1.095	0.275
High occupancy * 2009 (interaction)	0.08891	0.46587	168.30	0.191	0.849
Medium occupancy * 2011 (interaction)	0.41893	0.49004	167.20	0.855	0.394
High occupancy * 2011 (interaction)	0.40686	0.48354	167.68	0.841	0.401
Medium occupancy * 2012 (interaction)	0.40324	0.49004	167.20	0.823	0.412
High occupancy * 2012 (interaction)	0.48223	0.48354	167.68	0.997	0.320
Medium occupancy * 2013 (interaction)	-0.07130	0.44217	167.15	-0.161	0.872
High occupancy * 2013 (interaction)	0.20519	0.44805	167.61	0.458	0.648

Different levels of statistical significance attributed to each factor by the model are indicated by the following codes: *** = p<0.001; ** = p<0.01; * = p<0.05; . = P<0.1. Values indicate the probability that the estimate associated with a given effect differs from zero due to chance alone.

At the highest level of occupancy, the parameter estimates are positive in most years as might be expected from an adjustment in vegetation composition to wetter conditions. However, the size of this difference relative to the baseline year when compared to the low occupancy lochs relative to their baseline year is not significant in any year. Therefore the analysis presented in Table 10 yields no evidence of a systematic adjustment of shoreline vegetation towards a flora that is tolerant of increased soil moisture. This may reflect the limitations of the F indicator scores themselves, the relatively short time scale of the study, or the fact that some shoreline quadrats will naturally lie within the zone of annual water level fluctuations and therefore already support an inundation-tolerant flora. The changes in Dubh Loch are visually striking and suggest that if widespread damming and significant water level rise occurred in comparable situations elsewhere there would be significant adjustment in vegetation composition over a 5-year period.

5.3 General patterns of herbivory and foraging

Table 11 provides a semi-quantitative indication of the extent of feeding on different macrophyte species across the beaver-occupied lochs based purely on field signs (examples in Figure 23). These reinforce the results of the polygon and transect surveys described in 5.1 and 5.2. Five species were commonly utilised by beavers, *N. alba*, *S. lacustris*, *C. mariscus*, *E. fluviatile* and *C. rostrata*. The latter was consumed across all the inhabited lochs but only in small quantities. *N. alba* leaves were well-utilised in Lochan Buic and Un-named Loch (North) during 2011 but only rather sparingly in subsequent years. The peak exploitation amounted to a very small proportion of the total standing stock of floating leaves (less than 2%). After this, the grazing on *N. alba* appeared to shift to uprooting of the rhizome, as indicated by discarded roots or basal rosettes. There was a similar level of utilisation of *N. alba* in Loch Coille-Bharr in late summer 2013 following the movement there of the breeding pair from Dubh Loch. Grazing on *S. lacustris* in Lochs Linne and Fidhle was readily visible from floating stems severed from the rhizome with a single oblique cut. The lengths of these discarded stems indicate that these were typically gathered in water 1.5-2.5 m deep.

Small quantities of uprooted isoetid plants were often found floating amongst the residue from feeding by beavers on *N. alba*, *S. lacustris* or *E. fluviatile* (Figure 24). It is assumed that these plants represent collateral damage resulting from uprooting of rhizomes of the target species. There was no evidence that uprooted isoetids had been grazed, but these species commonly grow weakly anchored and at high densities in quiescent areas amongst the stems of *N. alba*, *S. lacustris* or *E. fluviatile*. Thus disturbance during feeding on target species would be likely to result in their detachment from the substrate.

Table 11. Summary interpretation of field signs recorded during macrophyte surveys (2009-2013) indicating the patterns of herbivory or foraging across the eight lochs lying within existing beaver territories

		Dubh	Coille-Bharr	Linne	Fidhle	Creagmhor	un'd North	Buic	un'd South
Nymphaea alba	White water lily	●	●	•	•	•	●	●	•
Cladium mariscus	Saw Sedge	•		•	●	●		●	
Schoenoplectus lacustris	Common Club-rush		•	●	●				
Equisetum fluviatile	Water Horsetail	●	●	•		•	•	•	•
Carex rostrata	Bottle Sedge	●	•	•	•	•	•	•	•
Menyanthes trifoliata	Bogbean	•	•						
Phragmites australis	Common Reed		•					•	
Sparganium erectum	Branched burr reed	•			•				
Potamogeton natans	Broad-leaved Pondweed					•			
Carex paniculata	Tussock Sedge	•							

Size of circle reflects the extent or frequency of observation of associated field signs. Large circles (widespread and/or commonly observed), medium circles (local and/or occasionally observed), small circles (very local and/or rarely observed).

Although it is generally assumed that plant material removed by beavers was utilised for feeding, there was also evidence in each territory of incorporation of macrophyte material into the structure of the lodge. This was especially noticeable at Lochan Buic, where the lower parts of the lodge were commonly draped with plants of *Cladium mariscus*. In the case of Loch Coille-Bharr, the temporary lodge in the sheltered south-west bay that was used by the breeding pair from Dubh Loch was observed to be covered in *N. alba* and locally excavated mud in which isoetid plants and *Elodea canadensis* were visible (Figure 25). It is also possible that fresh macrophyte material or litter was collected and used by beavers as bedding within lodges.
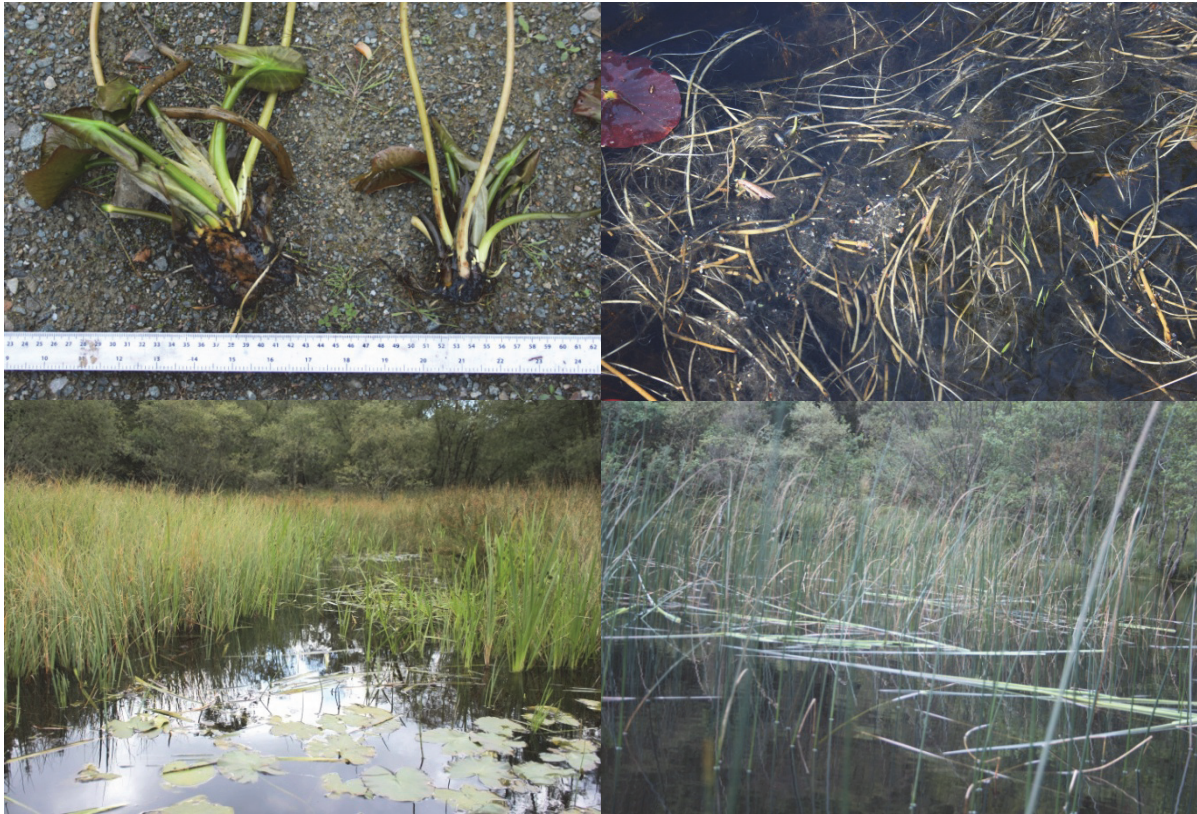
Figure 23. Examples of feeding on aquatic plants by beavers. Top left: basal rosettes of N. alba remaining after consumption of uprooted rhizome (Lochan Buic, September 2011). Top right: roots of N. alba remaining after consumption of uprooted rhizome (Un-named Loch (North), May 2013). Bottom left: grazing on above ground parts of S. erectum (Fidhle, September 2013). Bottom right: stems of S. lacustris remaining after uprooting and feeding on rhizome (Fidhle, September 2011).

Figure 24. Uprooting of isoetids by beavers during feeding on (left) E. fluviatile and N. alba at Lochan Buic (mainly uprooted L. dortmanna) and (right) at Loch Coille Bharr during feeding on N. alba (mostly uprooted Isoetes). Both pictures taken September 2013.

Figure 25. Use of foraged macrophyte material in lodge construction. Left: C. mariscus *draped on lower parts of lodge on Lochan Buic in May 2012. Right:* N. alba*, isoetids and* E. canadensis *packed onto surface of temporary lodge on Loch Coille-Bharr in September 2013.*

5.4 Geospatial surveys and Shoreline Development Indices

At Dubh Loch the increased water levels created by the dam constructed over the winter of 2009-10 resulted in a large increase in water surface area. Geospatial data collected around Dubh Loch during May 2011 were used to construct the outline of the new perimeter and calculate the new surface area. The surface area increased by approximately 337% from 0.38ha (Ordnance Survey 1:10 000 scale data from 2005) to an area measured in May 2011 of 1.66ha, inundating 1.28ha of willow and birch woodland and scrub to a depth of around 1m (±0.5). By May 2012 the total area had increased by a further 8% to 1.79ha, partly through the excavation of canals by beavers and probably aided by an abnormally wet preceding winter. This represented a total increase in surface area of 371% following construction of the dam, i.e. the surface area of the water body was 4.71 times its original size. In 2013, spring and summer water levels were lower than at any time over the previous 3 years. This resulted in significant exposure of previously inundated areas and there was no evidence that the overall area of Dubh Loch had increased since 2012. The drop in water level probably reflects a relatively dry preceding winter and spring, possibly coupled with an increase in dam porosity. The increase in surface area of Dubh Loch from 2009-2012 is shown in Figure 26. In May 2014, despite an exceptionally wet preceding winter, there was extensive exposure of marginal wet mud similar to the situation noted in the spring and summer of 2013. In May 2014, the water level on the original stage board was 0.25 m lower than the values noted in May 2011 and 2012, yet the level was only fractionally below the crest of the dam. This clearly indicates a reduction in dam height due to compaction and settlement of material and failure by beavers to offset this by the addition of new material.
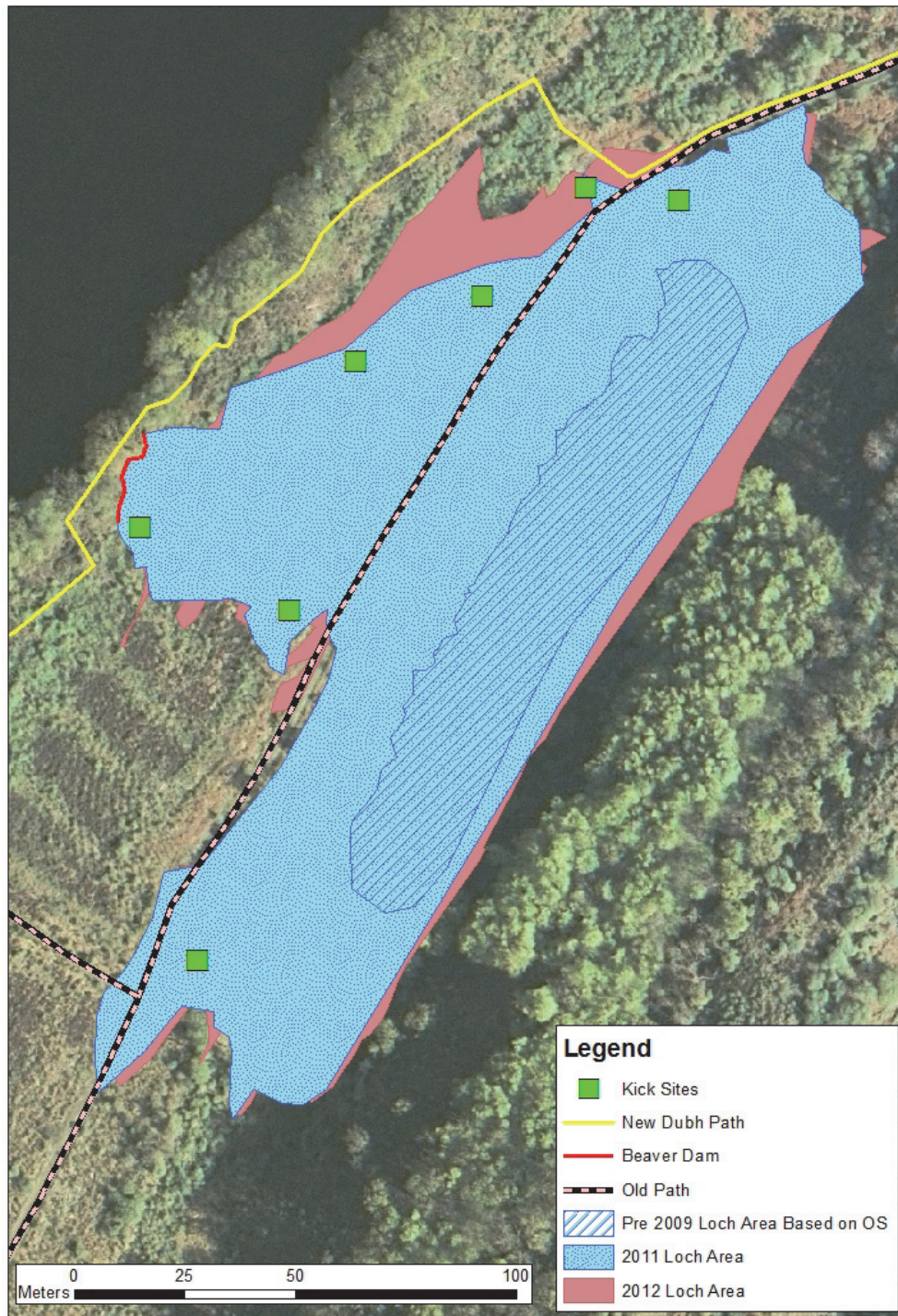
Figure 26. The outline of Dubh Loch in May 2011 and 2012, relative to the outline according to Ordnance Survey data and 2005 aerial photography. Green squares indicate invertebrate sampling sites.

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The Shoreline Development Index (SDI) was calculated for all Knapdale lochs, including the enlarged Dubh Loch, based on their perimeters and areas. Values for all lochs pre-damming ranged between 1.1 and 2.2 with a median of 1.3. These SDI values are low and reflect the typically rather simple shape of most of the Knapdale lochs due to the strongly folded nature of the local geology (see section 3.4). The SDI value for Dubh Loch increased by 21% following damming consistent with the change in shape illustrated in Figure 26.

There was a more modest increase in the area of Un-named Loch (North), where the small outflow was first dammed in autumn 2011, causing a maximum water level rise of about 0.3 m and a 10% increase in loch area (Figure 27). In this water body the SDI increased by 5% following damming.

Figure 27. The outline of Un-named Loch (North) in May 2012, relative to the outline according to Ordnance Survey data and 2005 aerial photography

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5.5 Germination study

The propagule bank experiment confirmed the presence of viable seeds or vegetative propagules of a wide range of species, including bulbous rush *Juncus bulbosus*, jointed rush *J. articulatus*, soft rush *J. effusus*, *Equisetum fluviatile*, *Carex rostrata*, star sedge *C. echinata*, floating club-rush *Eleogiton fluitans*, many-stalked spike-rush *Eleocharis multicaulis, L. uniflora* and *Nymphaea alba* in the sediment. Of these, the *Juncus* species accounted for 84% of the germination. Figure 28 illustrates the appearance of the trays after 12 months of germination. This experiment was continued for a further two months but was terminated after this as no further germination was recorded in this period. The results strongly suggest that *C. mariscus* does not have a viable, persistent propagule bank at this site that could accelerate recolonisation in the absence of grazing. Dominance by rush species is a common feature of aquatic seed banks (Abernethy and Willby 1999) and the vegetation observed under greenhouse conditions closely resembled the observed vegetation in strandline areas of Loch Fidhle and Lochan Buic, adjacent to where *C. mariscus* had formerly occurred.

None of the treatments (loch (i.e. Creagmhor or Fidhle), source of sediment (i.e. collected within former *C. mariscus* bed or elsewhere in loch), or presence of overlying litter (i.e. litter-covered or bare)) had a significant effect on the number of species germinating. In terms of the numbers of individuals germinating, material from Loch Creagmhor produced fewer individuals and germination tended to be poorer with the addition of a litter layer, but both of these effects were only significant at a probability threshold of $p = 0.1$ ($p = 0.075$ in both cases). Source of sediment had no effect on the numbers of individuals germinating ($p = 0.34$) indicating that *C. mariscus* beds do not trap seeds any more than they accumulate naturally elsewhere near the shoreline. There were no significant interactive effects of any treatments.
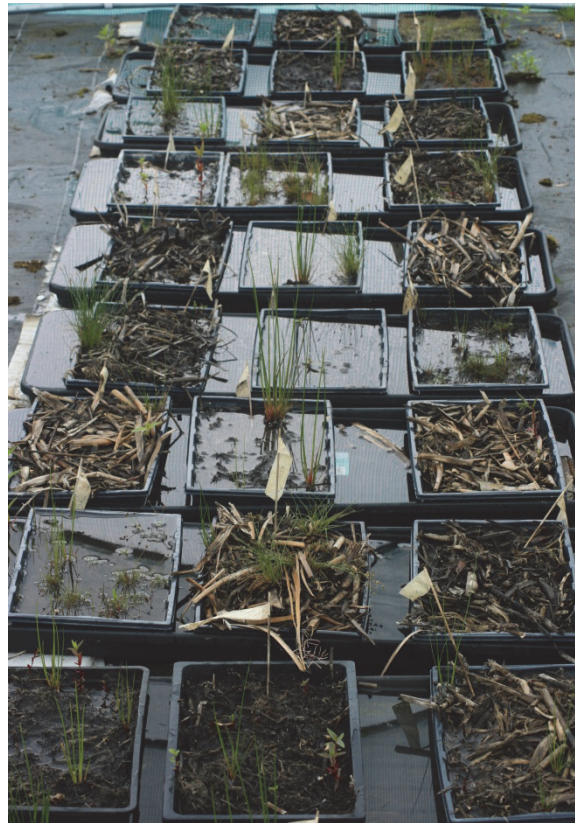
Figure 28. Polytunnel germination experiment after 12 months

5.6 Comparison of effects of beaver activity in different territories

In this section the water bodies occupied by beavers are considered according to the four territories now established. Changes in vegetation are described relative to the baseline data and the repeat surveys of fixed transects carried out in 2009-2013 are used to illustrate the trajectory of change.

5.6.1 Dubh Loch and Loch Coille-Bharr

Dubh Loch experienced the most significant hydromorphological changes and was the location where water level changes resulted in the most marked response in the macrophyte community (Figure 29). The main phase of dam construction by beavers on Dubh Loch was during late autumn 2009. This led to a rapid water level rise that affected the whole loch over the growing season of 2010. In 2011 these newly formed areas of aquatic habitat were still un-vegetated by aquatic plants since they largely comprised flooded birch woodland understorey shaded by standing trees. Between 2011 and 2013, Dubh Loch experienced a rapid transition to a well-vegetated aquatic habitat.

Figure 29. Fixed point photography of the southern end of Dubh Loch showing the vegetation present in September 2008 (left) and September 2011 (right)

Figure 30. Benthic peat that had surfaced in Dubh Loch, at various stages of colonisation (mainly by C. rostrata *and* Juncus *spp), in September 2011*

One of the major changes in Dubh Loch, besides the increased water level and loss of vegetation, was the appearance of large floating platforms of benthic peat bound together by rhizomes of *N. alba* and *E. fluviatile* (Figure 30). Indeed, although water depths generally increased in Dubh Loch relative to an absolute datum (this evidence will be reviewed in a separate report on hydrology), at some locations water depths were in fact *lower* in some years following impoundment due to the mobility and buoyancy of the submerged peat. In some cases, peat platforms almost completely replaced the beds of *N. alba*, *E. fluviatile* and *P. natans* that originally occurred in these locations. These peat platforms appear to be caused by a build-up of gases in rhizomes and surrounding sediment caused by anaerobic respiration as below-ground plant parts are no longer being ventilated via contact with the atmosphere. Coupled with the greatly reduced weight of the overlying plants and reduced solubility of gases during the summer, the buoyancy of the peat causes it to rise to the surface. Such processes are likely to be a key element in the development of quaking bogs or schwingmoor that encroach across small bodies of open water in boreal landscapes (Mitsch and Gosselink 2000).

This phenomenon has been reported from much larger lakes, such as Derwentwater in the Cumbrian Lake District. Here a floating island of decaying vegetation and soil, buoyed up by trapped gases, and sometimes as much as 0.5ha in area, achieved local fame during the nineteenth century (Martineau 1855). Peat 'heave' following the removal of surface sediment by suction dredging has also commonly been observed in shallow lakes in the Norfolk Broads. Here, benthic peat expands in response to the removal of the weight of overlying material (Andrea Kelly, Broads Authority, pers. comm). There appears to be a significant sediment propagule bank associated with such material that results in rapid colonisation, mainly by seedlings of *Carex* spp. or *Juncus* spp. The phenomena of floating peat platforms is not unique to Dubh Loch and was observable in several other Knapdale Lochs (Losgunn and Un-named (North)) prior to beaver introduction, albeit on a much smaller scale.

Whilst buoyancy of benthic peat has readily observable effects, it should be noted that this same property also applies to much of the fringing vegetation and wetter woodland at Dubh Loch. In the middle of the armoured track which formerly ran alongside this Loch, but which is now mostly submerged, water depths reached a maximum of 1.2m. However, rather than being completely drowned, the *C. mariscus* and greater tussock sedge *C. paniculata* mire that surrounds Dubh Loch was able to adjust to this change in water level, due to its natural buoyancy and the loose anchorage of the peat in which these plants are rooted. This effect also extends to willow trees (*Salix* spp.), which in places have risen by 0.5 m, exposing adventitious roots formed during their initial period of submersion (Figure 31). The larger alders and birch growing on more solid ground were unable to make this adjustment and were either dead or showed very restricted growth after three seasons of inundation.

From 2011 onwards, plant cover in six additional quadrats was monitored regularly. These quadrats were inundated to varying levels and had previously had a subsurface water table and in some cases were the understorey of the former birch woodland. Figure 32 illustrates the substantial year on year increase in plant cover, mostly associated with increases in *P. natans* (Figure 33). It is likely that heightened cover of wetland species was strongly favoured in 2013 by lower water levels (Figure 33) coupled with a decline in tree canopy associated with the death and subsequent wind blow of drowned trees (Figure 34). One consequence of the high variation in water depth, light, and extent of woody debris is to create a highly heterogeneous habitat in which macrophytes are patchily distributed (Figure 33). This is in marked contrast to the relatively uniform habitat that existed previously where plants followed a classic hydroseral zonation with large, homogeneous stands of the major species.

Figure 31. Emergence of willows at Dubh Loch revealed by exposure of adventitious roots formed during periods of submergence, in September 2011
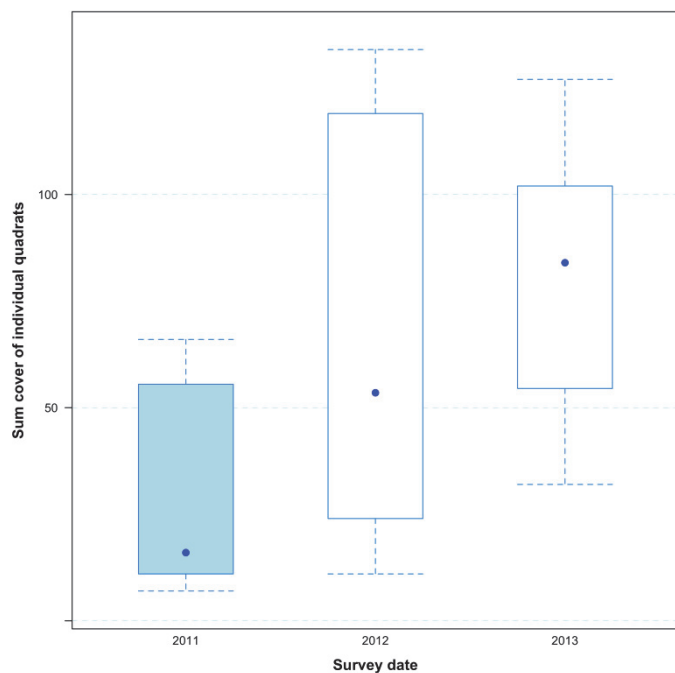
Figure 32. Change in mean plant cover at fixed quadrats in newly inundated part of Dubh Loch from 2011-2013. Each bar is based on six sample points.

The responses of macrophyte communities in Dubh Loch are undoubtedly mostly attributable to the increased water level, but it is likely that direct herbivory also contributed to these changes prior to 2011. A comparison of survey data from September 2008 (prior to beaver introduction) and September 2009, about a month after beavers colonised Dubh Loch from Loch Coille-Bharr, revealed only limited reductions in the cover of water mint *Mentha aquatica*, *E. fluviatile* and *C. rostrata*. Since no sampling was carried out in 2010, the scale of direct herbivory during the 2010 growing season is unknown. There are, however, photographs and observations by SBT staff of beavers feeding on *N. alba*

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rhizomes at Dubh Loch in 2010 and therefore, given the small size of the site relative to the number of beavers resident, herbivory might also have exerted some control on vegetation.

In this beaver family, activity was focused on Dubh Loch. However, from the outset of the trial, there was evidence of limited use of the sheltered and well-vegetated bay in the south-west corner of Loch Coille-Bharr for feeding. This was a location at which animals were originally released in May 2009. Generally, this feeding amounted to occasional grazing of *E. fluviatile* or *N. alba*. There was negligible utilisation of *S. lacustris*. However, in autumn 2012 and 2013, the breeding adults from Dubh Loch relocated to a temporary lodge in the corner of Coille-Bharr. This might reflect the limited availability of preferred macrophyte species in Dubh Loch. In September 2013, the observed widespread feeding on *N. alba* in Coille-Bharr is consistent with polygon survey data that indicate a 33% reduction in the area of the species between 2008 and 2013 (*Figure 11*). Given the generally favourable growing conditions in 2013, this is a marked reduction and suggests fairly extensive utilisation of *N. alba* by beavers. At this site, feeding-remains indicated that uprooting of rhizomes rather than browsing on floating leaves was the predominant method of feeding on *N. alba* and this would account for the size of the observed reduction. Possibly related to the scale of the decline in *N. alba*, *P. natans* was more than twice as extensive in Coille-Bharr in 2013 than in the baseline survey in 2008, although it remained at a lower abundance than *N. alba*.

*Figure 33. Dubh Loch in 2013, approaching four years after dam construction. Top left: high heterogeneity in emergent plant beds (*C. rostrata*, Ranunculus flammula*, Juncus effusus and* S. erectum*). Top right: vigorous growth of* Callitriche stagnalis*, Ranunculus flammula and* Juncus *species on mud of inundated zone exposed during May 2013. Bottom left: scale of colonisation by* P. natans *beneath former birch woodland. Bottom right: dense stands of* P. natans *with* N. alba *with drowned birch trees in the background.*

Figure 34. Dubh Loch in late May from 2012 (top) to 2014 (bottom), showing the increase in unshaded open water following die-back of birch trees in area inundated by beaver dam. The original area of Dubh Loch is visible to the lower left in the pictures for 2013 and 2014. Loch Coille-Bharr is situated in the background of the picture.

5.6.2 Linne-Fidhle system

Figure 35 shows the change in *S. lacustris* densities at the southern end of Loch Linne by the boat jetty (upper) and in the outflow bay (lower). There were clear signs of feeding on *S. lacustris* in Linne as early as September 2009 when Willby and Casas-Mulet (2010) noted several thousand cut stems of this species around the shore or forming rafts in open water. From 2011 onwards, beavers also exploited stands of *S. lacustris* at the northern end of Loch Linne and within Loch Fidhle, which had not previously been utilised. The early losses appeared potentially sustainable with sufficient regrowth. However, as a result of persistent foraging on *S. lacustris* by beavers, the stand area of this species was reduced by 95% and 76% in Linne and Fidhle respectively between 2008 and 2013.

During summer 2009, beavers constructed a number of small dams on the outflow of Loch Linne which resulted in a recorded water level rise of approximately 0.3m in September 2009, though this was probably exacerbated by an unusually wet August (rainfall of almost twice the 30 year mean). The regular removal of these dams until November 2011 (as required at the time by the terms of the release licence) ensured that they did not result in any permanent hydromorphological change on the Loch Linne-Fidhle system. Despite a change in the licence conditions after this time that would have allowed any subsequent dams to remain in place, no further dams of any significance were built. Thus the effects of the water level rise on aquatic vegetation in 2009 reported in Willby and Casas-Mulet (2010) were not observed in 2011 (Willby and Perfect, 2014) or thereafter and thus appear to have been temporary.

Figure 35. Fixed point photography from the southern end of Loch Linne showing the change in density and extent of S. lacustris *in September 2008 (left upper) and September 2013 (right upper), and in the outflow bay in September 2009 (left lower) and September 2013 (right lower). Note the generally superior conditions for plant growth in 2013.*

C. mariscus had a rather restricted distribution in Linne compared to Fidhle and was grazed much less extensively than in Fidhle. Nevertheless, the overall cover of *C. mariscus* in Linne declined by two-thirds. Unusually for this species, *C. mariscus* stands in Linne were growing in a rocky, coarse-gravel substrate, which may have reduced accessibility of its below-ground organs to beavers.

In Loch Linne, there was almost no evidence of feeding on *N. alba*, with animals apparently preferring to feed on emergent species. The extent of *N. alba* in Linne in 2013 was almost twice as high there as in the baseline year. Few signs of indirect damage by beavers to isoetid beds were observed in Linne over the duration of the trial. In common with most of the lochs coverage of *Lobelia* was apparently slightly higher in Linne in 2013 than in 2008, which probably reflects improved underwater viewing conditions for surveys in 2013.

Notable changes were observed in Loch Fidhle and captured by the transect surveys. Most evident was a marked reduction in the extent of *C. mariscus*, as shown in Figures 11 and 36. At a loch level, the overall reduction in this species was almost 100% based on the polygon surveys, with most (80%) of this decline having occurred by May 2011. Precisely when this decline happened is unclear, since macrophyte surveys were not undertaken between September 2009 and May 2011. However, there was already limited feeding on *C. mariscus* in September 2009, and in September 2011 colonisation by *N. alba* of areas formerly occupied by *C. mariscus* had begun. At this time the *C. mariscus* litter was either dry and well fragmented or fully submerged on the bed suggesting that most of the *C. mariscus* decline in Fidhle took place over the winter of 2009-10. *N. alba* seedlings also germinated on sediment from this site used in the greenhouse trial and could be seen in the field amongst adult plants that had presumably spread through rhizome fragments or lateral (shoreward) extension from existing *N. alba* beds. By 2013 there had been an expansion of *N. alba* into areas formerly occupied by *C. mariscus* and partly as a result of this, the overall extent of *N. alba* was 57% higher in Fidhle in 2013 than in the baseline survey year (2008). Isoetid species, such as *L. uniflora* or *L. dortmanna*, are likely to show much slower spread into the areas formerly occupied by *C. mariscus*. Given the extent of persistent *C. mariscus* litter still present on the bed in 2013 (Figure 37) it seems unlikely in the short term that isoetid species would be able to establish successfully in areas where *C. mariscus* formerly grew. Even if conditions did become suitable our observations to date suggest that *N. alba* would pre-empt establishment by isoetids.

As with Linne, the *S. lacustris* beds in Fidhle were heavily exploited by beavers, resulting in a 76% reduction in their stand area. In Fidhle, there was a delay in the full onset of grazing on *S. lacustris* until 2011, which coincided with the near-exhaustion of the available *C. mariscus* resource. Although *S. lacustris* was initially far less abundant in Fidhle than in Linne, by the close of the trial, as a result of grazing by beavers, there was a similarly low coverage of this species in both Linne and Fidhle.

Figure 36. Transect 3 on Loch Fidhle, in September 2009 (left) and September 2011 (centre). A comparison shows the loss of a band of C. mariscus *between surveys. In September 2011, washed up litter from* C. mariscus *partially obscured Quadrat 1 (right).*

Figure 37. Persistent accumulation of leaf and stem litter from former C. mariscus *bed in south west corner of Loch Fidhle through which* N. alba *plants can be seen establishing. May 2013.*

5.6.3 Creagmhor Loch and Un-named Loch (North)

Beaver activity on Creagmhor was primarily restricted to selective felling of riparian trees, especially rowan *Sorbus aucuparia*, and from the outset of the trial, animals had an irregular presence on this loch, eventually moving to the adjacent Un-named Loch (North). There was only sparse and intermittent feeding on macrophytes (mostly *S. lacustris*, *E. fluviatile* and *N. alba*) in Creagmhor Loch in the period 2009-2012, but during this time, no reduction in cover was observed in any of the transects. The stand of *C. mariscus* in the south-west corner of the Loch was ignored. However, over the 2012-13 winter, the single beaver remaining on the adjacent Un-named Loch (North) began feeding on this *C. mariscus* stand, such that by May 2013 most of the stand had disappeared (*Figure 11* and Figure 36). By September 2013, very few *C. mariscus* plants remained and by November 2013, even a small patch of *C. mariscus* in the outflow channel had been lost (C. Perfect and A. Law pers. obs).

Figure 38. Beaver grazing on C. mariscus *bed in Creagmhor Loch in May 2013*

From mid-2010, there was increased tree-felling activity on the watershed between Creagmhor Loch and Un-named Loch (North). In May 2011, there was no evidence that beavers were feeding directly on macrophytes in Un-named Loch (North), but by July 2011, clear evidence of grazing in open water on *N. alba* beds was noted and a new lodge was under construction. The area of feeding had increased between July and early September 2011 and on the basis of beaver-cut stems was visually estimated to represent a 5% loss of the standing stock of *N. alba* surface leaves (Figure 39).

The transect data for Un-named (North) suggest a decline in macrophyte cover in 2012 and 2013 (Figure 19) that is borne out by the relative decline in cover of both *N. alba* and *P. natans* (by 28% and 34% respectively) in this loch as indicated by the polygon data (*Figure 11*). In the case of *N. alba*, the physical removal of entire plants to access the rhizome probably contributed disproportionately to overall loss of cover, compared to grazing on expanded leaves. This type of feeding appears to be more common over the winter months and may be facilitated by the shallow depths. Although feeding on *P. natans* was not observed in this loch, it is possible that this species was affected indirectly by disturbance associated with beavers (e.g. transport and caching of felled trees), coupled with the water level rise and, potentially, reduced water clarity.

Figure 39. Effects of grazing of N. alba *leaves by beavers in Loch Un-named (North), late July 2011*

In November 2011, beavers constructed a low dam on the outflow of Un-named Loch (North), which, by May 2012, had resulted in water level rise of about 0.3m (section 5.4). By May 2013, there was a vigorous growth of *Sphagnum* (mostly *S. squarrosum*) on the inundated areas with plants extending from areas of adjoining mire (Figure 40).

Figure 40. Growth of Sphagnum *spp. on saturated land adjoining Un-named Loch (North) in May 2013 following water level rise*

5.6.4   Lochan Buic and Un-named Loch (South)

During summer 2011, there was widespread feeding on *Nymphaea alba* in Lochan Buic with animals grazing leaves *in situ*, mainly in shallow water, as observed in Un-named Loch (North), or uprooting entire plants to feed on the rhizome. In all cases this activity took place outwith sampled transects. Grazing of surface leaves typically occurred in patches of 5-20 m^2 in extent. The total loss of area of surface leaves of *N. alba* in Lochan Buic in 2011 was visually estimated to be less than 5% of the standing stock of floating leaves at the peak of the growing season. During 2012 and 2013, there was less evidence of feeding on *N. alba*, although some areas of more intense foraging could still be found in 2013 (Figure 41). Some contraction of the overall area of *N. alba* was expected, but the polygon survey data imply that the cover of *N. alba* in Lochan Buic in 2013 was twice as high as in the baseline survey year (2009). This level of increase was unusually high, despite the favourable growing conditions in 2013, although it was not dissimilar to the magnitude of increase observed in Loch Linne. Some of this increase was associated with colonisation of new areas associated with beaver feeding or from expansion into areas formerly occupied by *C. mariscus* (Figure 41). Beavers in Lochan Buic also regularly utilised *E. fluviatile* for feeding, mostly in the north of the loch. The 22% decline in cover of this species in Lochan Buic was similar to the decline observed in several medium occupancy lochs, and was inside the global inter-quartile range of variation in cover between baseline surveys and 2013. However, the initial cover of *E. fluviatile* in Lochan Buic was higher than in any other beaver-occupied loch implying that the losses in absolute terms were higher in this water body than elsewhere.

Until autumn 2011, beavers in Lochan Buic ignored the stands of *C. mariscus* in this water body, despite the largest stand being less than 20 m from the lodge entrance. However, over the winter of 2011-12, this *C. mariscus* was intensively grazed (Figure 42). In September 2012, small numbers of fresh *C. mariscus* shoots sprouting from drifting sections of rhizome could be found (Figure 43), but it appears that these were unable to establish. In September 2013, there was very limited growth of young *C. mariscus* plants higher up the shore. By September 2013, the remapping of polygons indicated that 87% of the original area of *C. mariscus* had been lost and was undergoing colonisation by other species, such as common reed *Phragmites australis* (Figure 43).

In Un-named Loch (South), minor grazing of several species, mainly *N. alba*, was observed in July 2011. This was unchanged in September 2011 and there was no further evidence of feeding by beavers in this Loch in any subsequent year. No other field signs of beaver presence in the riparian zone were observed. The feeding signs in 2011 may have been associated with exchange of animals between Lochan Buic-Un-named Loch (South) and Loch Creagmhor-Un-named Loch (North) territories.

In 2012 and 2013, there were regular signs of beaver presence, including tree felling and limited feeding on *E. fluviatile*, in a small pond (known as the 'Ford Pond' within the Scottish Beaver Trial), situated 0.5 km north of Lochan Buic.

Figure 41. Left: area of grazing on N. alba *and* E. fluviatile *at south end of Lochan Buic. Right: regeneration of* N. alba *plants from seed and fragments in beaver feeding area in former* C. mariscus *bed on north west shore of Lochan Buic. Both September 2013.*

Figure 42. Left: ungrazed bed of C. mariscus *in Lochan Buic in May 2012. Right: the same bed from reverse angle in May 2013.*

Figure 43. Left: fresh shoots of C. mariscus *growing from drifting rhizome fragments in Lochan Buic in September 2012. Right: expansion of* P. australis *into a former* C. mariscus *bed.*

5.7   General vegetation surveys

An overall summary of the vegetation composition data in line with the protocol of Lassiere (1998) is given in Tables 12 and 13. Given the frequency and intensity of sampling, the

outputs of these surveys may not be strictly comparable with results that would be generated from one-off surveys undertaken of these lochs, although the baseline and 2013 survey results should be comparable. The basic conclusion from a comparison of these surveys is that none of the lochs, with the exception of Dubh Loch, have changed fundamentally between 2008 and 2013. A comparison between the baseline surveys carried out in 2008 and surveys of some of the same lochs conducted in the period 1989-2004 (e.g. Murphy *et al.,* 2002) is provided by Willby and Casas-Mulet (2010). They concluded that the vegetation had remained stable over this period, the most notable change being the invasion of some lochs by *E. canadensis*. Results presented in Tables 12 and 13 reveal four basic types of variation between surveys conducted during the 2008-2013 monitoring period:

(i)   small variations in the cover of common species between surveys which reflect a combination of interannual variation and surveyor perception (for example whether a species is generally or locally abundant). This typically applies to species such as *N. alba* or *P. natans*.

(ii)   low probability of detection of intrinsically rare species in all surveys which ensures that the main source of apparent turnover between consecutive surveys is the occurrence of rare species. In such cases finding or not finding a species must not be confused with gaining or losing that species.

(iii)   occurrence of a small group of species at moderate to high local abundance that were previously unrecorded. Examples of such species include *Potamogeton* x *zizzi* in Loch Barnluasgan, *Potamogeton alpinus* in Loch Linne and *Potamogeton polygonifolius* in Dubh Loch. In such cases these species are abundant enough to suggest that they would not have been overlooked in the baseline surveys. The last confirmed occurrence of *P.* x *zizzi* in Barnluasgan was in 1999 but there are no previous records of the other species in the lochs in question. Therefore they are presumably either genuinely new arrivals or, as a result of a change in growing conditions (including possible disturbance of propagules by beavers), their probability of detection has increased significantly (albeit perhaps only temporarily).

(iv)   conspicuous species that have changed in abundance across several classes (e.g. abundant to rare) where this change is beyond that likely to occur due to interannual fluctuations in growing conditions or detectability and is therefore likely to reflect the influence of an external factor. Herbivory of species such as *C. mariscus* by beavers is the most obvious example.

Table 12. Composition of aquatic vegetation (floating and submerged species) of the Knapdale lochs in the baseline survey year and 2013

	Low occupancy								Medium occupancy						High occupancy							
	Barnluasgan		Losgunn		McKay		Un-named S		Coille-Bharr		Creagmhor		Un-named N		Buic		Dubh		Fidhle		Linne	
	2008	2013	2008	2013	2009	2013	2009	2013	2008	2013	2008	2013	2008	2013	2009	2013	2008	2013	2008	2013	2008	2013
Callitriche stagnalis	R				R	R												LF				
Chara virgata	R	R			D	LD	LF	LF	LA	LA					O	LF						LF
Eleogiton fluitans															LA	A						
Elodea canadensis	LA	LF							LA	A					LF	O						
Fontinalis antipyretica	O	O																			O	O
Isoetes lacustris	R	R							LF	LF	LF	LF			O						R	R
Juncus bulbosus			LA	LA	O	O	LA	LA			LF	LF	R	R	F	F		O	LF	LF	R	R
Lemna minor																	O	F				
Littorella uniflora	O	O	LF	LF	LF	LF			A	A	LF	LF			O	LF			F	LF	A	A
Lobelia dortmanna	R	R	LF	LF	LF	LF			LF	A	LF	LF			F	LA			R	O	A	A
Myriophyllum alterniflorum									LA	LF	O	O			R	R			O	R	LF	O
Nitella opaca/flexilis											R											
Nitella translucens			O		LA			O	R						LF							
Nuphar pumila	R	O	O	O		O	R	R											LF	LF		
Nymphaea alba	A	A	LA	A	LA	A	A	A	LA	LA	F	LA	LA	A	A	A	F	O	A	A	LA	A
Potamogeton alpinus									LF	LF												LO
Potamogeton berchtoldii	O	R							O	O	O											
Potamogeton lucens	LF	LA							LF	LA												
Potamogeton natans	A	A	A	A	F	F	A	A	F	LA	O	F	A	A	LA	LA	A	LA	A	A	LA	LA
Potamogeton obtusifolius									R	O								LA				
Potamogeton perfoliatus									LF	LF	R	R			R	O						
Potamogeton polygonifolius			LA	LA	LF	LF	O	O					O	O				LF	LF	R	O	R
Potamogeton praelongus	LA	LD							LF	LF												
Potamogeton x zizii		LF							LF	LF	LF	LA										
Sparganium angustifolium	LF	LA	F	LF	R	R	R	R	LF	LF					O	LF			R	R	O	R
Utricularia intermedia																				R	R	

D - Dominant; A - Abundant; F - Frequent; O - Occasional; R - Rare. Values prefixed by L - Local, e.g. LA - Locally Abundant

Table 13. Composition of emergent vegetation of the Knapdale lochs in the baseline survey year and 2013

	Low occupancy								Medium occupancy						High occupancy							
	Barnluasgan		Losgunn		McKay		Un-named S		Coille-Bharr		Creagmhor		Un-named N		Buic		Dubh		Fidhle		Linne	
	2008	2013	2008	2013	2009	2013	2009	2013	2008	2013	2008	2013	2008	2013	2009	2013	2008	2013	2008	2013	2008	2013
Caltha palustris	R	R									R	R						O				
Carex lasiocarpa																			LF	LF	LF	LF
Carex nigra					O	O					R				O	O			O			
Carex paniculata			R	R	R	R						R					LA	LA				
Carex rostrata	F	LA	F	F	F	F	A	A	F	F			LF	LF	LF	LF	LF	LA	F	F	F	F
Cladium mariscus											LA	R			LA	R	LA	LF	LA	R	LA	LF
Eleocharis multicaulis			LF	LF	O	R	LF	O			O	O							O	O	O	LF
Eleocharis palustris	O	R			O	O	O	R	LF	LA	R	R			R		R	O	R		O	O
Equisetum fluviatile	F	F			A	A	F	F	F	LA	O	O	O	O	F	F	A	F	O	O	F	LF
Glyceria fluitans							R															
Hydrocotyle vulgaris	R	R			O	O	O	O									O	O	R	R	R	
Iris pseudacorus	R	R			R	R	O	LF	O	R												R
Juncus acutiflorus	O	R	R	LF	LF	LF	F	F			O							LF	LF	LF	O	R
Juncus articulatus			LF	O		R	LF	O	R		R	O	R	O	R	O		LF	O		R	O
Juncus effusus	R	R	R	O		R			R									LF		R	R	
Lycopus europeaus																		O				
Lythrum salicaria	R								O	R												
Mentha aquatica	R	R							R	R							LF	O	R			
Menyanthes trifoliata	LF	LF			R	R			R	R			R	R			LF	O	O	R	O	R
Myosotis laxa																		R				
Myosotis scorpioides					R																	
Oenanthe crocata									O	R												
Phalaris arundinacea									LF	LF												R
Phragmites australis	LA	LA	O	O					LA	LA	LF	LF	O	O	A	A						
Potentilla palustris	O	O		R	R		O	O	R						R	R		LF				
Ranunculus flammula	R				O	O												LF	R	R	R	
Schoenoplectus lacustris	LA	A			LA	A	F	F	LF	LF	LA	LF							LF	O	LF	O
Scutellaria galericulata									O	O								R				
Sparganium erectum									R	R			R					LF	R	LF		
Sphagnum auriculatum				LF													O	LA		LF		
Sphagnum recurvum																		LF				
Sphagnum sp			O	R	R	R												R	LA			
Veronica scutellata																		R	R	R		

D - Dominant; A - Abundant; F - Frequent; O - Occasional; R - Rare. Values prefixed by L - Local, e.g. LA - Locally Abundant

5.8 Invertebrate colonisation of Dubh Loch

Seven fixed locations at Dubh Loch were sampled each May from 2011-2013 to assess the colonisation of newly formed habitat by aquatic invertebrates. In the 21 samples collected during the period 2011-2013, 87 species were found amongst 27,355 individuals (mean of approximately 1,300 individuals per sample, range: 520-5,910). Larval species of the families Chironomidae (20,305 individuals) and Corixidae (2,713) were present in all samples and made up the vast majority (84%) of individuals found. This number of species is very high for a small shallow water body in the early stages of colonisation (Williams *et al.,* 2008), including other water bodies formed through damming by beavers (Law and Willby, submitted). This almost certainly reflects the connectivity of the dammed area to a pre-existing well-vegetated water body, as well as the close proximity of other water bodies to act as a supply of colonists. However, the large numbers of individuals and dominance by one or two families is more symptomatic of the early stages of colonisation.

The number of species recorded per sample, or across all samples, was similar in 2012 and 2013, being approximately 50% higher than in 2011 (Table 14). Conversely, following a reduction in the density of chironomid midge larvae, the numbers of individual animals sampled was lower in the later years. Values of the Shannon Diversity Index did not change significantly between years and appear higher in 2012 mostly as a consequence of the smaller numbers of individuals recorded. The Bray Curtis dissimilarity index indicates that biological turnover between samples reduced over time. This effect is clearly visible in Figure 44 from the reduced dispersion of samples in 2013 compared to earlier years as indicated by the smaller ellipse. Possible underlying causes are that sampling sites were becoming environmentally more similar (e.g. woody debris inputs and aquatic vegetation establishment show less fine scale spatial variation) or because individual population sizes and local dispersal had increased sufficiently to homogenise the faunal composition. It is also possible that a drop in water level in 2013 caused organisms to be concentrated into a smaller area of aquatic habitat thus increasing similarity between samples. To accommodate the change in water level between years the exact location of one sampling point had to be adjusted by 2 m to ensure that only aquatic habitat was being sampled. The major gradient in Figure 45 is from rather generalist highly mobile taxa on the left through to more specialist and in some cases less mobile taxa on the right, consistent with expected patterns of colonisation.

Table 14. Change in number and richness and diversity of macroinvertebrates in samples from Dubh Loch

Year	Mean taxa per sample (range)	Mean individuals per sample (range)	Total taxa recorded	Total individuals sampled	Bray Curtis dissimilarity	Shannon Diversity
2011	16 (12-25)	1,817 (520-5,910)	41	12,717	0.57 ± 0.04[a]	2.83 ± 0.34
2012	24 (19-28)	857 (545-1,141)	64	5,998	0.43 ± 0.03[ab]	5.34 ± 1.16
2013	25 (18-31)	1,235 (703-2,144)	57	8,643	0.39 ± 0.03[b]	2.99 ± 0.45

Note: for each year of sampling *n* = 7. For the Bray Curtis dissimilarity values years that share the same letter suffix were not significantly different from each other.

Figure 45 illustrates the individual-based taxon accumulation curves for the samples collected from 2011-2013. In 2012 the curve does not reach an asymptote suggesting that the fauna was potentially undersampled and that more taxa were actually present, although this is partly influenced by the fewer individuals sampled that year. In 2011 chironomids

were overwhelmingly dominant resulting in a very slow rate of taxon accumulation. Dominance of newly created wetlands by chironomids is a common phenomenon (e.g. Danell and Sjöberg 1982) and the results for 2011 suggest that even if sampling had commenced in May 2010, shortly after the formation of the enlarged Dubh Loch, the composition of the invertebrate community would probably have been very similar.
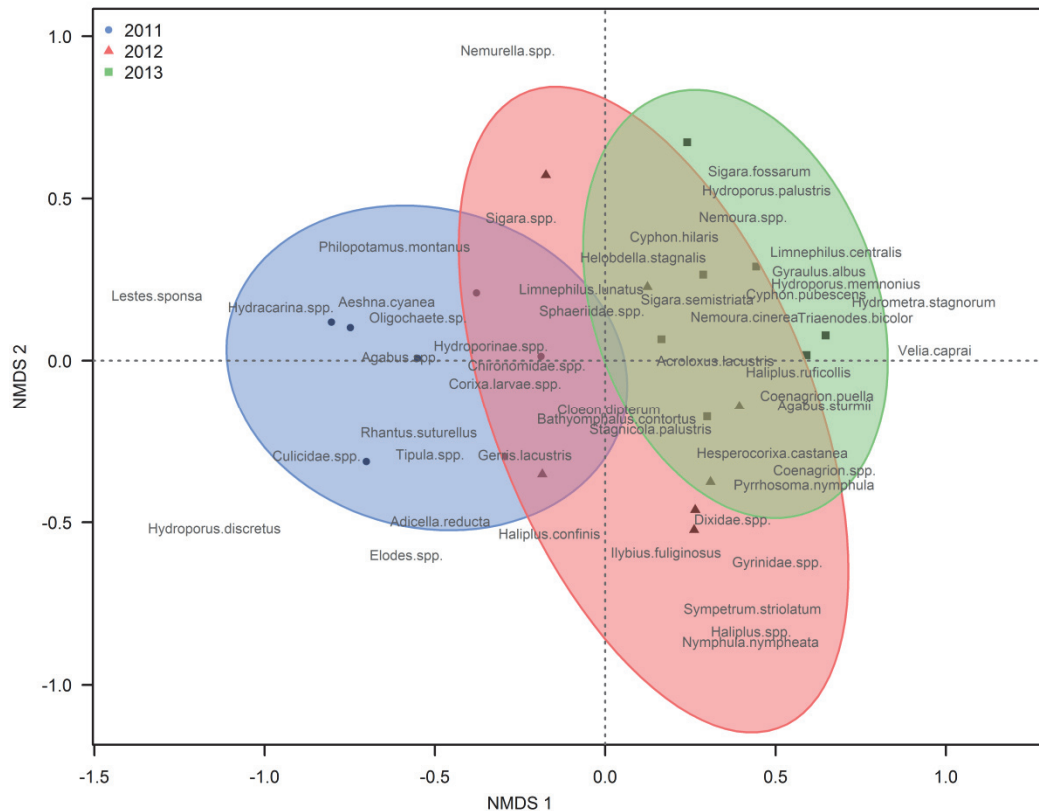
Figure 44. Non-metric multidimensional scaling ordination (NMDS) plot for macroinvertebrate species composition in Dubh Loch 2011-2013. All stress values < 0.1.

A total of 32 aquatic beetle species were found within the Dubh Loch from 2009-2013, with five species that were found in 2009 (Garth Foster, pers. obs.), shortly after beavers were released and before they were found regularly in Dubh Loch, not being found in samples collected during 2011-2013. Conversely an additional 20 species not recorded in 2009 were found in the period 2011-2013. Indeterminate individuals of the genera *Agabus* and sub-family Hydroporinae were numerically dominant in samples collected between 2011-2013. The species accumulation curve (Figure 46) is approximately asymptotic suggesting that a significant number of additional species would not be found with greatly increased sampling effort.
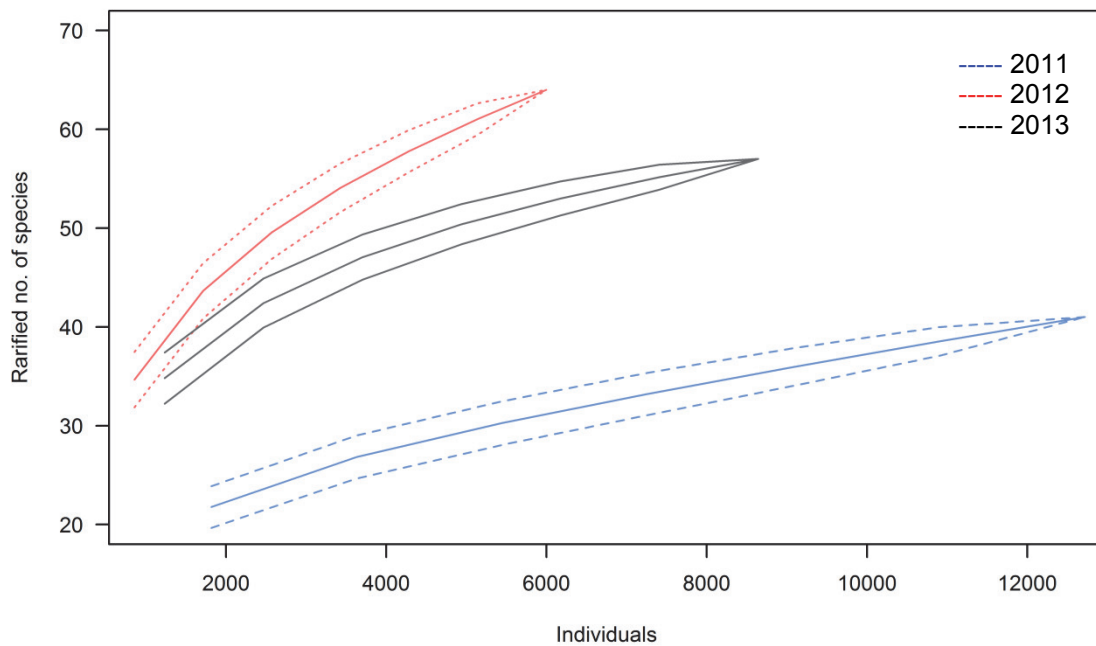
Figure 45. Individual based species accumulation curves for invertebrate taxa in Dubh Loch for three successive sampling years. Error bars represent the standard deviation in richness based on 1000 random resampling events.
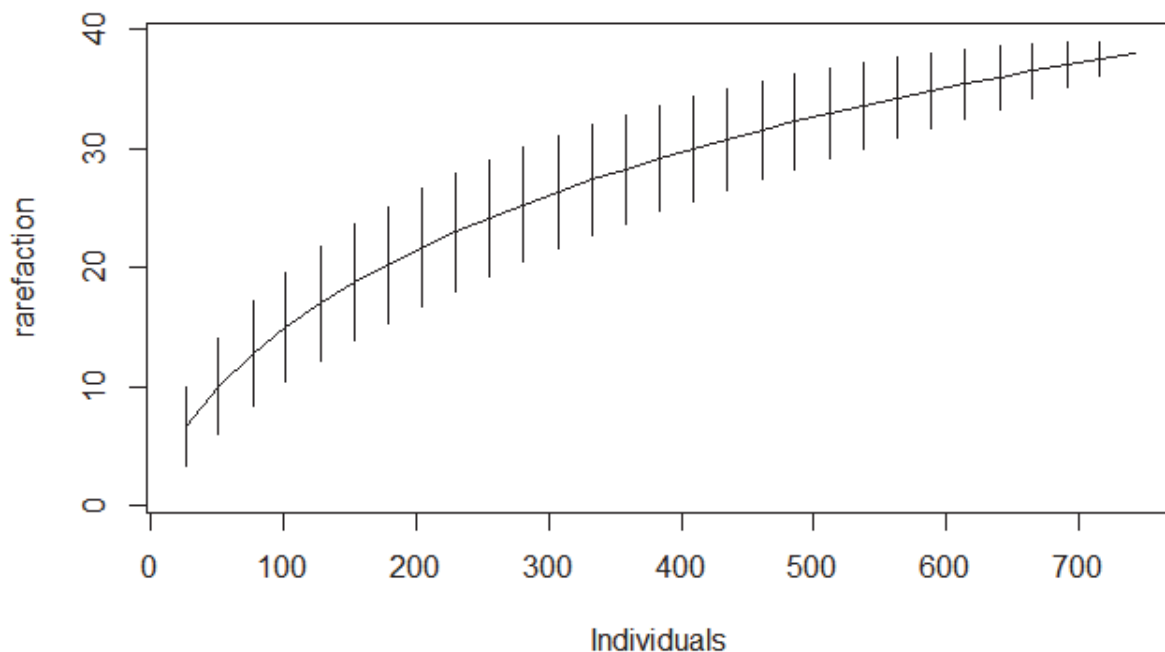
Figure 46. Individual-based species accumulation curves for water beetles in Dubh Loch for the period 2009-2013. Error bars represent the standard deviation in richness based on 500 random resampling events.

The number of beetle species and individuals recorded at Dubh Loch was high compared to beaver-generated and other naturally-occurring wetlands in Sweden sampled with similar effort (Willby *et al*., submitted), although the rate at which species accumulated with the

number of individuals sampled was higher in the Swedish sites. Newly-created ponds are known to be important habitats for water beetles, which are effective colonists due to their high mobility (Bloechl *et al*., 2010). Extensive woody debris may be an important component of habitat complexity in beaver ponds because it provides direct shelter and refugia from fish, as well as concealment for predatory species of beetles. In deeper water, or where the substrate is unstable, submerged wood may also sustain a scraper invertebrate fauna by enabling the growth of algal biofilm.

6. DISCUSSION

6.1 Overview of the effects of Knapdale beavers on loch macrophytes

The first part of this discussion is structured around the effects of beavers at Knapdale on aquatic vegetation, as summarised in Table 15.

6.1.1 Herbivory and foraging

6.1.1.1 Grazing and foraging on *Cladium mariscus*

The observed patterns of grazing by beaver on individual species are largely consistent with those reported from elsewhere in Europe, although there are no published accounts referring to herbivory of *C. mariscus*. One paper refers to herbivory by North American beavers (*C. canadensis*) of the closely-related *Cladium jamaicense* in Louisiana (Chabreck, 1958). Of the ten aquatic plant species on which beavers have been observed feeding at Knapdale (see Table 11), all, with the exception of *C. mariscus,* are common and widely distributed in lochs either in Knapdale or Scotland in general.

Cladium mariscus is an uncommon species in Great Britain, occurring in about 8% of hectads, although it could not be described as rare and is frequently abundant where it occurs (Preston and Croft, 1997). In England, *C. mariscus* is commonest in calcareous fens in East Anglia, but in Scotland, it occupies a range of more distinctly aquatic, oligotrophic to mesotrophic peaty wetlands, mostly along the west coast. The area of the north Kintyre peninsula and Islay supports one of the larger concentrations of *C. mariscus* in Great Britain. Outside Britain, *C. mariscus* is common in Ireland (26% of hectads) and has a near-global distribution, tending to be most abundant in subtropical regions. There is no particular reason to suspect that beavers could adversely affect the status of *C. mariscus* in Great Britain as a whole, although this species is evidently highly palatable and beavers thus have the potential to reduce its abundance at sites where it occurs. It is therefore unlikely that *C. mariscus* could coexist at high cover in the long term at sites utilised by beavers.

Germination studies on *C. mariscus* or the closely related *C. jamaicense* show that *Cladium* germinates preferentially on saturated peat and compared to other emergent species germination rate in the dark is high (Ponzio *et al*., 1995; Lorezen *et al*., 2000). *Cladium* is an evergreen genus that accumulates dense persistent litter and the near-ground microclimate in *Cladium* stands is therefore conducive to promoting germination of *Cladium* and suppressing germination of other emergent species (Meredith, 1985). The greenhouse germination trials in this study were conducted under conditions that should have favoured germination of *C. mariscus* (i.e. saturated peat with overlying *C. mariscus* litter, natural light cycle and fluctuating temperatures with a day time peak of $25^{o}C$). The absence of any germination over a period of 14 months therefore implies that the seedbank of *C. mariscus* in the Knapdale lochs is very small and that the population is maintained by vegetative means. This is consistent with the low frequency of flowering observed in the field.

In East Anglia, *C. mariscus*-dominated fens are harvested on a rotational basis to supply materials for thatching (Conway 1942). Mowing is also carried out to prevent succession of sedge fen to carr. Various studies show that this process reduces the depth of the litter layer, thus favouring germination of other species that are unable to establish in unmanaged *C. mariscus* stands (Conway 1942; Meredith 1985; Gusewell and Le Nedic 2004). Studies in East Anglia suggest that mowing on a shorter cycle than four years is unsustainable and ultimately leads to the loss of *C. mariscus* (Meredith 1985). Although there are some basic similarities between manual harvesting and herbivory, the former will be relatively benign since the below ground organs remain *in situ* and are undamaged, whereas these are actively uprooted by beavers. Consequently beaver herbivory is likely to represent a more severe and long-lasting pressure.

Table 15. Summary of observed and potential effects of beavers on aquatic vegetation at Knapdale

Observed or potential effect	Main locations	Classification	Basis for interpretation
Grazing and foraging on *Cladium mariscus*	Buic, Creagmhor, Fidhle	Negative	Uncommon species subject to almost complete loss in several lochs. Very limited evidence of recolonisation. Populations present in other sites and not universally depleted
Grazing on *Schoenoplectus lacustris* or *Equisetum fluviatile*	Fidhle, Linne	Neutral	Common species, present elsewhere in Knapdale and small residual populations in lochs affected so potential for rapid re-establishment. Possible loss of hydraulic refuge for some aquatic biota
Grazing and foraging on *Nymphaea alba*	Buic, Dubh, Coille-Bharr, Un-named (North)	Neutral	Common species, losses small and sustainable. Little evidence of compensatory growth or expansion of understorey species due to high level of dominance. Possibility of greater utilisation in future if preferred foods exhausted
Uprooting of isoetids	Buic, Coille-Bharr	Neutral	Losses trivial in relation to other forms of disturbance. Apparently collateral damage from feeding on *Schoenoplectus* or *Nymphaea* and no evidence that isoetids specifically targeted.
Major water level rise	Dubh	Positive	Promotes fine to medium scale heterogeneity. Rapid recolonisation by macrophytes and invertebrates. Generates novel habitat conditions and niche for early colonists.
Minor or temporary water level rise	Fidhle, Linne, Un-named (North)	Neutral-Positive (taxa dependent)	Reversible shift in relative abundance of more moisture tolerant species. Possible niche for scarce species associated with fluctuating water levels.
Removal of tree shade	Linne, Coille-Bharr, Creagmhor, Buic, Dubh	Neutral	Potential to increase diversity of understorey vegetation or increase aquatic vegetation if resulting habitat suitable. Increased risk of desiccation of bryophytes associated with high shade and humidity. Multivariate effects preclude assessment.
Accumulation of woody debris	Coille Bharr, Linne, Buic, Creagmhor	Neutral-Positive (taxa dependent)	No clear effect on aquatic vegetation. May lead to erosional losses but also likely to increase complexity of littoral habitat for other aquatic biota
Changes in water chemistry	Dubh, Un-named (North)	Uncertain	Potential for increase in DOC in smallest lochs with raised water levels. May reduce macrophyte growth but insufficient evidence from water quality monitoring
Spread of *Elodea canadensis*	Dubh Loch	Negative	First recorded in Dubh Loch in May 2014 by dam, although impossible to state categorically that spread was due to beavers

Cladium mariscus is a rare plant in Scandinavia (Mossberg and Stenberg 2003), confined to scattered locations in southern Sweden where beavers are presently sparse (Hartman 2011), although it was reportedly commoner in Sweden 6000-8000 years ago (Conway 1942). Thus it is exceptionally unlikely that the beavers imported to Knapdale from Norway could have had prior experience of *C. mariscus* and were probably feeding on this species opportunistically. Other large fleshy emergent species on which beavers have been observed to feed elsewhere (e.g. branched bur-reed *Sparganium erectum*, reedmace *Typha latifolia*, iris *Iris pseudacorus*, bogbean *Menyanthes trifoliata*) are scarce at Knapdale or absent and this may be reflected in the scale of feeding on *C. mariscus*. The almost complete loss of large stands of *C. mariscus* in several lochs, the lack of evidence for a significant propagule bank to aid their re-establishment and the dispersion of litter necessary to create a favourable microclimate for germination implies that recovery may be a long process. In some cases loss of *C. mariscus* from deeper water was also followed by a surprisingly rapid expansion of *N. alba* into the gaps created. Other studies indicate that nymphaeids are common beneficiaries of the decline of emergent vegetation from lake shorelines (Crivelli *et al.*, 1995). This may further impede re-establishment by *C. mariscus*. The only possible mitigating effect of beaver feeding is that any dam building may cause sufficient increase in water level to saturate the upper part of the littoral zone where litter and, potentially, seeds of *C. mariscus* may accumulate. This may encourage germination and re-establishment. However, on present evidence, our overall interpretation is that this beaver effect is negative.

6.1.1.2 Grazing on *Schoenoplectus lacustris* and *Equisetum fluviatile*

Due to direct grazing by beavers, stands of *S. lacustris* were reduced by 92% and 75% in Lochs Linne and Fidhle respectively, with a smaller reduction of 25% in Creagmhor Loch. *E. fluviatile* was reduced by 22% in Lochan Buic. Beavers typically uprooted the entire *S. lacustris* plant before consuming the lower section of the stem and part of the rhizome. There was vigorous feeding on *S. lacustris* in Linne and Fidhle from the first summer of the trial.

There are few published accounts of beavers specifically grazing *S. lacustris* on the scale observed in Linne-Fidhle, although Danilov *et al.* (2011a) list it amongst the preferred macrophyte diet of beavers in Karelia. Valta-Hulkkonen *et al.* (2004) describe marked changes in the extent of this species in a Finnish lake associated with grazing and nest building by muskrats (*Ondatra zibethica*). In addition, extensive feeding by beavers has been observed on *S. lacustris* in the Dalälven system in central Sweden (Willby and Law personal observation, 2012). *E. fluviatile* is a more commonly reported constituent of the diet of beavers (e.g. Histøl 1989).

Both *S. lacustris* and *E. fluviatile* are common species occurring very widely in standing waters throughout Scotland, often forming sizeable stands in shallow lochs. They frequently coexist and extend into deeper water than other emergent species, which may partly explain their attractiveness to beavers. *S. lacustris* was not completely eliminated from Linne or Fidhle and would be expected to regain its original cover in the absence of beavers. This species is likely to be able to resist physical disturbance more effectively than *C. mariscus*, possibly due to its multiple tillers and early-forming floating leaves, and is regularly harvested for its biomass in parts of Asia or to maintain flow in river channels. However, under the constraints of low fertility, re-establishment is expected to take longer to achieve. Because *S. lacustris* in particular occurs as a low density of robust stems it provides ideal sheltered habitat for isoetids and pondweeds. No adverse effects on these associated species were noted from the loss of this habitat over the duration of the trial but confirmation of this by monitoring over a longer period would be desirable. Our overall interpretation is that the effect of grazing on *S. lacustris* and *E. fluviatile* is neutral.

6.1.1.3 Grazing and foraging on *Nymphaea alba*

A tendency for beavers to feed on nymphaeids, especially their rhizomes (Northcott 1972), is widely reported in the literature. In the present study, *N. alba* showed a significant reduction in cover in several sites that appeared to be the consequence of persistent uprooting of rhizomes, perhaps in some cases, coupled with small rises in water level, or feeding on floating leaves. In the latter case, it was possible to quantify the actual size of leaves grazed, because the petiole projects above the water surface upon removal of the weight of the floating blade and there is a simple biometric relationship between petiole diameter and leaf size. Based on this relationship, and from sampling grazed and ungrazed leaves in Lochan Buic and Un-named Loch North, Law *et al.* (2014a) demonstrated that beavers fed selectively on larger leaves mostly situated in shallow water. It was speculated that smaller leaves tend to be avoided because, being characteristically red in colour, they are likely to be better chemically defended due to their higher anthocyanin content (Lev-Yadun and Gould 2009). Law *et al.* (2014a) showed that the loss of floating leaves due to herbivory was small (2% of the leaf 'population'). This suggests that although leaf feeding is common, it is the uprooting of rhizomes that has the most destructive effect on *N. alba*.

Larger, floating-leaved and emergent species, such as *N. alba* and *S. lacustris*, create quiescent habitat in lochs and are often the front line in dampening down wave action in deeper water before it reaches the shallowest parts of the littoral zone. Such habitat often supports isoetid plants and there might therefore be a decline in isoetids if there were to be a large-scale decline in their supporting habitat. Extensive recession of lily beds due to feeding by beavers might lead to increased disturbance of hitherto sheltered shallow water areas by wave action, mimicking the effects of eutrophication reported in some lakes (Madgwick *et al.*, 2011). However, no indication of such an effect was observed in any of the lochs inhabited by beavers. Indeed, there may even be some benefit to isoetids from a local reduction in shading by the canopy of floating *N. alba* leaves. In more productive lochs, or those with a diverse sediment propagule bank, a more rapid response of other species to the formation of gaps in the dominant plant canopy might be expected. Our overall interpretation is that this aspect of beaver effects is neutral.

6.1.1.4 Uprooting of isoetids

In terms of the specific elements of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea* plant associations (principally *L. uniflora*, *L. dortmanna*, *Isoetes lacustris*, *M. alterniflorum* and *J. bulbosus*) that form part of the basis of the SAC designation for the Knapdale lochs, there is no evidence of adverse effects associated with beavers. Records of beavers elsewhere utilising any of these species are unusual, although Histøl (1989) reports Norwegian beaver feeding on both *L. dortmanna* and *I. lacustris*. Limited collateral damage to some beds of *L. uniflora* and *L. dortmanna* was observed in Loch Fidhle, Lochan Buic and Loch Coille-Bharr where beavers had been uprooting them whilst feeding on *S. lacustris* or *N. alba*. Such effects are probably inevitable and likely to be not much greater than the disturbance associated with annual monitoring of macrophytes by surveyors or launching boats for fishing. Compared to the losses incurred by isoetids during winter storms, the losses imposed by beaver feeding are trivial; a simple comparison of the extent of drifting plants versus their standing stock suggests that such losses will equate to less than 0.1% of the population annually in individual sites. Redistribution of uprooted plants to other parts of a lake by wave action could potentially prove beneficial if this allows colonisation of new habitat or areas disturbed by beavers. However, evidence for this could not be found over the duration of this study. Our overall interpretation is that this aspect of beaver effects is neutral.

6.1.2 Water level change associated with dam building

6.1.2.1 Major water level rise

In the case of Dubh Loch, damming of the outflow resulted in a major transformational change, inundating an additional 1.41 ha to an average depth of 1m. While depth *per se* is an important determinant of vegetation development in beaver wetlands, several studies emphasise the greater significance of water level regime and its interaction with microtopography (Pollock *et al.*, 1998; Sturtevant 1998). In 2013, the partial exposure of large areas of wet mud at Dubh Loch appeared to significantly accelerate vegetation development.

The rapidity of establishment by aquatic macrophytes in the newly-flooded areas at Dubh Loch was surprising, especially given that plants were establishing in the former understorey vegetation of a birch woodland. There was very little colonisation of these areas in 2011, but from 2012 onwards colonisation was rapid, potentially aided by tree collapse and increased recession of the surviving tree canopy. Colonisation may also have accelerated in 2013 due to a combination of good weather and lower water levels. Two species, *Potamogeton natans* and blunt-leaved pondweed *P. obtusifolius* were especially prevalent in the newly flooded area in 2013. The latter was already common in this area in 2012, yet was not recorded in the baseline survey in 2008, indicating that it was either absent or rare enough at that time to be overlooked.

Pondweed species characteristically form large seedbanks that can remain viable for centuries (Skoglund and Hytteborn 1990). Therefore, one explanation for rapid plant establishment is that the newly inundated area of Dubh Loch was colonised through rewetting of a pre-existing seedbank associated with a historic wetland. There is certainly evidence of successional encroachment by mire-forming species at the south end of Dubh Loch, indicating that it was formerly much larger. There is no indication from the oldest available Ordnance Survey maps for this area (1870) that Dubh Loch was larger in the recent past (1870-1940) than at present, which implies that most of the change in area must have occurred well before this date. Pollen and plant macrofossils from a sediment core would be needed to verify the post-glacial history of Dubh Loch. Given its topography, it is conceivable that a former beaver-generated wetland existed at this location. The much slower establishment of *N. alba* is consistent with the results of successional studies of beaver ponds (Ray *et al.*, 2001), which indicate that nymphaeids are characteristically the last group of species to colonise new water bodies in view of their low mobility. Unpublished data from a survey of Swedish beaver ponds of a variety of ages (Willby and Law, personal data), plus studies carried out in the US (McMaster and McMaster 2001; Ray *et al.*, 2001) indicate that isoetid species are unlikely to be a significant beneficiary of beaver ponds, being absent from or rare in studied sites.

The presence of beaver ponds is widely reported to increase landscape-scale diversity (Wright *et al.*, 2002), partly because of the presence of a specialist or early successional biota and because the rotational use of wetlands by beavers creates a mosaic of wetlands at different stages of maturity, use or abandonment. In terms of habitat structure no other water bodies in Knapdale present a dynamic combination of water, extensive dead wood, re-establishment by macrophytes and intermittent exposure of wet mud. Thus, while the altered Dubh Loch does not yet appear to support any unique species that can be attributed to the effects of beavers, at a landscape scale it represents novel habitat which independent evidence demonstrates is of value to a wide range of aquatic biota, including birds (Nummi 1992; Danilov *et al.*, 2011b), bats (Nummi *et al.*, 2011), amphibians (Dalbeck *et al.*, 2007), invertebrates (Rolauffs *et al.*, 2001) and fish (Hägglund and Sjöberg 1999). The current window of monitoring is also relatively narrow given that Ray *et al.* (2001) found by studying beaver ponds of different ages that plant species richness continued to increase in ponds up

to 40 years old. More widespread development of beaver-generated wetlands in Scotland might be expected to yield the landscape-scale benefits for biodiversity observed elsewhere in Europe or North America, and for a disparate range of biota. Therefore our overall interpretation is that this aspect of beaver effects is positive.

6.1.2.2   Minor or temporary water level rise

Depending on the bank profile, small dams on the outflow will result in shallow inundation of marginal areas. This was evident in Lochs Linne and Fidhle during 2009, after which the dams were removed, and in Un-named Loch (North) from 2012 onwards (Figure 47). Analyses of quadrat level data using the Ellenberg moisture indicator scores provide little evidence for a systematic shift in vegetation composition of these marginal areas towards increased cover of species associated with soil saturation. Eventually vegetation composition in such areas should achieve equilibrium with the new water level position, although this adjustment might be expected to take a decade or more to stabilise and it is uncertain if the water level rises imposed would be maintained for this length of time. Plant zonation around standing waters follows broadly predictable patterns, but the water depth tolerance of many common marginal species is fairly wide (±0.2m) (Spence, 1964). The rise in water level associated with beaver dams on these lochs is likely to fall inside the natural window of intra-annual variation in water level (approximately 0.5m) that existed prior to damming. Therefore major floristic changes in these lochs are unlikely. However, there are a variety of uncommon amphibious plant species, such as pillwort *Pilularia globulifera* or bog hair-grass *Deschampsia setacea*, which may benefit from creation of this inundation zone habitat, particularly where damp bare ground is exposed. However, none of these species are currently recorded in Knapdale. In May 2014 the somewhat commoner ivy-leaved crowfoot *Ranunculus hederaceus* was found, for the first time, growing on wet mud on the margin of Dubh Loch, a typical habitat for this species. *R. hederaceus* was not recorded in any of our earlier surveys of water bodies at Knapdale, or to our knowledge in previous recording there by other botanists, but was also found to be common in shallow beaver-created habitats at a study site in Perthshire (Willby, unpublished data). In view of the possibilities for recruitment of additional specialist taxa the overall interpretation is that this aspect of beaver effects is neutral or positive.

Figure 47. Left: water level rise associated with a small dam at Un-named Loch (North) in May 2013. Right: inundated Myrica *mire at fixed transect on Loch Fidhle in September 2009.*

6.1.3 Other observed or potential indirect effects

6.1.3.1 Removal of tree shade

Trees were regularly felled within 5 m of the shoreline around five of the lochs inhabited by beavers. *Salix* spp, *Sorbus aucuparia* and *Betula pubescens* were the commonest felled species recorded, in line with the findings of surveys by the James Hutton Institute which has been monitoring the effects of beavers on the Knapdale woodlands (Iason *et al.*, 2014). Where trees directly overhang the water surface, this felling will increase light availability unless there is compensatory growth into the gaps by adjacent trees. There were no sites where the entire shoreline was extensively felled, so any effect of tree felling by beavers on aquatic vegetation is probably too localised to be detected. In Dubh Loch, there was extensive die-back of the former birch woodland due to water level rise and the extent of colonisation of flooded areas by aquatic plants was probably partly regulated by the loss of shade created by standing dead trees (see Figure 34). In Loch Losgunn, the conifer forestry above the north-west shore of the loch was harvested in 2012, this representing the single largest change in the catchment of any of the lochs studied during the trial period. This felling is likely to have reduced shading of the water surface and may have contributed to the significant expansion in cover of *N. alba* on this loch. It is interpreted is that this aspect of beaver effects is neutral.

6.1.3.2 Accumulation of woody debris

Beavers did not actively cache woody material in any of the Knapdale lochs beyond the immediate vicinity of their lodges. This may reflect the lack of prolonged ice cover and provision of resources afforded by aquatic vegetation (Gorshkov and Gorshkov 2011). Although rarely found in the fixed transects, beaver-cut woody debris was commonly observed around the shoreline of a number of lochs, especially Linne, Buic, Creagmhor and Coille-Bharr (Figure 48). Occasionally this material coincided with a lawn of isoetids, typically *L. uniflora*. It is expected that through the patchy occurrence of shading, nutrient input and physical shelter, this woody debris will generate a more heterogeneous environment for macrophyte growth and associated organisms. Woody debris presence may also partially compensate for the loss of physical complexity and shelter associated with the submerged stems of species such as *S. lacustris*. However, traction of woody debris during storm events could potentially also result in some erosion of beds of macrophytes in shallow water areas.

Habitat complexity associated with woody debris in streams is widely agreed to be a major influence on the composition and distribution of invertebrates and fish (Gurnell *et al.*, 1995), but the influence of woody debris within the littoral zone is less well-studied. In principle, twigs and branches found on lake shorelines and generated by tree felling in the adjacent riparian zone will have a different habitat value from large sections of dead timber produced by felling or wind-blow in pond-like environments such as Dubh Loch. France (1997) found that densities of macroinvertebrates, fish and amphibians were significantly elevated near beaver lodges and wood caches compared to the typical sand and gravel dominated habitats of lakes in Ontario. It is therefore concluded that for fish and invertebrates in lakes, the effect of woody debris accumulation will usually be positive. Recent evidence (Langford *et al.*, 2012) suggests that coarse woody debris in streams favours selected fish species and their ontogenic stages, rather than being universally beneficial, and the same principle is likely to apply in lakes. The overall interpretation is that this aspect of beaver effects is neutral or positive, depending on the taxa concerned.

Figure 48. Beaver-cut woody material on the loch bed, observed around the margins of Loch Linne in September 2012

6.1.3.3   Changes in water chemistry

In the absence of regular monitoring of water chemistry at all sites pre- and post-beaver introduction, it is difficult to conclude whether there have been changes in water chemistry that may have a direct impact upon macrophytes.   The most critical determinant for macrophytes at Knapdale is probably DOC, as this will dictate water colour, which has a significant impact on water column transparency.   Inundation of surrounding peatland, accompanied by significant inputs of organic matter from felled or dead trees might be expected to increase DOC water column levels, as reported elsewhere (Peczula and Szczurowska 2013).   However, the scope for an increase in DOC concentration is probably limited to the smallest sites (i.e. Dubh Loch and Un-named Loch (North) where DOC level is already high.   In both Dubh Loch and Un-named Loch (North), there was a decline in *P. natans* in open water areas that cannot be attributed to herbivory. A similar decline was noted in floating-leaved pondweed species (*P. natans* and bog pondweed *P. polygonifolius*) at a site in Perthshire where these species were also ungrazed (Law *et al.*, 2014b).   It is speculated that the modest decline of *P. natans* in Dubh Loch and Un-named Loch (North) is partly associated with decreased water transparency. However, no quantitative evidence for this is available from the water chemistry data provided by SEPA and therefore any such effect is considered to be uncertain.

6.1.3.4   Spread of *Elodea canadensis*

The invasive *E. canadensis* was present in two lochs occupied by beavers: Buic and Coille-Bharr. In the case of the latter site, there was a small risk of transfer into Dubh Loch, as animals moved regularly between these water bodies.   Despite regular inspection, *E. canadensis* was never found over the formal macrophyte survey period (2008-2013) in Dubh Loch, suggesting that the risk of transfer is low.   However, in May 2014 ten stems of *E. canadensis* were noted growing within the enlarged Dubh Loch next to the dam.   It is impossible to prove that the spread of *E. canadensis* to Dubh Loch, presumably from the immediately adjacent Loch Coille-Bharr, was caused by beavers, though the position of the plants would suggest this. Merely by increasing the proximity of the uninvaded Dubh Loch to the invaded Loch Coille-Bharr beavers increase the risk of transmission by other vectors.

Aquatic plants are highly prone to desiccation and the chance of viable overland dispersal of vegetative material is therefore low.   Propagules of other species might conceivably be

spread by beavers via their faeces or attachment to fur, but there are no reports of this in the literature. Packing of dams and lodges with mud and vegetation is likely to be the major way in which beavers cause local dispersal of vegetation. If this causes non-native plant material to be moved from an invaded site to an adjacent uninvaded site the risks of invasion are increased. Under these circumstances the effect of beavers could be regarded as negative.

6.2 Effects of beavers on aquatic vegetation at Knapdale compared to effects observed elsewhere

6.2.1 Herbivory

It is well-known that beavers graze on aquatic plants (Svendsen 1980; Histøl 1989, Milligan and Humphries 2010). However, although there is a sizeable literature listing the plant species consumed, very few studies are sufficiently detailed to quantify the scale of biomass loss associated with herbivory or its consequences or lack the necessary control treatment or baseline data. Those studies that do exist confirm that losses of biomass or cover of preferred species can be substantial, with values in line with those recorded in the present study. For example, Parker *et al.* (2007) documented a 60% decrease in plant biomass in areas open to grazing by North American beaver, *C. canadensis*. In addition, Law et al. (2014b) showed that biomass of *Menyanthes trifoliata* was 45% lower in areas open to grazing by European beavers than in plots from which animals were excluded, based on a study of a semi-captive population in Perthshire living on a small shallow loch. In this same study several hundred square metres of *Iris pseudacorus* were almost entirely eliminated over a five-year period due to intense grazing by beavers. While this was a semi-captive beaver population, similar levels of loss have been reported for other aquatic rodents such as muskrat (Danell 1977; Smirnov and Tretyakov 1998) and the observed losses due to beavers are comparable with those recorded for several plant species at Knapdale.

Beavers are often referred to as choosy generalists in terms of their dietary habits. The importance and identity of aquatic plants in beaver diet varies spatially and seasonally, depending on the availability of preferred species, their palatability and nutritional content (Milligan and Humphries 2010). Beyond the more obvious generalisations that utilisation of aquatic plants tends to increase during the summer, and is mainly directed at larger rhizomatous species, it is therefore difficult to predict precisely what beavers will eat, or where and when.

Both Parker *et al.* (2007) and Law *et al.* (2014b) reported significant changes when monitoring aquatic vegetation in grazed areas compared with exclosure plots, and over time in open habitat following foraging by beavers. Some changes were mediated via shifts in the interaction between dominant species, others resulted in unpalatable species expanding at the expense of preferred edible ones. The end result was an overall reduction in the cover of dominant species that favoured increased richness by permitting recruitment or expansion of competitively inferior plants. For example, Law *et al.* (2014b) reported that a decline in cover of the dominant species, *I. pseudacorus*, increased cover of *Hippuris vulgaris* and *Juncus effusus*, which were the two least palatable species in a 'cafeteria' study, and saw a trebling of species richness measured at the quadrat ($1m^2$) scale. This scale of increase in richness may be unusually high in the context of beavers. Significantly increased richness has been reported in association with muskrat grazing (Bhattacharjee *et al.*, 2007), though other studies indicate that richness may also decline due to an increase in the abundance of grazing-tolerant species (Smirnov and Tretyakov 1998).

Herbivory is a form of disturbance in the sense that it destroys existing plant biomass. The effects of disturbance are, however, likely to be mitigated by other factors such as productivity, as summarised by the Dynamic Equilibrium Model (Huston 1994). This model attempts to unify the effects of productivity and disturbance, both of which are expected to

yield greatest diversity at intermediate values and are likely to have interactive effects. The effects of herbivory by aquatic rodents are therefore likely to be regulated by the underlying fertility of the system (Danell 1996), tending to become negative in the least productive sites (because disturbance by grazing acts as an additional pressure on a nutrient-stressed system where growth rates will be naturally low), and positive in more productive sites, (because competitive dominance by preferred high-yielding rhizomatous species is reduced). Law et al. (2014b) suggest that the generally positive effects of herbivory that they observed were potentially contingent on high background productivity and that such effects should not be assumed to be universal.

6.2.2 Dam building

The ecological effects of dam building are the most widely studied aspects of habitat engineering by beavers (Rosell et al., 2005) with biological changes typically attributed to the increase in geomorphological and hydrological heterogeneity that is associated with dam building.

Although the dam on the outflow of Dubh Loch resulted in a substantial rise in water level, inundating an additional hectare of land to an average depth of 1m, beaver dams will have similar ecological consequences with much smaller water level rises. In Sweden for example, due to the topography, beaver-generated wetlands tend to be much larger (2-5ha) and shallower than the habitat formed at Dubh Loch, yet by inundating formerly forested areas, the changes in tree cover, vegetation composition and patchiness tend to be manifested across the entire wetland. While Dubh Loch was exposed to a single very pronounced change in water level over a short period of time, after which beavers exerted a relatively minor effect on aquatic vegetation, experience elsewhere (Sweden and Perthshire) and published evidence (e.g. Ray et al., 2001) suggests that continuing activity by beavers (tree felling, herbivory on herbaceous plants, canal building) in shallower wetlands are all a significant source of within-wetland heterogeneity (Figure 49). Thus Willby et al. (submitted) found that in Swedish wetlands, diversity of aquatic plants (and water beetles) was higher at the patch, site and landscape scale than in other non-beaver-related wetland types within the same area. Contrasts at a site-scale were especially pronounced as a result of high species turnover between plots within beaver wetlands. This serves to increase site-scale richness. Turnover was associated with microtopographical differences, and perturbations caused by herbivory, and wind-throw of dead trees which together increase spatial complexity relative to non-beaver wetlands. The presence of beaver wetlands within an extensively wooded landscape, high connectivity with surrounding wetlands and a high quality plant propagule pool due to the extent of other little-impacted water bodies within the landscape may be integral to these differences (Ray et al., 2001) and in prolonging residency of beavers at a site. In a different and more fragmented landscape, such as that found in the UK, beavers might be expected to abandon wetlands on a shorter rotation, while the water bodies they create are likely to be colonised more slowly by aquatic biota.
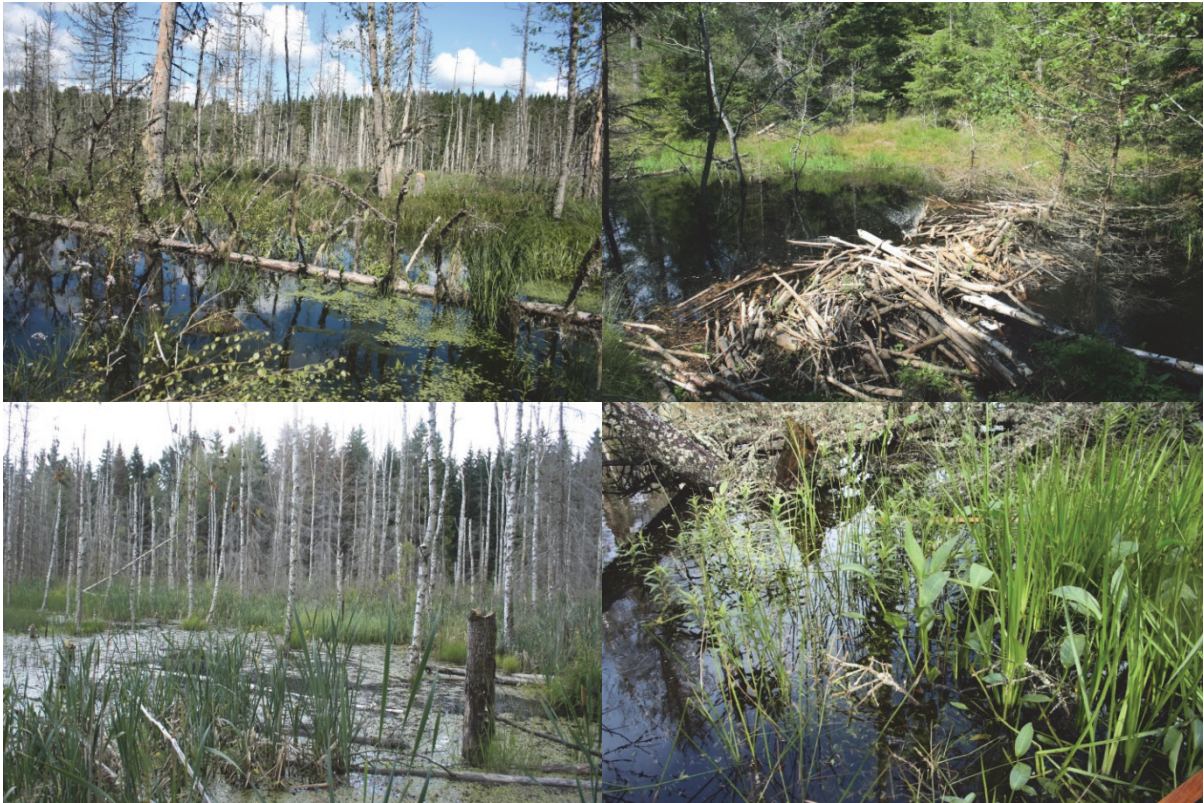
Figure 49. Beaver-generated wetlands in central southern Sweden formed by damming of small forested streams. All pictures © N Willby.

The above findings highlight some basic differences between impoundments formed from dams built by beavers and those constructed artificially. Habitat-engineering by beavers is an on-going process and the use and alteration of beaver ponds maintains a dynamic state whereas artificial impoundments tend to be one-off constructions. Small water bodies, such as farm reservoirs, fishing lakes, curling ponds and ornamental water bodies are mostly created in a single step by a combination of excavation and impoundment of a water course rather than by damming the outflow of an already existing water body. In such cases, the objective is commonly storage of water and stabilisation of water levels. Woody debris, which is a major source of heterogeneity in beaver ponds, is likely to be eliminated from these small-scale artificial impoundments prior to or soon after their creation. Studies of successional processes in such water bodies typically reveal species accumulation plateaus after three to four years for macroinvertebrates and six years for aquatic plants (Williams *et al.*, 2008). In one of the most widely cited examples, Danell and Sjöberg (1982) describe the eight-year changes in vegetation in a shallow lake in Sweden formed by flooding a sedge meadow to increase duck production. Plant species richness and the cover of the dominant hydrophyte peaked after six to seven years, although there was a major reduction in the cover of emergent species. Expansion of aquatic vegetation and declining tree cover over a ten-year period are reported by Hyvonen and Nummi (2011) based on a study to simulate the effects of impoundment by beavers, but Ray et al. (2001) reported on the basis of a cross-sectional study of beaver ponds of different ages in Minnesota that plant species richness increased linearly over a time scale of 40 years. This suggests that species gain is likely to continue for much longer yet in beaver-created habitats at Knapdale than would be the case in artificial wetlands.

By contrast, in large water supply or pumped storage reservoirs used for hydropower there are pronounced and sometimes rapid water level fluctuations over a large range (5-15 m) that will effectively eliminate any functional littoral zone and completely dictate the

functioning of the lake (Moss 2008). Even where the water level regime is comparatively benign (range less than 3m) reservoirs are likely to experience occasional and traumatic drawdown and refilling phases due to periodic drainage for maintenance and dam inspection. Systematic negative effects of pronounced water level fluctuations on macrophytes are widely reported (Hellsten 2001, Thompson and Ryder 2008; Mjelde *et al.*, 2013).

Where existing lakes are adapted for water storage or flood control by raising the outflow, the water level rise that is imposed tends to be significant (2-5m) and much greater than that associated with damming by beavers. The water level regime in such schemes tends to result in an autumn or winter minimum to maximise spring storage (Mjelde *et al.*, 2013). The reported effects of such changes on vegetation are generally negative, with large-scale contraction of emergent vegetation most commonly reported (Crivelli *et al.*, 1995), especially where ice cover is common (Hellsten 2001).

Small modifications to the outflow of existing standing waters are probably very common in Scotland and are often undertaken for fisheries purposes, the aim being to increase the extent of shallow littoral habitat and thus stimulate fish production. In other cases small outflow structures allow increased water storage. It is likely that outflow structures installed for fisheries purposes have already caused modest changes in some of the Knapdale lochs, such as Loch McKay. There is little published research on the effects of such modifications. This is perhaps because the changes themselves are considered too modest to merit attention, or because they are likely to result in subtle ecological adjustments that require a commitment to monitoring for long periods in order to be detected. Such interventions have a parallel with the construction of small dams by beavers on the outflow of Lochs Linne and Un-named North because the water level rise is too small to inundate adjacent woodland and largely influences a 0.5 m zone that is already influenced by natural water level fluctuations.

These small modifications differ from the habitat engineering by beavers at Dubh Loch where the water level rise caused by damming is sufficient to fully inundate woodland and associated terrestrial habitats. Such changes thus result in water level rise that is well outside the window of natural water level fluctuations, which, in sites such as Dubh Loch, will be very small (less than 0.5 m). The subsequent wind-throw of drowned trees is a key architect of habitat complexity in such cases, which is rarely replicated by artificial impoundment (excluding tropical reservoirs). The lack of active flow regulation and the natural porosity of a beaver dam will favour low summer water levels and associated emergent or amphibious vegetation establishment and gradual rather than sudden changes in water depth. Vegetation development is likely to be accelerated by the existence of a ready supply of propagules from the pre-impoundment water body.

It is certainly the case that a subset of lowland, often more fertile reservoirs with a benign water level regime can have significant conservation value, especially for certain scarce shallow water or amphibious plant species, or wading birds and wildfowl, but the overall habitat structure and scale of such sites is very different from that associated with a typical beaver pond.

6.3 Responses of macro-invertebrates to changes at Dubh Loch

The effects of stream damming by beavers on aquatic macroinvertebrates have been long and widely studied (McDowell and Naiman 1986) and are generally positive at the landscape scale due to the introduction of novel habitat features and lentic conditions. These benefits appear to apply even in agricultural landscapes (Law and Willby, submitted). However, the consequences for invertebrates of modifying pre-existing standing water habitat are less well known. Other studies of beaver wetlands (Danilov *et al.*, 2011b) or where wetlands have

been deliberately created to simulate the effect of impoundment by beavers (Nummi 1989) confirm the importance of beaver-generated wetlands as habitat for invertebrates and the rapid colonisation that takes place post-impoundment. Other studies of invertebrate colonisation of ponds are consistent with the patterns observed in the present study. For example Bloechel *et al.* (2010) classed *Sigara falleni* as a true pioneer species that disappears during pond succession due to competitive displacement by other corixids, whereas *Notonecta glauca* and *Corixa punctata* were ubiquitous, as in our results. The three heteropteran species of the genus *Hesperocorixa* (*H. castanea*, *H. linnaei* and *H. sahlbergi*) occurred mainly in ponds with abundant vegetation and increased in relative abundance over time in Dubh Loch, consistent with the widespread establishment of aquatic vegetation.

However, Dubh Loch demonstrates a more important principle of habitat alteration by beavers, namely the marked increase in local habitat heterogeneity that occurs when wetlands are generated through impoundment by beavers. Continued active use of a territory increases patchiness in vegetation cover due to herbivory and canopy gaps, whilst tree fall due to felling or windthrow of drowned trees creates a more finely dissected habitat that is rich in submerged wood. The excavation of canals by beavers for accessing new areas also ensures a high availability of edge habitat. Two recent studies, Hood and Larson (2014) and Willby *et al*. (submitted), confirm the importance of increased habitat heterogeneity in beaver ponds for aquatic invertebrates relative to other wetland types, especially predatory species.

Although the expanded Dubh Loch is broadly typical of the environment of beaver ponds and beaver-generated wetlands beavers will also dam the outflow of much larger water bodies. This will result in more modest water level rises over much larger areas. In large water bodies physical characteristics of the littoral zone such as substrate, depth and wave fetch are likely to remain the natural driving influence on benthic invertebrate populations and the changes observed in small sheltered water bodies such as Dubh Loch cannot be extrapolated to such situations.

6.4 Potential future changes in aquatic vegetation and associated features at Knapdale

If the population of beavers at Knapdale maintains its current size or experiences modest growth, various potential scenarios of ecological change may be proposed.

- There may be dispersal of beavers to new locations. Within the Knapdale area, relocation of the main residence of the Dubh Loch family to Loch Coille-Bharr, or establishment of a permanent lodge there by descendants of the Dubh Loch family, seems probable in the near future and observations in May 2014 suggest that this may have already occurred. Animals from Dubh Loch already use this site regularly and the sheltered south-west corner supports an abundance of preferred macrophyte species. A small pond 0.5 km north of Lochan Buic (sometimes referred to as the Ford Pond or Ford Lochan) has been visited by beavers since at least 2011 and may be suitable for damming. Un-named Loch (South), Loch McKay and to a lesser extent Loch Losgunn offer suitable habitat and feeding, though the availability of preferred species and sizes of trees at these sites may be too limited. Loch Barnluasgan also offers suitable habitat and feeding, but there is the potential for disturbance of beavers by dogs at this water body, as it is easily accessible and there is no evidence that beavers have utilised this site. Outwith the immediate Knapdale area, the most suitable site for colonisation would be Lochan Taynish, which lies only 5 km south-west of Loch Coille-Bharr and supports extensive aquatic vegetation with well wooded margins. There is no evidence to date that animals have ever visited this site (R. Campell-Palmer, pers. comm.).

- To date there have been very few incidences of stream damming at Knapdale and none outwith the immediate vicinity of the inhabited lochs. A reduction in the availability of preferred size and species of trees close to the existing loch shoreline may result in greater mobility of animals and a tendency for small-scale dam building on feeder streams. Since the Knapdale streams are small, heavily shaded and almost devoid of macrophytes there are few potential implications for aquatic macrophytes unless damming results in impoundment of existing water bodies or reduced inflows. In the event of new beaver pairs forming, it is more likely that new territories would be established on streams than on already-occupied lochs.

- Utilisation of macrophytes will continue. If animals remain in their present territories, a shift towards more intensive and potentially less sustainable feeding on *N. alba* seems likely since preferentially grazed species such as *C. mariscus* and *S. lacustris* may be scarce or no longer available. Grazing will continue at more sustainable levels if animals disperse to other locations or switch to a diet of terrestrial herbaceous species in place of macrophytes.

- Dubh Loch may be abandoned or experience a decline in use. This site may soon fail to provide suitable feeding on aquatic vegetation and relocation of this family to Loch Coille-Bharr in the next few years seems possible. If so, Dubh Loch is likely to experience successional changes as water levels decline due to lack of dam maintenance and will provide high habitat diversity for a range of biota over a transitional phase of a decade or so. The results of surveys carried out in 2013 and 2014 already suggest a contraction in loch area that appears to be associated with settlement of the dam and reduced water storage.

- A shift to herbaceous terrestrial feeding may continue. Over the duration of the trial we have noted increased evidence of grazing by beavers on terrestrial plant species, especially bracken *Pteridium aquilinum* and purple moor grass *Molinia caerulea*. If animals remain resident at the present sites, this trend is likely to continue since supplies of the preferred macrophytes, such as *C. mariscus*, have been largely exhausted.

- If animals fail to disperse more widely, continued modification of the riparian zone through increased felling is likely. This will input more woody debris to the littoral zone and may ultimately cause a change in the composition of terrestrial herbaceous vegetation. Changes in tree species composition and the structure of under-storey vegetation have been monitored by the James Hutton Institute.

If there is a gradual decline in the numbers of animals at Knapdale over the next five years, as would be possible in the absence of intervention, the following changes would be expected.

- Recovery of populations of grazed species. Aquatic vegetation typically responds rapidly to the removal or onset of herbivory. Where there are residual populations in place, species such as *S. lacustris* and *N. alba* might be expected to return to their original population size within five to ten years of the cessation of grazing. For slower-growing species such as *C. mariscus*, where the population has been heavily depleted, recovery might be expected to take several decades. Previous studies of muskrat grazing, for example, demonstrate that the impact of grazing and recovery from it are dependent on the productivity of the system (Toivonen and Meriläinen 1980; Danell 1996), with recovery of vegetation in some intensely grazed, unproductive systems taking as long as 30 years. In some cases, this recovery may be prevented or significantly delayed through colonisation by other species, such as *N. alba* or *P. australis*.

- Eventually breakdown and loss of woody debris accumulated in the loch littoral zone would be expected. These are rather unproductive systems and the rate of decomposition is therefore likely to be slow, with the largest pieces of wood likely to remain in place ten years hence.

- Drainage of inundated areas of Dubh Loch may occur due to lack of dam maintenance, thus initiating a cycle of terrestrialisation. Change in vegetation following abandonment of beaver-wetlands has been widely documented. A full return to the former woodland vegetation and the well-defined hydrosere found in the original Dubh Loch is likely to take several decades and to include some intermediate states of high plant diversity.

6.5 Implications of wider scale reintroduction of beavers in Scotland for aquatic vegetation and associated features.

Small, shallow and well-vegetated water bodies of the type found in Knapdale are extremely widespread and numerous in Scotland (approximately 10,000 mapped small to medium sized (less than 50 ha) shallow water bodies exist on the mainland) and are therefore unlikely to be a significant constraint on the size of any future beaver population. In lowland areas, many of these sites would be expected to support an abundance of the large, rhizomatous, floating-leaved or emergent macrophytes preferred by beavers. The limited connectivity of such water bodies and scarcity of suitable riparian woodland is likely to be the most significant constraint on the spread of beavers and their use of otherwise suitable habitat. At those sites that are successfully colonised, it is highly likely that beavers will modify the aquatic vegetation by selective feeding. In less productive habitats, this may result in a rapid decline in plant abundance, but little overall change in composition. However, in more productive habitats, selective reduction of dominant emergent and floating-leaved species is likely to result in a change in composition and increased plant diversity (Law *et al.*, 2014b).

The scope for major water level rise of the scale seen at Dubh Loch may prove to be limited in Scotland because this relies on a combination of favourable topography, abundant supply of suitably sized trees for dam and lodge building and an adjacent small water body with a stable water level in an undisturbed location. Beavers elsewhere in Europe will dam much larger lakes than any of the Knapdale lochs, provided the outflow channel is small enough (Willby pers. obs.), but sites in Scotland where this might happen are probably rather limited and such dams are easily managed or removed. Wetland creation, through the impoundment of small, wooded, medium gradient streams, may prove common on a small scale and the benefits for aquatic vegetation and associated biota will then depend on proximity to a source of suitable colonists and the availability of clear water with minimal shade. Numerous studies conducted over the last three decades confirm the transformational effects of beavers on invertebrate habitat, especially the uniquely high habitat heterogeneity that develops in beaver wetlands, and there is no reason to expect such benefits to be any less pronounced in Scotland.

Many sites offering suitable aquatic habitat and associated woodland for beavers in Scotland will occur in the vicinity of large rivers and their floodplains (e.g. Tay, Spey, Dee). However, high flow variability due to a low snow-melt influence and high frequency of Atlantic depressions could restrict the utility of these habitats unless beavers are also able to revert to burrows in higher ground during periods of flooding. There is evidence from the Netherlands that beavers can adjust rapidly to pronounced water level fluctuations (annual range 6-7 m) (Kurstjens and Bekhuis 2003). A pronounced trend for wetter winters and increased river flooding over the last 30 years in Scotland might therefore either limit the viability of some otherwise suitable floodplain areas as habitat, or expand the elevational range of beaver effects.

6.6 Appropriateness of methods for assessing effects of beavers on aquatic vegetation

The survey techniques used in this study rely on repeat observations at different spatial scales and assume that independent observations can be compared directly. Perhaps the biggest constraint in surveys of lake macrophytes is incomplete and indeterminate detectability. These issues were discussed in detail by Willby and Casas-Mulet (2010) in the context of the baseline macrophyte surveys. While these constraints apply to all biological data collection, they are accentuated in lakes for practical reasons. The problem is certainly more acute for submerged species and is emphasised further for inconspicuous species. Under poor viewing conditions and low water clarity, detectability is reduced which can potentially become a serious problem in making comparisons between surveys in which data were collected under different conditions. For example, in 2013 when water levels were slightly lower and the growing season conditions had been favourable (the best since 2006) we recorded *Potamogeton alpinus* in Loch Linne and *Potamogeton* x *zizzi* in Loch Barnluasgan, both for the first time, but in locations that had been checked on four occasions in the previous five years. In Loch Barnluasgan, *Potamogeton praelongus* was also more abundant than at any time in the previous five years. Fortunately, in the present study, the species of greatest relevance in terms of quantifying effects of beavers are for the most part, large, readily visible, easily identified taxa. Therefore, it should be possible to map these species with high precision and detect them with high reliability. If the effects of beavers were focused on small, inconspicuous submerged species, it is likely that a fundamentally different survey approach would be required.

Like all biological surveys, the present study utilised methods that were a compromise between rigor, repeatability and available resources. Using the same team of surveyors to collect all data introduces both advantages and disadvantages. Issues of variability between surveyors in assessment of cover will become more trivial but increased familiarity with site conditions and the species present probably serve to increase detection year on year up to a point of saturation. Given that the biggest effects of beavers are on the cover of selected species, reducing variability in cover assessments was more critical than reducing bias in species detection.

Fixed transects proved an effective way of demonstrating vegetation change (through data and photographs) at given points. Although the number of transects per loch was small, it was sufficient to demonstrate significant effects of beavers on plant cover and regular monitoring of these transects provided a temporal dimension to the coarser scale changes shown by the polygon mapping. Our analyses illustrate that the variation in richness and cover between transects within a loch is trivial compared to the variation between lochs and, especially, the variation between points along a transect running from the shore to open water. One alternative would have been to use randomly located transects on each visit thus probably reducing the artefact of increasing species richness through repeat sampling. However, a large number of transects would then have had to be surveyed in each year to reduce the effect of positional variation in species composition between transects as it is these compositional differences (rather than differences in overall richness or cover) that dictate the scale of losses due to herbivory. The transect data collected generally supported the trends evident from the polygon data although the scale of reductions shown by the latter were often more pronounced as highly patchily distributed species had a low chance of occurrence in individual transects. Establishing a larger number of fixed transects and resurveying these throughout the trial would probably have increased the conformity between transect and polygon survey data and may even have rendered the polygon mapping redundant. However, having more transects would have increased disturbance to vegetation and the use of fixed quadrats would fail to capture changes in the outer limits of vegetation as effectively as the polygon surveys. It would be possible through randomly subsampling the polygon data to determine the minimum number of transects required at a

site to achieve similar estimates of overall cover to those obtained via the polygon mapping surveys. However, our expectation is that this exercise would imply the need to sample an unsustainably large number of transects in most sites.

Although the Knapdale lochs are superficially similar in their environment and are not strongly differentiated on the basis of vegetation, between loch effects were still a substantial source of variation in richness and cover on transects. This almost certainly reflects the influence of differences in size, depth, exposure and fertility between lochs. Eleven is a modest number of lochs to use for this kind of study but it did allow for sufficient site-scale replication at all levels of beaver occupancy. Increasing the number of lochs used might have proved beneficial but this would almost certainly come at the expense of increased between-loch variation since expanding the area of study to supply additional lochs would introduce more underlying environmental variation. At larger scales, additional geographical factors, such as proximity between water bodies, would also become increasingly important.

Polygon mapping in the field and subsequent construction and checking of maps in GIS is time consuming and this approach is somewhat dependent on subjective evaluation of stand boundary and identity. Potentially this could be streamlined in future studies using unmanned aerial vehicles (drones) which are readily portable and can collect high resolution aerial imagery (sub-decimetre resolution) at low elevations. This technique has already been successfully exploited in grassland assessments (Rango *et al*., 2009) and shows considerable promise for mapping aquatic and riparian vegetation (Husson *et al*., 2014). The quality of the data is sufficient to not only allow species level identification of emergent and floating leaved species but would also allow additional data to be derived (e.g. leaf or flower density, tissue pigmentation, species richness) at variable spatial scales. Whilst such aerial data require ground-truthing and carry significant costs in terms of image processing and interpretation, the high repeatability, reduced field time, ease of access and increased flexibility in terms of data extraction make this technology highly attractive.

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 Main findings

Through a combination of direct grazing or foraging and associated activity (trampling or tree felling and removal), alongside dam building and water level change in some cases, beavers have exerted clear and measurable effects on aquatic vegetation in most of the Knapdale lochs in which they are now resident. These effects are evident at a water body scale through fixed-point photography, remapping of vegetation at coarse scales, and at a local scale through resampling of fixed quadrats. Four main species, *Nymphaea alba*, *Schoenoplectus lacustris*, *Cladium mariscus* and *Equisetum fluviatile* have been exploited to a greater or lesser extent, with populations of some of these species in those lochs with the greatest duration and density of occupancy (Dubh, Buic and Linne-Fidhle) being substantially reduced. The most obvious adverse effect was on *C. mariscus*, a notable (though not rare) species in Great Britain, which was virtually eliminated from Lochan Buic, Creagmhor Loch and Loch Fidhle. There was very little evidence of regrowth at these locations, and none in germination trials, although smaller, less heavily exploited populations persisted in Loch Linne and Dubh Loch.

The analyses indicate that beaver impacts on aquatic vegetation increase with the duration of occupancy and the number of animals present at a site. Over the period of monitoring, the effects of intermittent occupancy by one or two non-breeding animals were indistinguishable from the inter-annual variation in total vegetation cover that occurred at sites unoccupied by beavers.

Transferability of findings between families was limited. While all animals fed on large, rhizomatous, aquatic plants, the timing of feeding on individual species and the choice of those species varied significantly between families. Herbivory and foraging by beavers resulted in significant reductions in plant cover in their own right based on a subsample of those lochs that were unaffected by major water level rise from dam building.

At the outset of the SBT management of dams was required, as a condition of the release licence, to prevent significant water level change and potential adverse effects on features of the lochs within the SAC. Thus, sustained and pronounced water level rise due to dam building occurred at only a single site (Dubh Loch) which did not contain the SAC qualifying aquatic vegetation. This water level change resulted in major alteration in the abundance and distribution of aquatic and terrestrial vegetation. However, the period of adjustment to this change was shorter than anticipated, which may have been due to a pre-existing persistent seed bank of wetland species. Beaver effects at this site could be considered positive in the sense that they increased the extent of aquatic habitat and re-established a naturally more dynamic state, in addition to promoting habitat complexity and conditions that closely resemble those found in beaver wetlands in Sweden. Two water bodies (Lochs Linne/Fidhle and Un-named North) experienced a smaller temporary rise in water level due to dam building from which subtle adjustments in floristic composition occurred and were on-going at the conclusion of the formal monitoring period.

Effects of beavers developed rapidly at some sites, but were more evident after two seasons than a single season of occupancy. In principle, this suggests that effects might also be relatively quickly reversed over a small number of years, if animals were to be removed or to naturally vacate a site. This may not apply equally to all grazed species and experience of other aquatic mammalian herbivores, such as muskrat (Danell 1996), indicates that impact times are shorter and recovery times longer in less productive habitats, such as those found at Knapdale.

There was no evidence of significant adverse effects of beavers specifically on the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea* plant associations that form part of the basis of the Taynish and Knapdale Woods SAC designation. Thus beavers could not be considered to have had a detrimental impact on the specific aquatic vegetation features for which the SAC has been designated.

7.2   Wider perspectives

In standing water habitats, the effects of beavers will generally be to alter the macrophyte community and associated habitat structure through reductions in targeted species. This results mainly in local scale changes. Viewed at the coarser, whole loch scale, it is unlikely that such sites would deviate significantly outside the range of variation in community structure already found for lochs of a similar type elsewhere in Scotland. The effects of herbivory or foraging by beavers on aquatic vegetation observed in this study might be regarded as neutral, because there was usually compensatory growth by other existing common species in the gaps created, but not colonisation by new species. Changes of the latter type might however, be expected to occur in more productive, lowland environments, or over decadal time scales. Fundamental alteration in standing water habitat and associated vegetation is only likely in the event of dam building that promotes a major increase in water depth. Such changes are likely to be confined to small, undisturbed water bodies, with a well-wooded riparian zone and where the topography of the outflow is conducive to dam building.

8. REFERENCES

Abernethy, V.J. and Willby, N.J. 1999. Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. *Plant Ecology*, **140**, 177-190.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4.
URL: http://CRAN.R-project.org/package=lme4.

Bloechl, A., Koenemann, S., Philippi, B. and Melber, A. 2010. Abundance, diversity and succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in the North German Lowlands. *Limnologica – Ecology & Management of Inland Waters*, **40**, 215–225.

Bonner, J.L., Anderson, J.T., Rentch, J.S. and Grafton, W.N. 2009. Vegetative composition and community structure associated with beaver ponds in Canaan valley, West Virginia, USA. *Wetlands Ecology & Management*, **17**, 543–554.

Bhattacharjee, J., Haukos, D. and Neaville, J. 2007. Vegetation response to disturbance in a coastal marsh in Texas. *Community Ecology*, **8**, 15–24

Brzyski, J.R. and Schulte, B.A. 2009. Beaver (*Castor canadensis*) Impacts on Herbaceous and Woody Vegetation in Southeastern Georgia. *American Midland Naturalist*, **162**, 74-86.

Chabreck, R.H. 1958. Beaver-Forest Relationships in St. Tammany Parish, Louisiana. *Journal of Wildlife Management*, **22**, 179-183.

Colwell, R.K., Mao, C.X. and Chang, J. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.

Conroy J.W.H. and Kitchener A.C. 1996. The Eurasian beaver (*Castor fiber*) in Scotland: a review of the literature and historical evidence. *Scottish Natural Heritage Review No. 49.*

Conway, V.M. 1942. One British species - *Cladium mariscus* (L.) R.Br. (*C. germanicum* Schrad.; *C. jamaicense* auct. non Crantz; *Mariscus serratus* Gilib.). *Journal of Ecology*, **30**, 211-216.

Crivelli, A.J., Grillas, P. and Lacaze, B. 1995. Responses of vegetation to a rise in water-level at Kerkini Reservoir (1982-1991), a Ramsar site in northern Greece. *Environmental Management*, **19**, 417-430.

Dalbeck, L., Luscher, B. and Ohlhoff, D. 2007. Beaver ponds as habitat of amphibian communities in a central European highland. *Amphibia-Reptilia*, **28**, 493–501.

Danell, K. 1977. Short-term plant successions following the colonization of a northern Swedish lake by the muskrat, *Ondatra zibethica*. *Journal of Applied Ecology*, **14**, 933–947.

Danell, K. 1996. Introductions of aquatic rodents: lessons of the muskrat *Ondatra zibethicus* invasion. *Wildlife Biology*, **2**, 213–220.

Danell, K. and Sjöberg, K. 1982. Successional patterns of plants, invertebrates and ducks in a man-made lake. *Journal of Applied Ecology*, **19**, 395-409.

Daniels M.J., Rao S.J., Balharry D. and Ratcliffe P.R. 2000. The suitability of Knapdale and Polloch for a trial reintroduction of beavers. *Scottish Natural Heritage Commissioned Report* (unpublished).

Danilov, P., Kanshiev, V. and Fyodorov, F. 2011a. Characteristics of North American and Eurasian beaver ecology in Karelia. *In*: Sjöberg, G and Ball, J.P. (eds) *Restoring the European beaver: 50 years of experience*. Sofia-Moscow: Pensoft, pp. 55-72.

Danilov, P., Kanshiev, V. and Fyodorov, F. 2011b. The role of beavers in the European Taiga ecosystem (NW Russia). *In*: Sjöberg, G and Ball, J.P. (eds) *Restoring the European beaver: 50 years of experience*. Sofia-Moscow: Pensoft, pp. 173-193.

France, R.L. 1997. The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. *Canadian Journal of Zoology*, **75**, 1009-1013.

Fryxell, J.M. and Doucet, C.M. 1993. Diet choice and the functional response of beavers. *Ecology,* **74**, 1297–1306.

Fuller, M.R. and Peckarsky, B. L. 2011. Does the morphology of beaver ponds alter downstream ecosystems? *Hydrobiologia*, **668**, 35-48

Gorshkov, D. and Gorshkov, Y. 2011. Feeding strategy of beavers in Tatarstan Republic. *In*: Sjöberg, G and Ball, J.P. (eds) *Restoring the European beaver: 50 years of experience*. Sofia-Moscow: Pensoft, pp. 149-159.

Goslee, S.C. and Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1-19.

Gunn, I. D. M., Carvalho, L, Darwell, A.M., Roy, D.B., Rothery, P., Wade, P.M., Stewart, N., Dent, N.M., Kirika, A., James, J.B., Hodgson, P.M. and Abel, D.V. 2004. Site Condition Monitoring of Standing Waters Phase 1, Report 1: Aquatic Macrophyte Method Development. *Report by CEH to Scottish Natural Heritage*.

Gurnell, A.M., Gregory, K.J. and Petts, G.E. 1995. The role of coarse woody debris in forest aquatic habitats-implications for management. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **5**, 143-166

Gusewell, S. and Le Nedic, C. 2004. Effects of winter mowing on vegetation succession in a lakeshore fen. *Applied Vegetation Science*, **7**, 41-48.

Hägglund, A. and Sjöberg, G. 1999. Effects of beaver dams on the fish fauna of forest streams. *Forest Ecology & Management*, **115**, 259-266.

Harrington, L.A., Feber, R., and Macdonald, D.W. 2012. The Scottish Beaver Trial: Ecological monitoring of the European beaver *Castor fiber* and other riparian mammals – Second Annual Report 2011. *Scottish Natural Heritage Commissioned Report* No. 510.

Hartman, G. 2011. The beaver (*Castor fiber*) in Sweden. *In*: Sjöberg, G. and Ball, J.P. (eds) *Restoring the European beaver: 50 years of experience*. Sofia-Moscow: Pensoft, pp13-17.

Hellsten, S.K. 2001. Effects of lake water level regulation on aquatic macrophyte stands in northern Finland and options to predict these impacts under varying conditions. *Acta Botanica Fennica*, **171**, 1-47

Hellsten, S., Willby, N., Ecke, F., Mjelde, M., Phillips, G., Tierney, D. and Poikane, S. 2014. *Water Framework Directive Intercalibration Technical Report: Northern Lake Macrophyte ecological assessment methods.* Luxembourg: Publications Office of the European Union.

Hill, M.O, Mountford, J.O, Roy, D.B and Bunce R.G.H. 1999. *Ellenberg's indicator values for British plants*. ECOFACT Volume 2, Technical Annex. Centre for Ecology & Hydrology.

Histøl, T. 1989. Summer diet of beavers *Castor fiber* L. in some small lakes in Vennesla, Vest Agder. *Fauna*, **42**, 96-103 [in Norwegian].

Hood, G.A. and Larson, D.G. 2014. Beaver-created habitat heterogeneity influences aquatic invertebrate assemblages in boreal Canada. *Wetlands*, **34**, 19-29.

Husson, E., Hagner, O. and Ecke, F. 2014. Unmanned aircraft systems help to map aquatic vegetation. *Applied Vegetation Science,* **17**, 567-577.

Huston, M.A. 1994. *Biological Diversity: the coexistence of species on changing landscapes.* Cambridge: Cambridge University Press.

Hutchinson, G.E. 1957. *A Treatise on Limnology. Vol.1. Geography, Physics and Chemistry.* John Wiley & Sons. 1015pp.

Hyvonen, T. and Nummi, P. 2011. Plant succession in beaver patches during and after flooding. *In*: Sjöberg, G. and Ball J.P. (eds) *Restoring the European beaver: 50 years of experience*. Sofia-Moscow: Pensoft, pp. 164-171.

Iason, G.R., Sim, D.A., Brewer, M.J. and Moore B.D. 2014. The Scottish Beaver Trial: Woodland monitoring 2009 – 2013, final report. Scottish Natural Heritage Commissioned Report No. 788.

Jones, K., Gilvear, D., Willby, N. and Gaywood, M. 2009. Willow (*Salix* spp) and aspen (*Populus tremula*) regrowth after felling by the Eurasian beaver (*Castor fiber*): implications for riparian woodland conservation in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **19**, 75-87.

Kemp, P.S., Worthington, T.A., Langford, T.E.L., Tree, A.R.J. and Gaywood, M.J. 2011. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries*, **13**, 158–181.

Kitchener A.C. 2001. *Beavers*. Suffolk: Whittet Books.

Kindt, R. and Coe, R. 2005. *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies.* Nairobi: World Agroforestry Centre (ICRAF), ISBN 92-9059-179-X.

Kurstjens, G. and Bekhuis, J. 2003. Adaptation of beavers (*Castor fiber*) to extreme water level fluctuations and ecological implications. *Lutra*, **46**, 147-151.

Langford, T. E. L., Langford, J. and Hawkins, S. J. 2012. Conflicting effects of woody debris on stream fish populations: implications for management. *Freshwater Biology*, **57**, 1096-1111.

Lassiere, O. 1998. *Botanical survey of Scottish freshwater Lochs: Methodology*. Scottish Natural Heritage, unpublished.

Law, A, Bunnefeld, N. and Willby, N.J. 2014a. Beavers and lilies: selective herbivory and adaptive foraging behaviour. *Freshwater Biology*, **59**, 224-232.

Law, A., Jones, K. and Willby, N.J. 2014b. Medium- versus short-term effects of herbivory by Eurasian beaver on aquatic vegetation. *Aquatic Botany*, **116**, 27-34.

Law, A. and Willby, N.J. submitted 2014. A reintroduced habitat engineer, the beaver, enhances aquatic biodiversity and ecosystem function in agricultural streams.

Lev-Yadun S. and Gould K.S. 2009. Role of anthocyanins in plant defence. *In*: Gould, K., Davies K. and Winefield, C. (eds) *Anthocyanins: Biosythesis, Functions, and Applications.* Berlin: Springer, pp. 21–48.

Little, A.M., Guntenspergen, G. R. and Allen, T.F.H. 2012. Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. *Ecoscience*, **19**, 246-257

Lorenzen, B., Brix, H., McKee, K.L., Mendelssohn, I.A. and Miao, S.L. 2000. Seed germination of two Everglades species, *Cladium jamaicense* and *Typha domingensis*. *Aquatic Botany*, **66**, 169-180

MacDonald D.W., Maitland P. and Rao S.J. 1997. Development of a protocol for identifying beaver release sites. *Scottish Natural Heritage Commissioned Report* No. 93.

McDowell, D.M. and Naiman, R.I. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, **68**, 481-489.

McMaster, R.T. and McMaster, N.D. 2001. Composition, structure, and dynamics of vegetation in fifteen beaver-impacted wetlands in western Massachusetts. *Rhodora*, **103**, 293–320.

Madgwick, G., Emson, D., Sayer, C, Willby, N.J., Rose, N.L., Jackson, M.J. and Kelly, A. 2011. Combining historical records and palaeolimnology to reconstruct centennial-scale changes in the aquatic vegetation structure of a shallow lake. *Freshwater Biology*, **56**, 2620-2636.

Martineau, H. 1855. *A Complete Guide to the English Lakes*. London: John Garnett, Windermere, Westmorland, and Whittaker & Co.

Meredith, T.C. 1985. Factors affecting recruitment from the seed bank of sedge (*Cladium mariscus*) dominated communities at Wicken Fen, Cambridgeshire, England. *Journal of Biogeography*, **12**, 463-472.

Mjelde, M., Hellsten, S. and Ecke, F. 2013. A water level drawdown index for aquatic macrophytes in Nordic lakes. *Hydrobiologia*, **704**, 141-151.

Milligan, H.E. and Humphries, M.M. 2010. The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. *Oikos*, **119**, 1877-1886.

Mitsch, W.J. and Gosselink, J.G. 2000. *Wetlands*. Wiley, 600 pp.
Moss, B. 2008. The kingdom of the shore: achievement of good ecological potential in reservoirs*. Freshwater Reviews*, **1**, 29-42.

Mossberg, B. and Stenberg, L. 2003. Den nya nordiska floran. Sweden: Wahlström & Widstrand, 928 pp.

Murphy, K.J., Wallace, G. and Drummond, J. 2002. *Aquatic macrophyte and bankside vegetation of the beaver re-introduction lochs: Knapdale, Argyll 2002.* Scottish Natural Heritage, Edinburgh, UK. Report ID BAT/AC322/01/02/94.

Naiman, R.J., Johnston, C.A. and Kelley, J.C. 1988. Alteration of North American streams by beaver. *BioScience*, **38**, 753–762.

Northcott, T.H. 1972. Water lilies as beaver food. *Oikos,* **23**, 408-409.

Nummi, P. 1989. Simulated effects of the beaver on vegetation, invertebrates and duck. *Annales Zoologica Fennici*, **26**, 43-52

Nummi, P. 1992. The importance of beaver ponds to waterfowl broods: An experiment and natural tests. *Annales Zoologica Fennici*, **29**, 47–55.

Nummi, P., Kattainen, S., Ulander, P. and Hahtola, A. 2011. Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation*, **20**, 851-589.

Nummi, P. and Kuuluvainen, T. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. *Boreal Environment Research* 18, Special Issue Supplement A, 13-24.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.S. and Wagner, H. 2012. Vegan: Community Ecology Package. R package version 2.0-9. http://CRAN.R-project.org/package=vegan.

Orians, G.H. and Pearson, N.E. 1979. On the theory of central place foraging. *In*: Horn, D.J., Stairs, G.R. and Mitchell, R.D. (eds) *Analysis of Ecological Systems*. pp 155-177.

Parker, J.D., Caudill, C.C. and Hay, M.E. 2007. Beaver herbivory on aquatic plants. *Oecologia,* **151**, 616-625.

Peczula, W. and Szczurowska, A. 2013. Long term changes in phytoplankton in a humic lake in response to the water level rising: the effects of beaver engineering on a freshwater ecosystem. *Knowledge and Management of Aquatic Ecosystems*, **410**, 67-79.

Pollock, M.M., Heim, M. and Werner D. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. *American Fisheries Society Symposium*, **37**, 213–233.

Pollock, M.M., Naiman, R.J. and Hanley, T.A. 1998. Plant species richness in riparian wetlands: a test of biodiversity theory. *Ecology*, **79**, 94-105.

Ponzio, K.J.; Miller, S.I. and Lee, M.A. 1995. Germination of sawgrass, *Cladium jamaicense* Crantz, under varying hydrologic conditions. *Aquatic Botany*, **51**, 115-120.

Preston, C.D. 1995. *Pondweeds of Great Britain and Ireland*. BSBI Publications.

Preston, C.D. and Croft, J.M. 1997. *Aquatic Plants in Britain and Ireland*. Harley Books.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rango, A., Laliberte, A., Herrick, J. E., Winters, C., Havstad, K. and Steele, C. 2009. Unmanned aerial vehicle-based remote sensing for rangeland assessment, monitoring, and management. *Journal of Applied Remote Sensing*, **3**, 1–15.

Ray, A.M., Rebertus, A.J. and Ray, H.L. 2001. Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany*, **79**, 487-499.

Rich, T.C.G. and Jermy, A.C. 1998. *Plant Crib 1998*. London : Botanical Society of the British Isles.

Rolauffs, P., Hering, D. and Lohse, S. 2001. Composition, invertebrate community and productivity of a beaver dam in comparison to other stream habitat types. *Hydrobiologia*, **459**, 201–212.

Rosell, F., Bozser, O; Collen, P. and Parker, H. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, **35**, 248-276.

Skoglund J. and Hytteborn H. 1990. Viable seeds in deposits of the former lakes Kvismaren and Hornborgasjon, Sweden. *Aquatic Botany*, **37**, 271-290.

Smirnov, V.V. and Tretyakov, K. 1998. Changes in aquatic plant communities on the island of Valaam due to invasion by the muskrat *Ondatra zibethicus* L. (Rodentia: Mammalia). *Biodiversity and Conservation*, **7**, 673–690.

Spence, D.H.N. 1964. The macrophytic vegetation. *In*: Burnett, J.H. (ed) *The Vegetation of Scotland*. Edinburgh: Oliver & Boyd, pp 306-425.

Stephenson, D. and Merritt, J. 2010. *Argyll and the Islands: a landscape fashioned by geology*. Scottish Natural Heritage.

Stewart, N.F. and Church, J.M. 1992. *Red data books of Britain and Ireland*: Stoneworts. Peterborough: JNCC.

Sturtevant, B.R. 1998. A model of wetland vegetation dynamics in simulated beaver impoundments. *Ecological Modelling*, **112**, 195-225.

Svendsen, G.E. 1980 Seasonal change in feeding patterns of beaver in southeastern Ohio. *Journal of Wildlife Management*, **44**, 285-290.

Thompson, R. M. and Ryder, G. R. 2008. Effects of hydro-electrically induced water level fluctuations on benthic communities in Lake Hawea, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **42**, 197-206.

Townsend, P.A. and Butler, D.R. 1996. Patterns of landscape use by beaver on the lower Roanoke River floodplain, North Carolina. *Physical Geography*, **17**, 253-269

Toivonen, H. and Meriläinen, J. 1980. Impact of the muskrat (*Ondatra zibethica* L.) on aquatic vegetation in small Finnish lakes. *Developments in Hydrobiology*, **3**, 131-138.

Valta-Hulkkonen, K., Kanninen, A. and Pellikka, P. 2004. Remote sensing and GIS for detecting changes in the aquatic vegetation of a rehabilitated lake. *International Journal of Remote Sensing*, **25**, 5745-5758.

Webb A., French D. and Flitsch A. 1997. Identification and assessment of possible beaver sites in Scotland. *Scottish Natural Heritage commissioned report* No. 94.

Williams, P., Whitfield, M. and Biggs, J. 2008. How can we make new ponds biodiverse? A case study monitored over 7 years. *Hydrobiologia*, **597**, 137–148.

Willby, N.J. and Casas-Mulet, R. 2010. The Scottish Beaver Trial: Baseline survey of the aquatic and semi-aquatic macrophytes of the lochs 2008. *Scottish Natural Heritage Commissioned Report* No. 391.

Willby, N.J., Casas-Mulet, R. and Perfect, C. 2011. The Scottish Beaver Trial: Monitoring and further baseline survey of the aquatic and semi-aquatic macrophytes of the lochs 2009. *Scottish Natural Heritage Commissioned Report* No. 455*.

Willby, N.J. and Perfect, C. 2014. The Scottish Beaver Trial: Monitoring and of the aquatic and semi-aquatic macrophytes of the lochs 2011. *Scottish Natural Heritage Commissioned Report* No. 687*.

Willby, N.J., Law, A., Levanoni, O., Foster, G.N. and Ecke, F. submitted 2014. Engineering biodiversity: beavers enrich aquatic plant and beetle assemblages at multiple spatial scales.

Wright, J.P., Jones, C.G. and Flecker, A.S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.
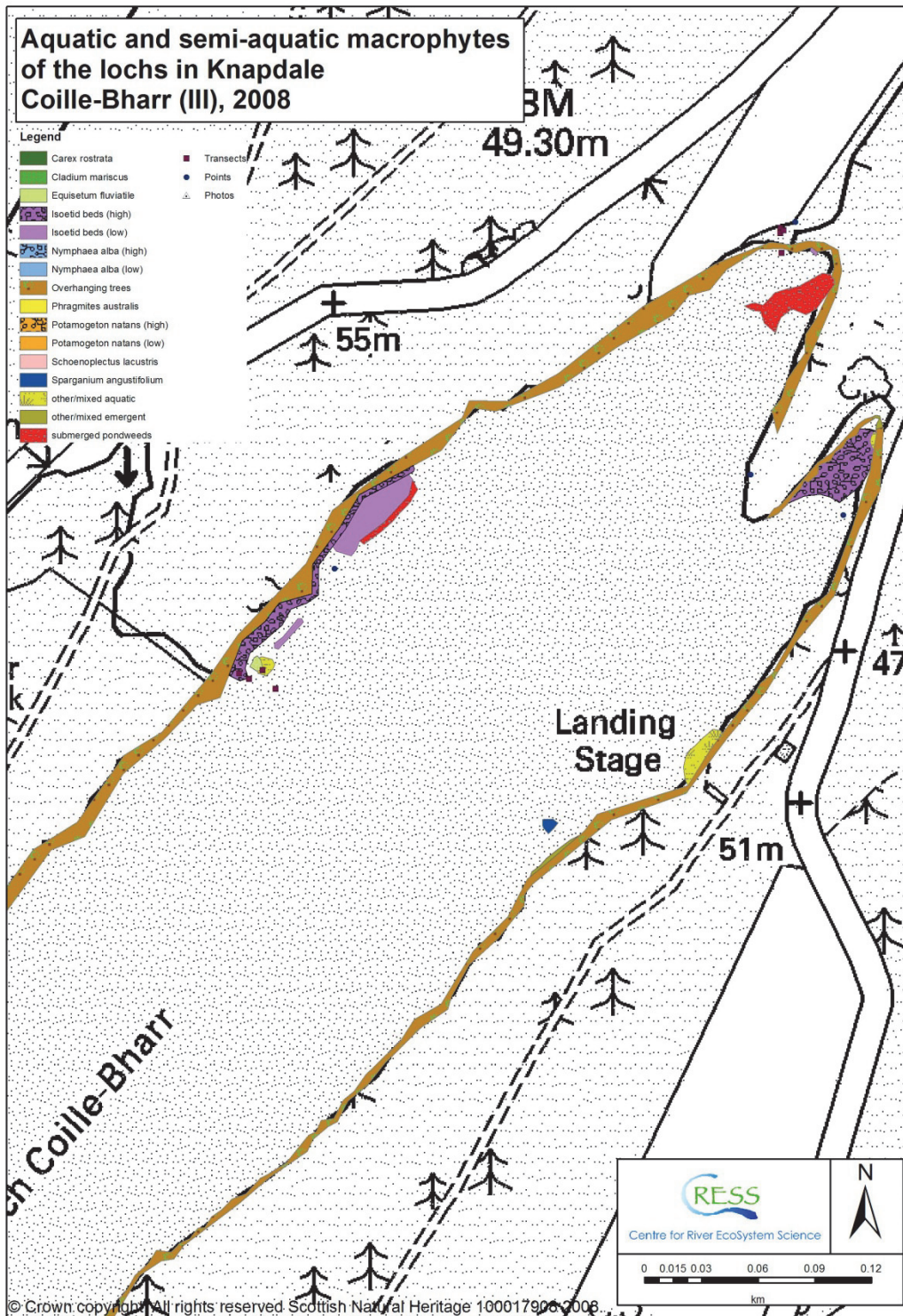
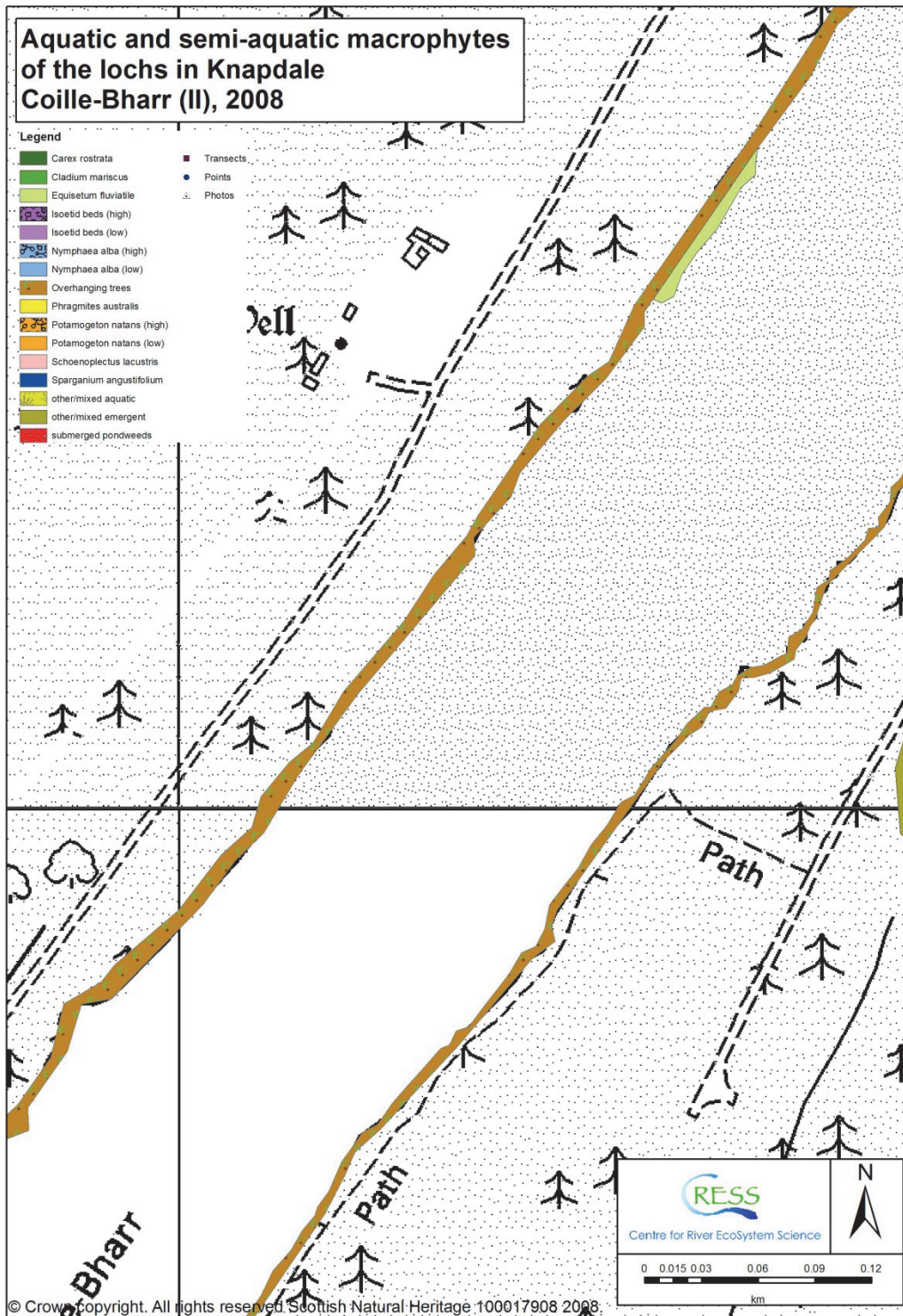**APPENDIX 1: VEGETATION POLYGON MAPS FOR PRIMARY LOCHS, BASELINE SURVEYS, 2008 AND 2009**
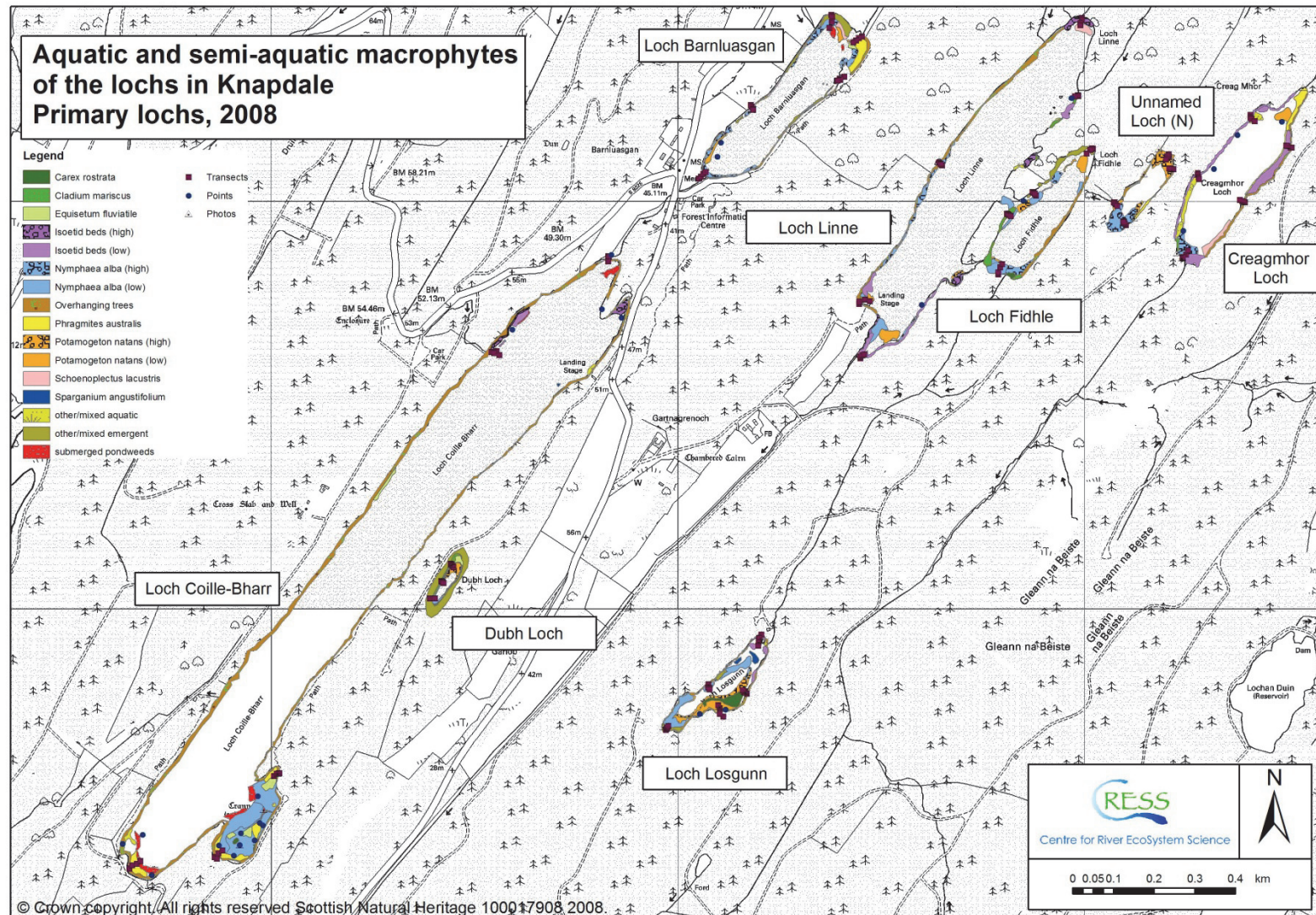
Map 1. Overview of polygon distribution in all primary lochs surveyed in 2008
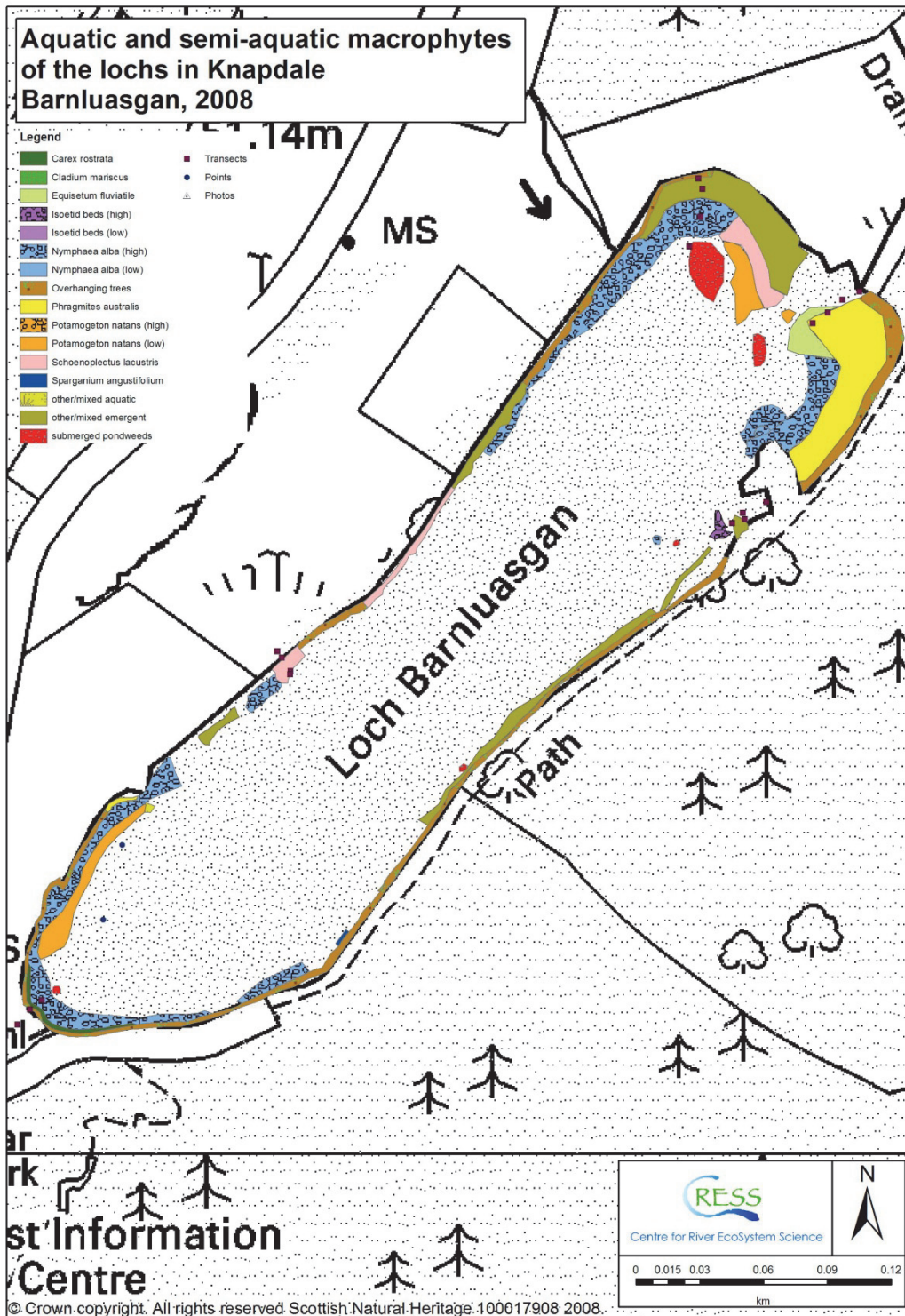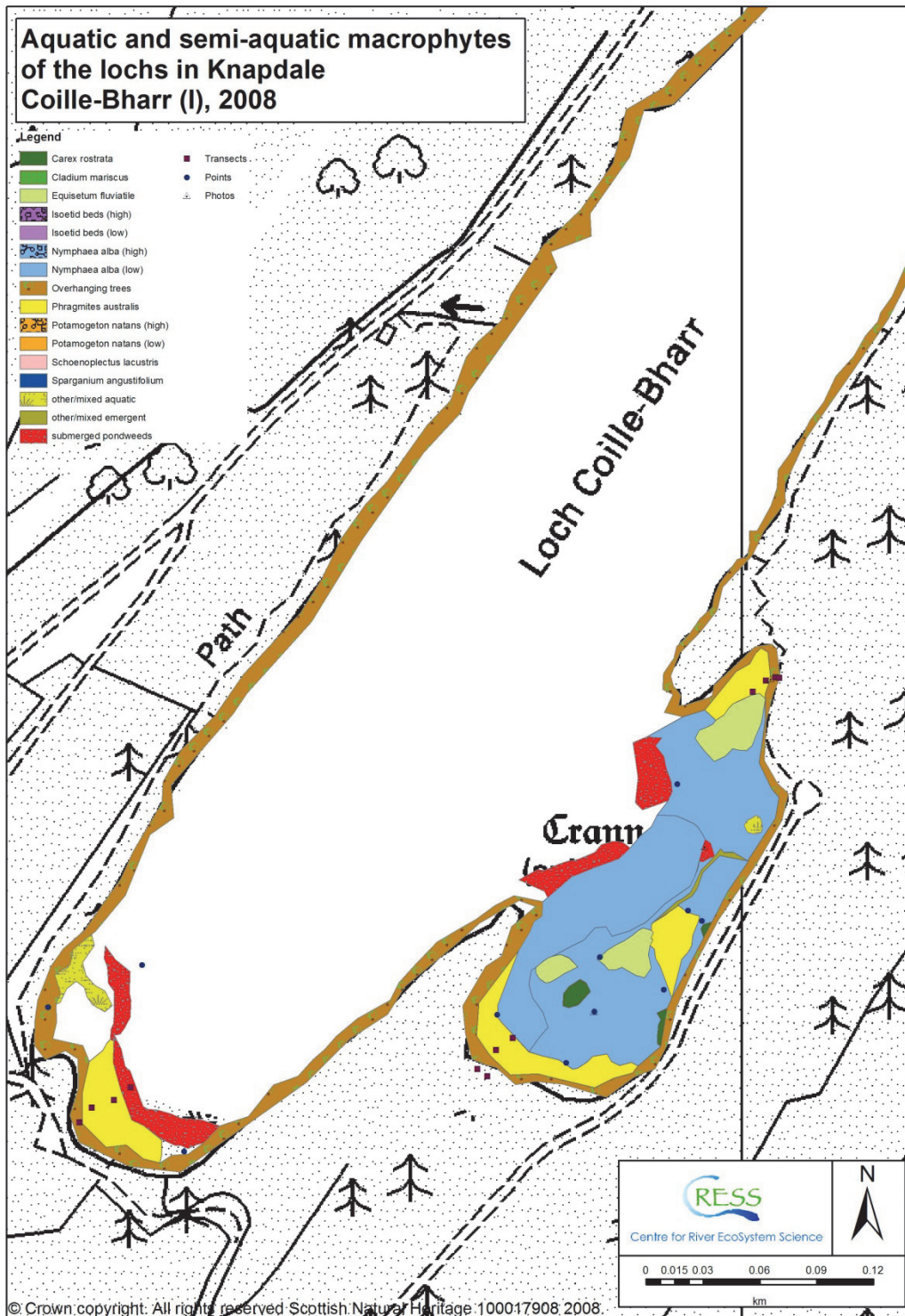
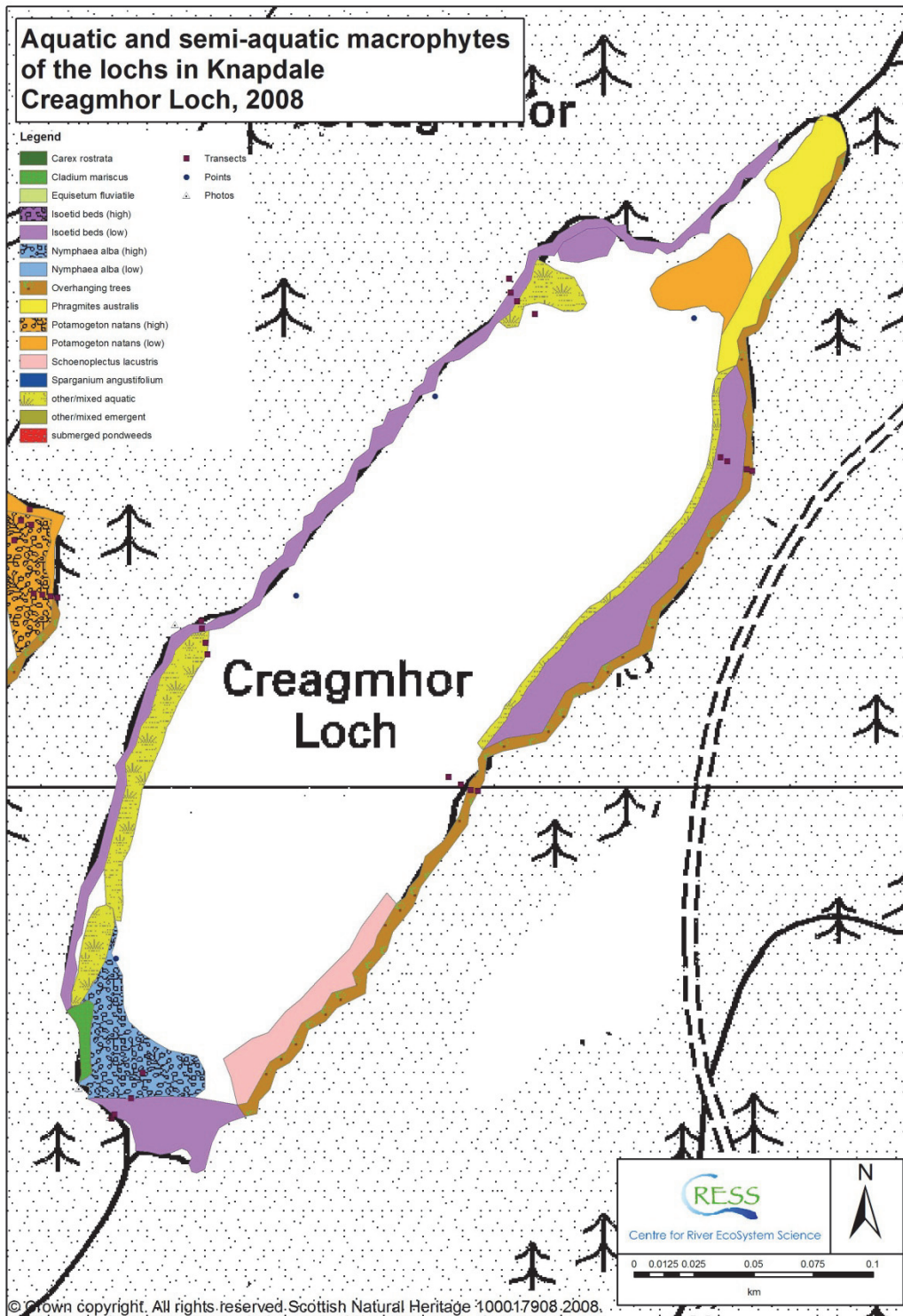*Map 2. Polygon, point and transect distribution in Loch Barnluasgan*

Map 3. Polygon, point and transect distribution in Loch Coille Bharr (north)

Aquatic and semi-aquatic macrophytes of the lochs in Knapdale Coille-Bharr (II), 2008

Legend

- Carex rostrata
- Cladium mariscus
- Equisetum fluviatile
- Isoetid beds (high)
- Isoetid beds (low)
- Nymphaea alba (high)
- Nymphaea alba (low)
- Overhanging trees
- Phragmites australis
- Potamogeton natans (high)
- Potamogeton natans (low)
- Schoenoplectus lacustris
- Sparganium angustifolium
- other/mixed aquatic
- other/mixed emergent
- submerged pondweeds

- Transects
- Points
- Photos

Dell

Path

Path

Bharr

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Centre for River EcoSystem Science
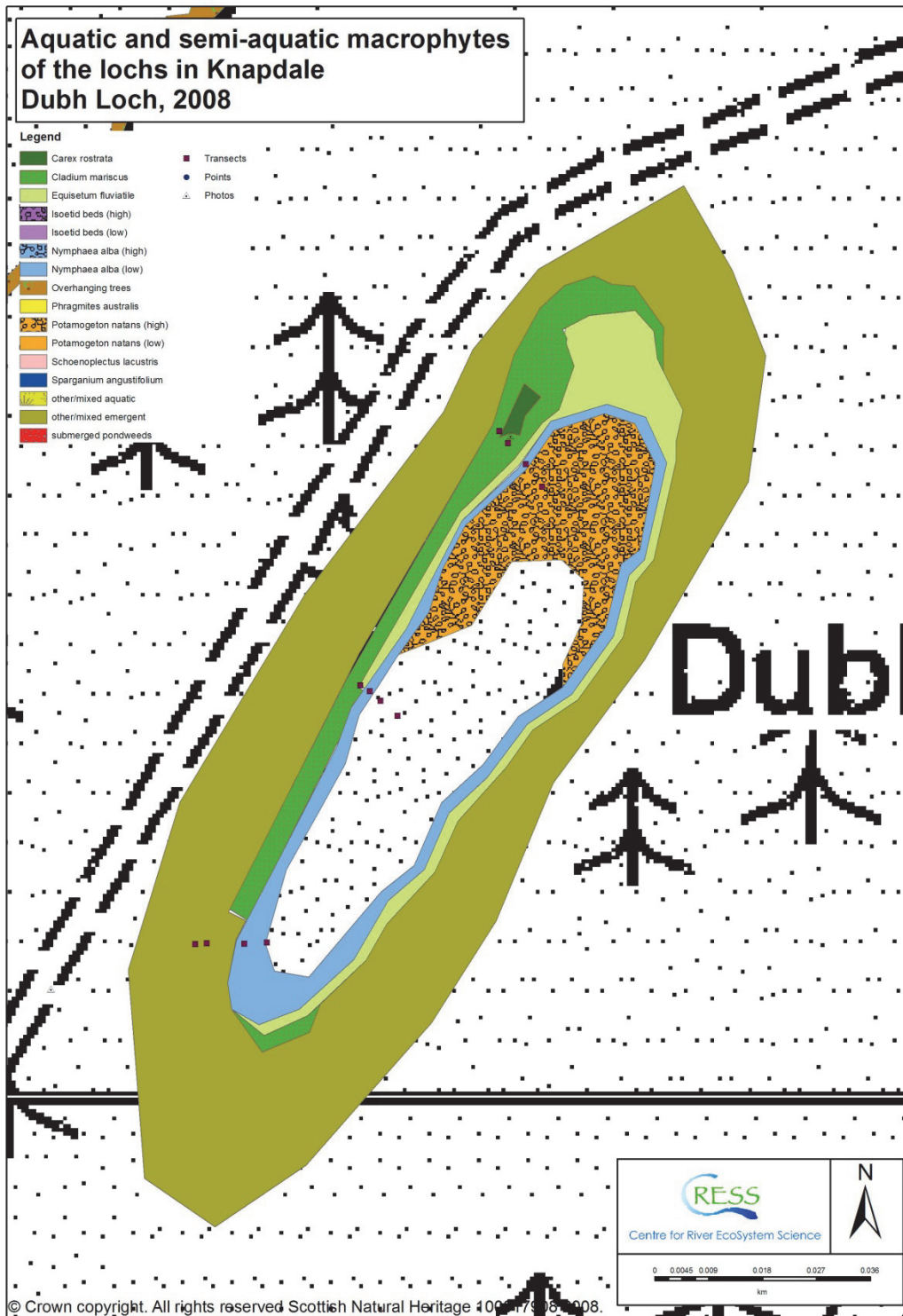
N

0 0.015 0.03 0.06 0.09 0.12
km

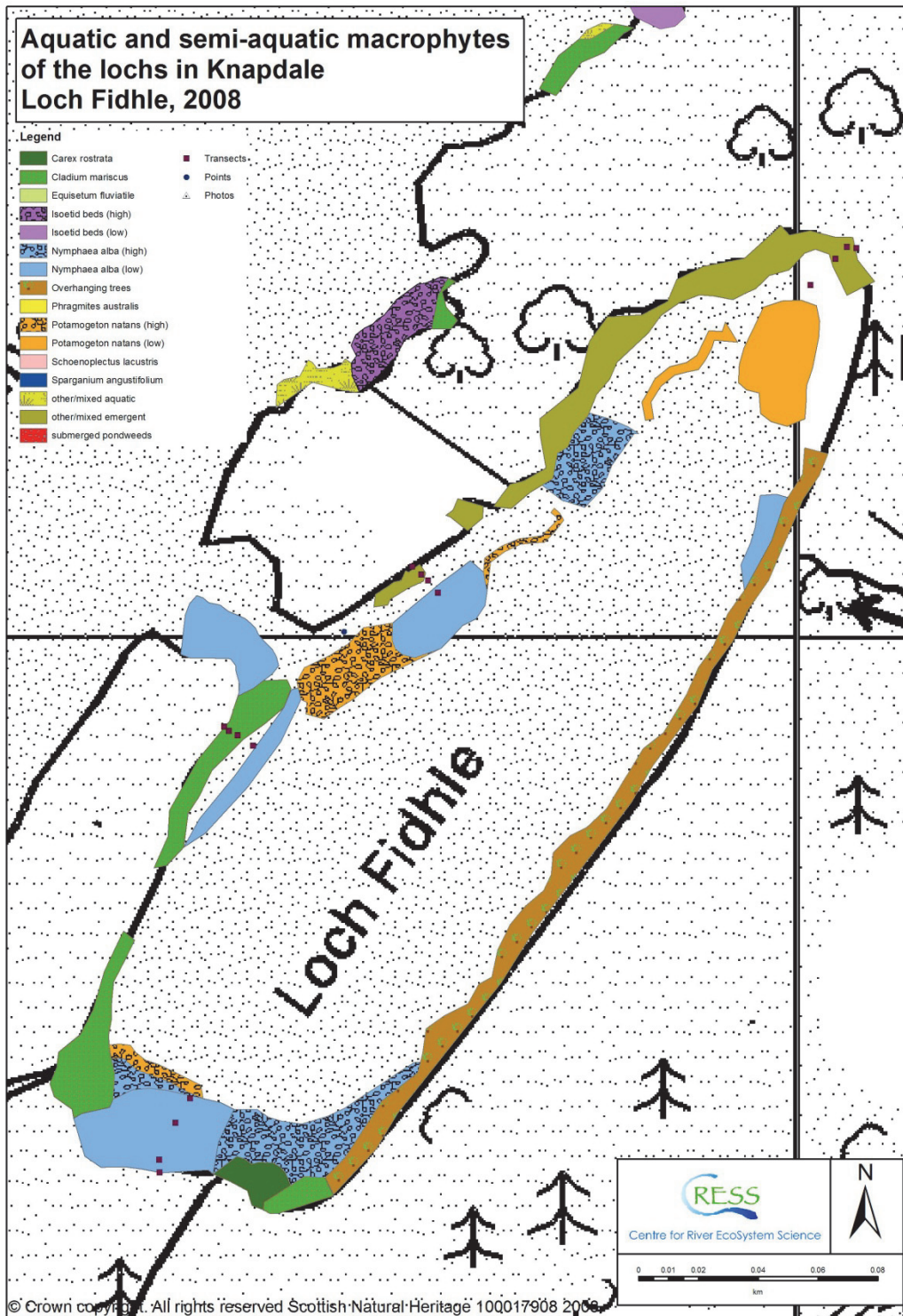*Map 4. Polygon, point and transect distribution in Loch Coille Bharr (mid)*

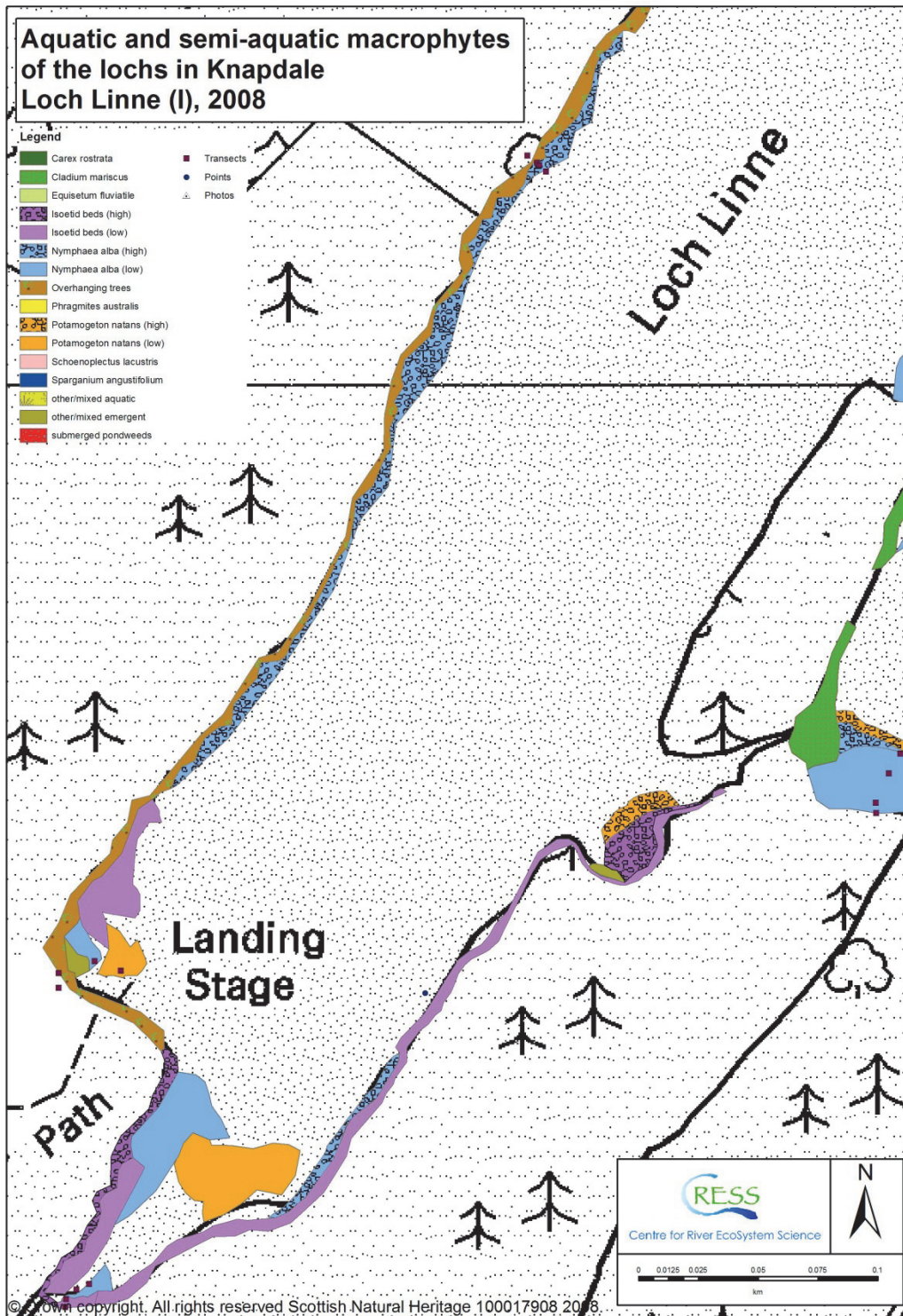*Map 5. Polygon, point and transect distribution in Loch Coille Bharr (south)*

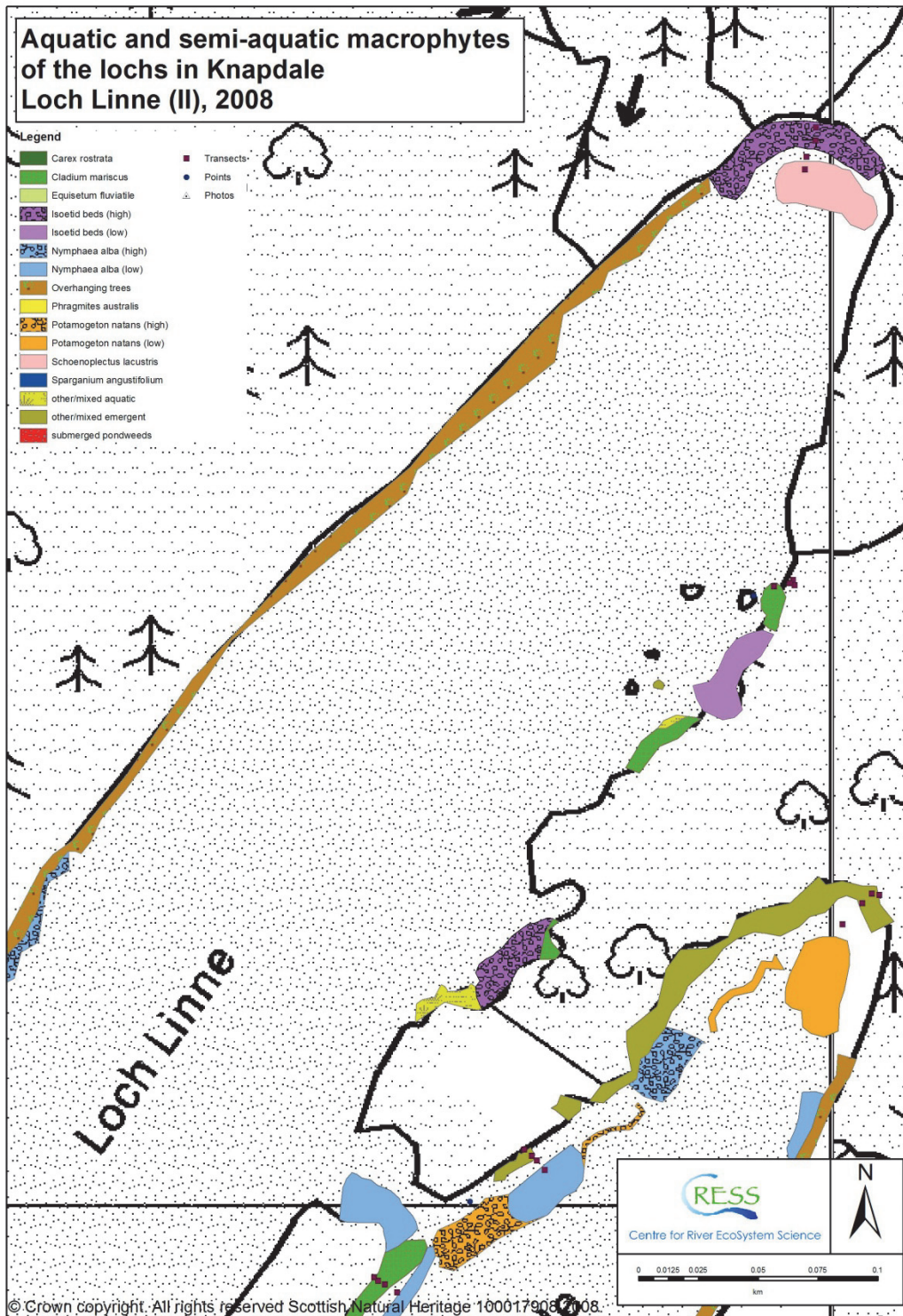*Map 6. Polygon, point and transect distribution in Creagmhor Loch*

Aquatic and semi-aquatic macrophytes of the lochs in Knapdale
Dubh Loch, 2008

Legend

- Carex rostrata
- Cladium mariscus
- Equisetum fluviatile
- Isoetid beds (high)
- Isoetid beds (low)
- Nymphaea alba (high)
- Nymphaea alba (low)
- Overhanging trees
- Phragmites australis
- Potamogeton natans (high)
- Potamogeton natans (low)
- Schoenoplectus lacustris
- Sparganium angustifolium
- other/mixed aquatic
- other/mixed emergent
- submerged pondweeds

- Transects
- Points
- Photos

Dubl

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0 0.0045 0.009   0.018   0.027   0.036
km

Map 7. Polygon, point and transect distribution in Dubh Loch

105

Aquatic and semi-aquatic macrophytes of the lochs in Knapdale
Loch Fidhle, 2008

Legend

- Carex rostrata
- Cladium mariscus
- Equisetum fluviatile
- Isoetid beds (high)
- Isoetid beds (low)
- Nymphaea alba (high)
- Nymphaea alba (low)
- Overhanging trees
- Phragmites australis
- Potamogeton natans (high)
- Potamogeton natans (low)
- Schoenoplectus lacustris
- Sparganium angustifolium
- other/mixed aquatic
- other/mixed emergent
- submerged pondweeds

- Transects
- Points
- Photos

Loch Fidhle

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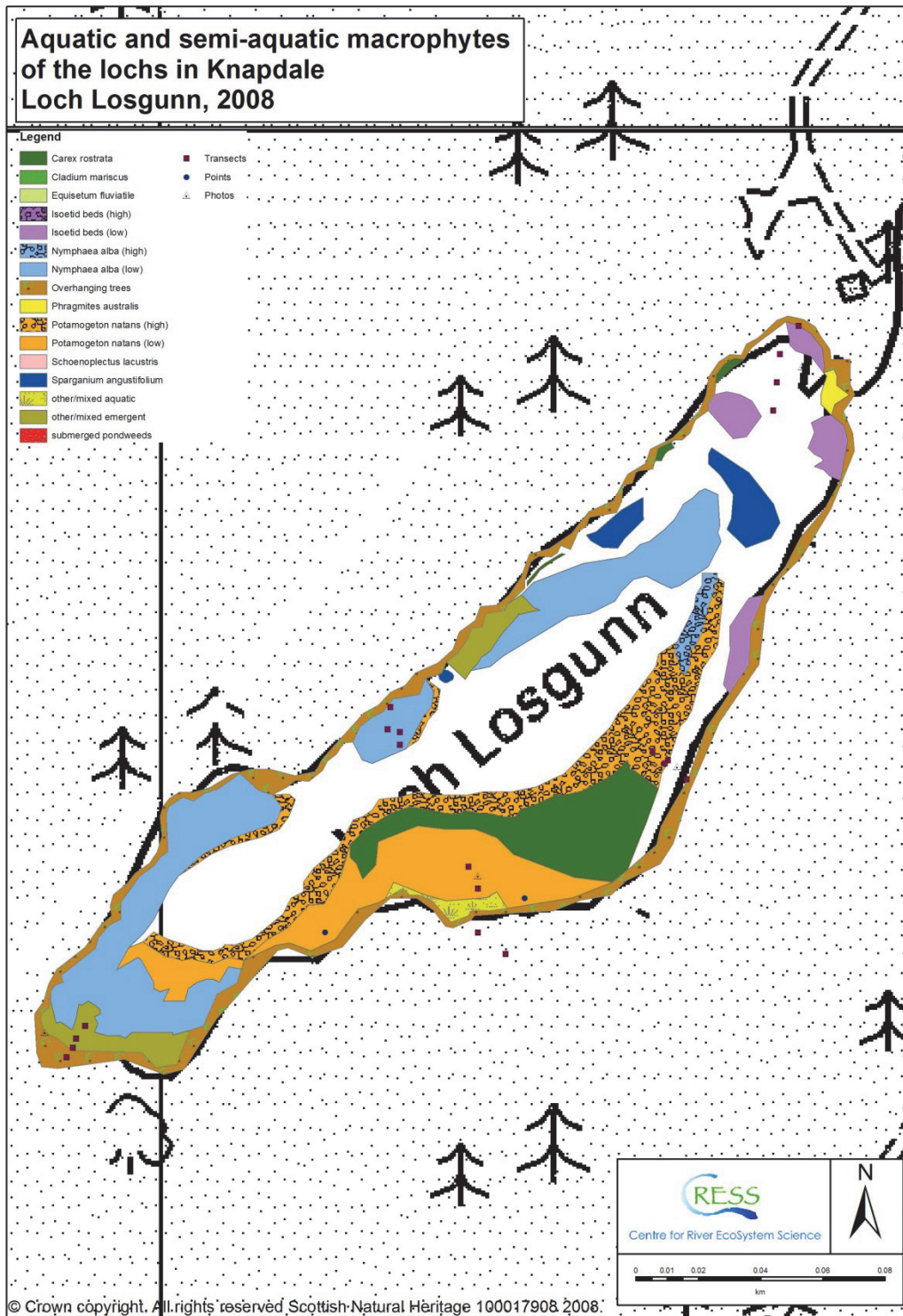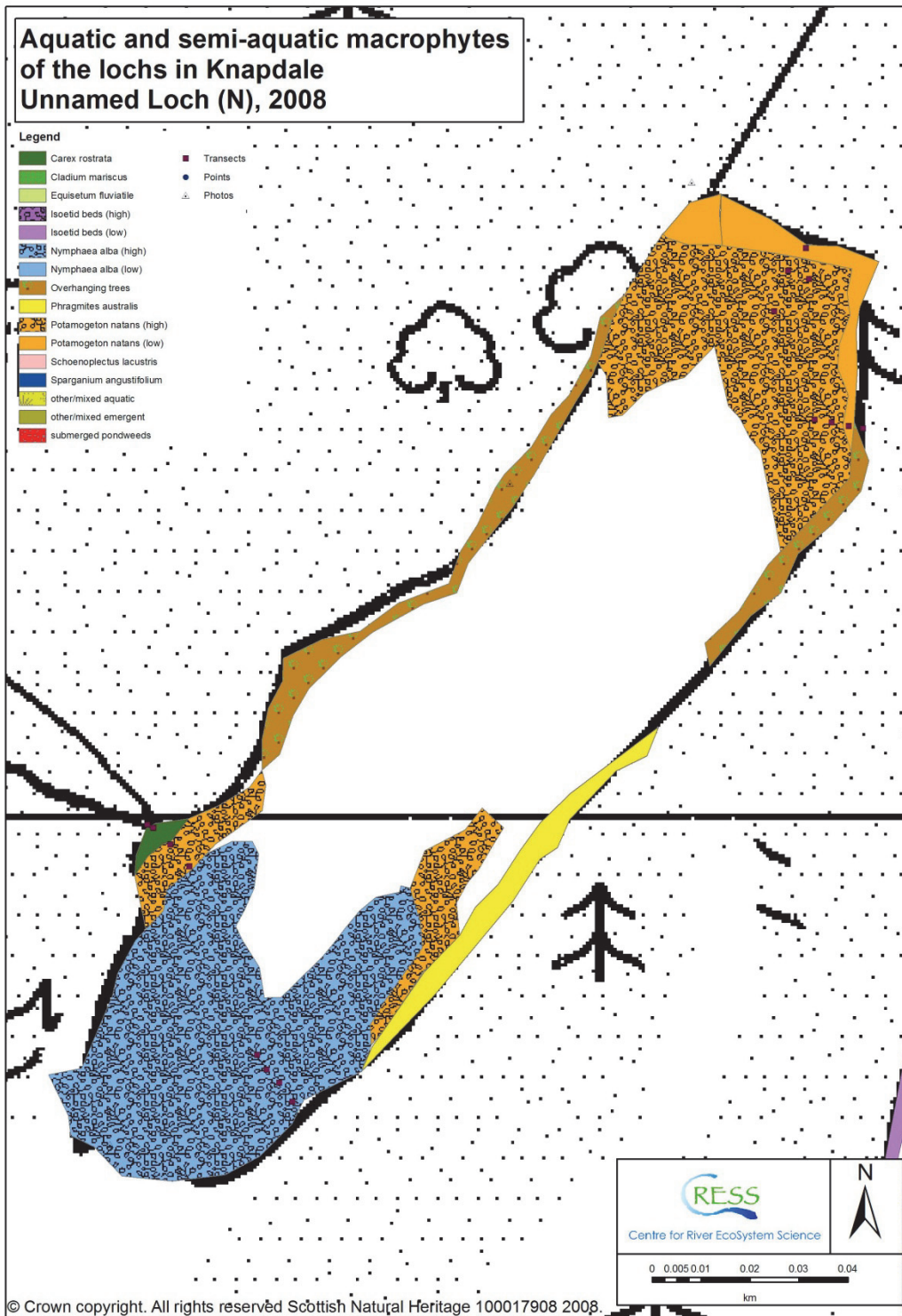
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| 0 | 0.01 | 0.02 | 0.04 | 0.06 | 0.08 |
km

Map 8. Polygon, point and transect distribution in Loch Fidhle

106

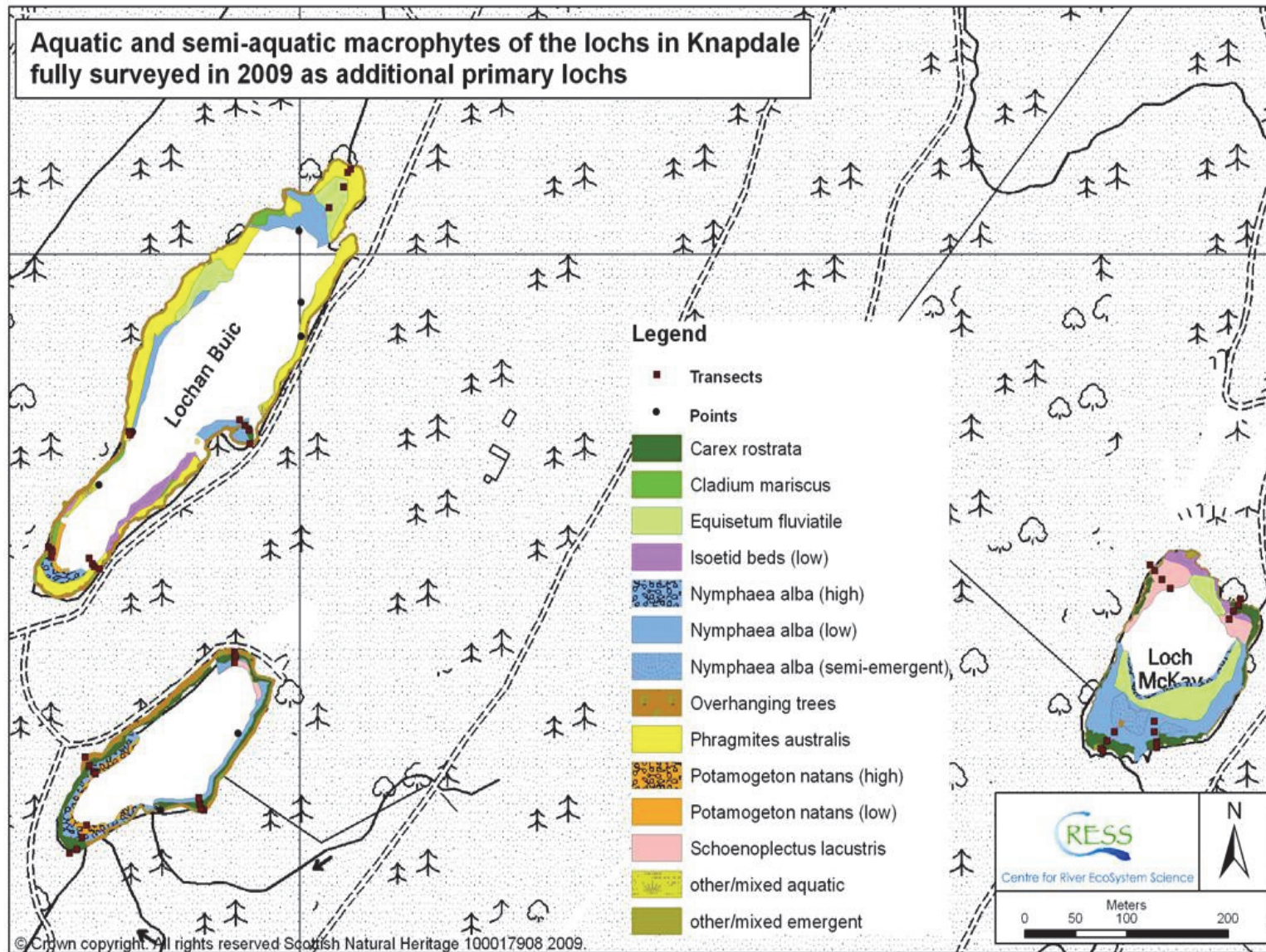*Map 9. Polygon, point and transect distribution in Loch Linne (south)*

Aquatic and semi-aquatic macrophytes
of the lochs in Knapdale
Loch Linne (II), 2008

Legend

Carex rostrata
Cladium mariscus
Equisetum fluviatile
Isoetid beds (high)
Isoetid beds (low)
Nymphaea alba (high)
Nymphaea alba (low)
Overhanging trees
Phragmites australis
Potamogeton natans (high)
Potamogeton natans (low)
Schoenoplectus lacustris
Sparganium angustifolium
other/mixed aquatic
other/mixed emergent
submerged pondweeds

Transects
Points
Photos

Loch Linne

Map 10. Polygon, point and transect distribution in Loch Linne (north)

108

Aquatic and semi-aquatic macrophytes of the lochs in Knapdale
Loch Losgunn, 2008

Legend

- Carex rostrata
- Cladium mariscus
- Equisetum fluviatile
- Isoetid beds (high)
- Isoetid beds (low)
- Nymphaea alba (high)
- Nymphaea alba (low)
- Overhanging trees
- Phragmites australis
- Potamogeton natans (high)
- Potamogeton natans (low)
- Schoenoplectus lacustris
- Sparganium angustifolium
- other/mixed aquatic
- other/mixed emergent
- submerged pondweeds

- Transects
- Points
- Photos

CRESS
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Map 11. Polygon, point and transect distribution in Loch Losgunn

Map 12. Polygon, point and transect distribution in Un-named Loch (North)

Table 1. Composition of vegetation in characteristic polygon types in 2008

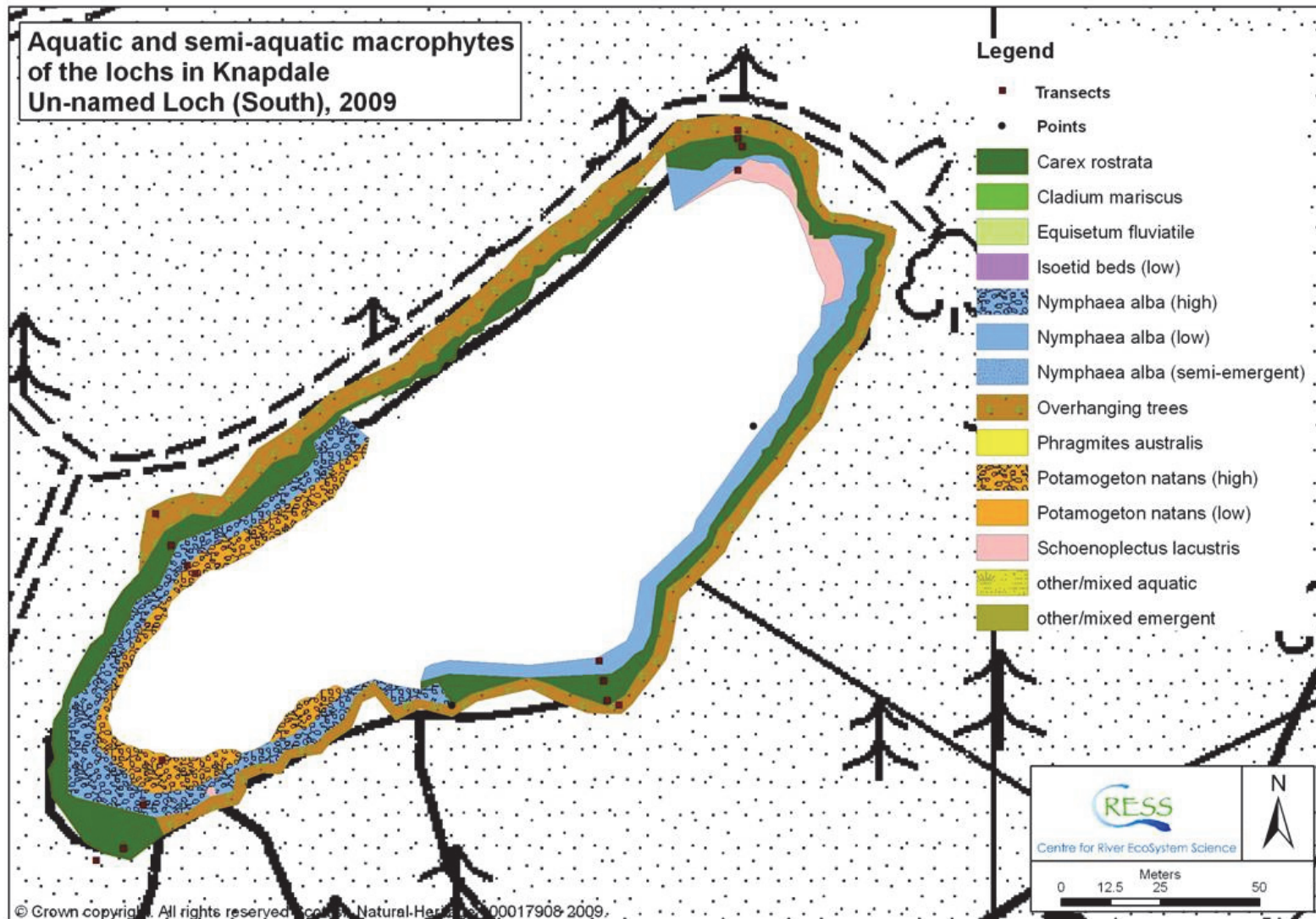| Polygon name	Description
Carex rostrata	stands dominated by *C. rostrata* in which other species (e.g. *L. uniflora*, *Juncus bulbosus*, *Juncus articulatus*) may occur as subordinates
Cladium mariscus	stands dominated by *C. mariscus* with occasional very limited cover of other species (e.g. *E. fluviatile*, *N. alba*)
Equisetum fluviatile	open stands dominated by *E. fluviatile* sometimes with associated *N. alba*, *S. lacustris* or *P. natans*
Isoetid beds (high)	stands with >50% cover of *L. uniflora* and/or *L. dortmanna*
Isoetid beds (low)	stands with <50% cover of *L. uniflora* and/or *L. dortmanna*, either intermixed with small emergents such as *C. rostrata* and *J. articulatus*, or overlain by *N. alba*
Nymphaea alba (high)	stands with >50% cover of *N. alba* with limited cover of associates, most commonly *P. natans*, *S. lacustris* or *E. fluviatile*
Nymphaea alba (low)	stands with <50% cover of *N. alba* intermixed with low density *P. natans*, *C. rostrata*, *E. fluviatile* or *S lacustris*. Often underlain by low density of *L. uniflora* or *L. dortmanna*
Other/mixed aquatic	stands dominated by species with very low overall frequency (e.g. *Nuphar pumila*, *P. polygonifolius*) or mixed stands with no clear dominant, but usually including *M. alterniflorum*, *J. bulbosus*, *L. uniflora*, *S. lacustris* or *E. canadensis*
Other/mixed emergent	stands dominated by species with very low overall frequency (e.g. *Eleocharis multicaulis*, *Phalaris arundinacea* or *C. paniculata*) or mixed stands with no clear dominant, but usually including *S. lacustris*, *P. australis*, *E. fluviatile* and/or *C. rostrata* plus a low density of *N. alba*)
Overhanging trees	range of fringing woody vegetation type in which *Betula pubescens* usually dominant or co-dominant
Phragmites australis	stands with cover dominated by *P. australis*, with *P. natans*, *L. uniflora* or *E. fluviatile* the most common associates
Potamogeton natans (high)	stands with >50% cover of *P. natans*, occasionally with sparse cover of *N. alba*
Potamogeton natans (low)	stands with <50% cover of *P. natans*, typically associated with sparse cover of *N. alba* and *S. lacustris*
Schoenoplectus lacustris	stands dominated by *S. lacustris* with occasional cover of *E. fluviatile* or *N. alba*
Sparganium angustifolium	stands dominated by *Sparganium angustifolium*, few associates (most commonly *N. pumila*)
Submerged pondweeds	Beds of *Potamogeton praelongus*, *P. lucens*, *P.x zizzii*, *P. perfoliatus*, sometimes mixed with *E. canadensis, Chara virgata* or *M. alterniflorum*

Map 13. Overview of polygon distribution in additional primary lochs surveyed in 2009
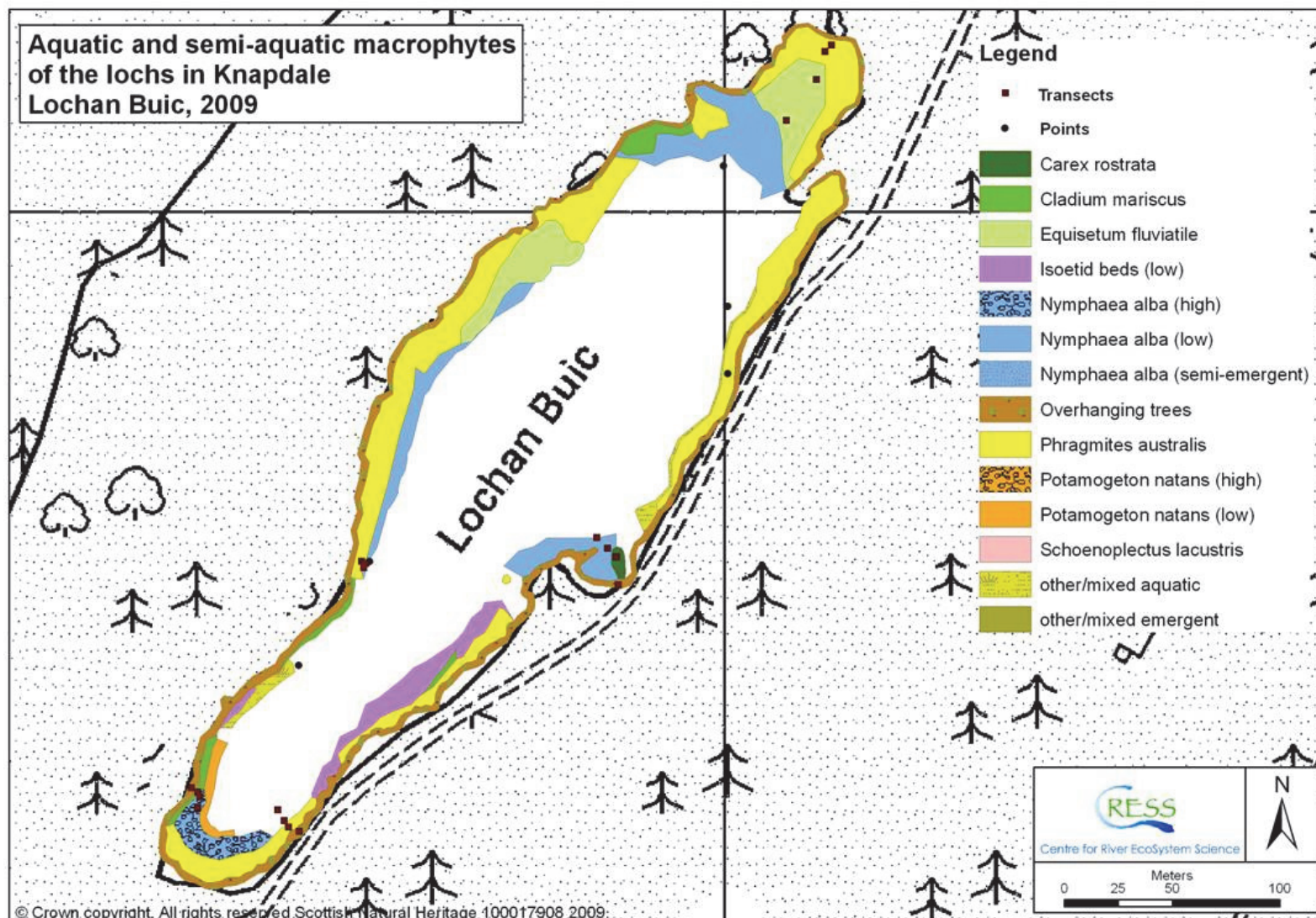
Map 14. Polygon, point and transect distribution in Lochan Buic
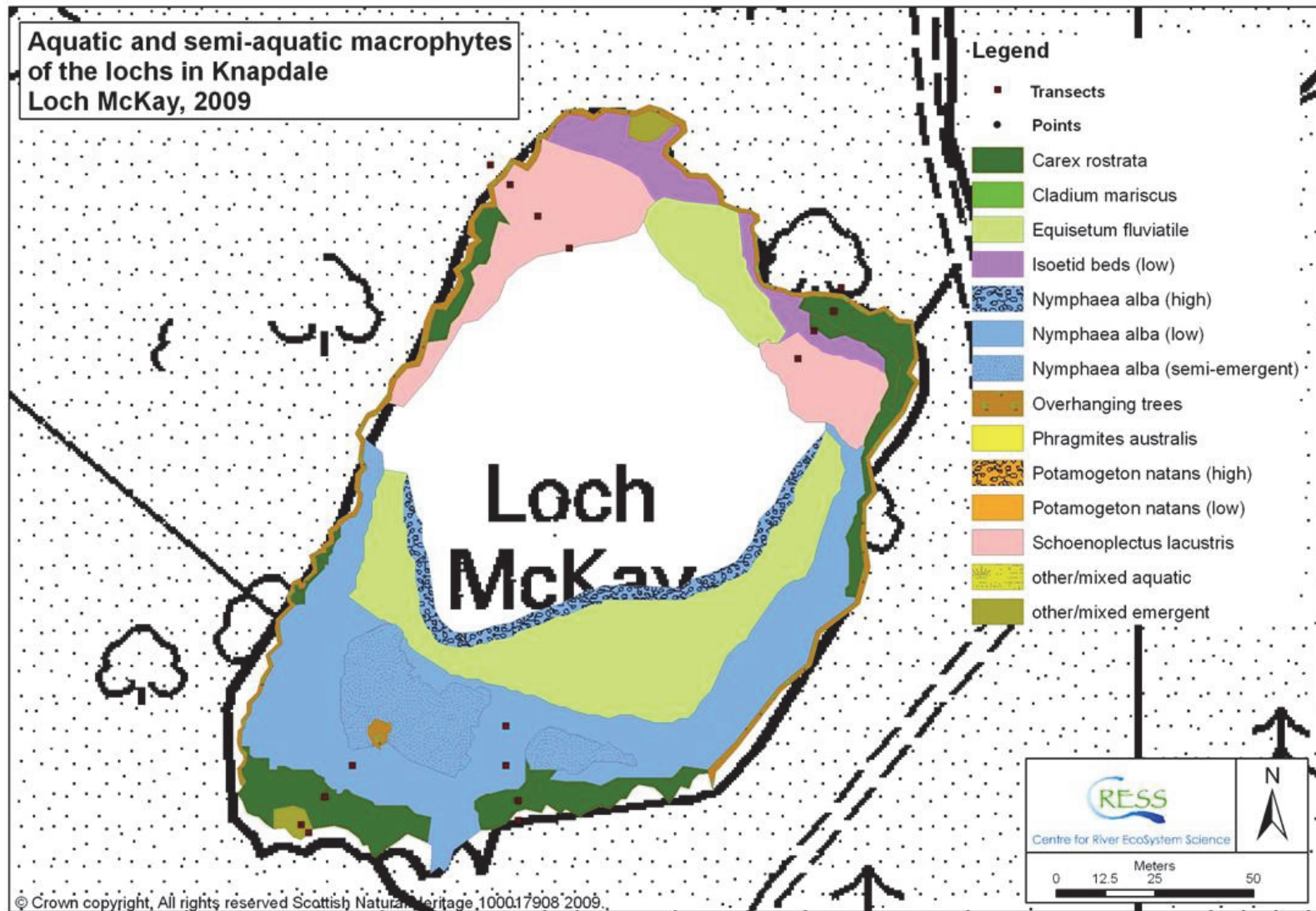
Map 15. Polygon, point and transect distribution in Loch McKay

Map 16. Polygon, point and transect distribution in un-named loch (S)

Table 2. Composition of vegetation in characteristic polygon types in additional primary lochs surveyed in 2009

Polygon name	Description
Carex rostrata	*stands dominated by C. rostrata in which other species (e.g. L. uniflora, J. bulbosus, J. articulatus) may occur as subordinates*
Cladium mariscus	*stands dominated by C. mariscus with occasional very limited cover of other species (e.g. E. fluviatile, N. alba)*
Equisetum fluviatile	*open stands dominated by E. fluviatile sometimes with associated N. alba, S. lacustris or P. natans*
Isoetid beds (low)	*stands with <50% cover of L. uniflora and/or L. dortmanna, either intermixed with small emergents such as C. rostrata and J. articulatus, or overlain by N. alba*
Nymphaea alba (high)	*stands with >50% cover of N. alba with limited cover of associates, most commonly P. natans, S. lacustris or E. fluviatile*
Nymphaea alba (low)	*stands with <50% cover of N. alba intermixed with low density P. natans, C. rostrata, E. fluviatile or S lacustris. Often underlain by low density of L. uniflora or L. dortmanna*
Nymphaea alba (semi-emergent)	*Stands of low density N. alba on partially exposed peat, usually with very low density of C. rostrata, plus a large number of emergent and marginal species at negligible cover.*
Other/mixed aquatic	*stands dominated by species with very low overall frequency (e.g. N. pumila, Eleogiton fluitans, P. polygonifolius) or mixed stands with no clear dominant, but usually including M. alterniflorum, J. bulbosus, L. uniflora, S. lacustris or E. canadensis*
Other/mixed emergent	*stands dominated by species with very low overall frequency (e.g. Eleocharis multicaulis, Phalaris arundinacea or C. paniculata) or mixed stands with no clear dominant, but usually including S. lacustris, P. australis, E. fluviatile and/or C. rostrata plus a low density of N. alba)*
Overhanging trees	*range of fringing woody vegetation type in which B. pubescens usually dominant or co-dominant*
Phragmites australis	*stands with cover dominated by P. australis, with P. natans, L. uniflora or E. fluviatile the most common associates*
Potamogeton natans (high)	*stands with >50% cover of P. natans, occasionally with sparse cover of N. alba*
Potamogeton natans (low)	*stands with <50% cover of P. natans, typically associated with sparse cover of N. alba and S. lacustris*
Schoenoplectus lacustris	*stands dominated by S. lacustris with occasional cover of E. fluviatile or N. alba*

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