Evaluation of the ecological impacts of beaver reintroduction on aquatic systems

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STATEMENT OF ORIGINALITY

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GENERAL ABSTRACT

The extent and quality of freshwater systems is declining globally. Combined with past drainage, straightening and flow regulation, current systems are often functional but not pristine. Conservation, creation and restoration of freshwater systems is common but requires significant planning, resources and active monitoring and may only be a short-term solution to the long-term problem of destruction and loss of riparian zones. Beavers (*Castor* spp.) have the ability to create physical and biological habitat heterogeneity through the construction of woody debris dams, thereby restoring lost natural discontinuities in freshwater systems. Beavers may thus offer a natural, more passive solution to the need for wetland restoration or creation and the problem of homogenisation of watercourses. As such, numerous beaver reintroductions and introductions have been undertaken based in part on restoring this lost natural heritage. However, it is crucial to be able to predict the potential effects on existing biota of physical modifications by beavers to ecosystems, especially in the light of further population expansion, whilst also disentangling these effects from other influences, namely herbivory. The impact of beavers on aquatic systems was studied using a combination of field-based surveys and experiments, using aquatic plants and macro-invertebrates as indicators of hydromorphological changes and to quantify the effects of direct foraging.

The research presented in this thesis demonstrates beaver adaptive foraging behaviours between terrestrial and aquatic habitats, whilst feeding highly selectively, optimally and opportunistically, using the white water lily (*Nymphaea alba*) as a model species. The effects of beaver foraging on the aquatic plant resource and diversity was low over short time spans (e.g. 1 year), but when selective foraging was assessed over greater time scales (e.g. 10 years) the effects of foraging were distinct. Significant changes in aquatic plant height, biomass, richness, diversity and composition were observed over this time period due to selective grazing on large rhizomatous species (e.g. *Menyanthes trifoliata*). These direct effects occurred even though changes in water levels, which are commonly believed to be the main driver of beaver influence on aquatic vegetation, were negligible. In a separate study in Sweden where beavers commonly constructed dams, with ponds then forming upstream, the aquatic plant and coleoptera species richness and composition differed in comparison to adjacent non-beaver created wetlands. Therefore, having a range of wetland types in the environment increases physical and biological heterogeneity creating unique niches that are exploited by disparate taxa. The construction of a series of dams within a single reach of stream flowing through a Scottish agricultural landscape also increased physical habitat diversity. Distinctive macroinvertebrate assemblages and modified functional diversity were associated with each dominant habitat type in the stream, resulting in increased landscape scale richness.

The findings of this thesis confirm that beaver engineering and foraging has the potential to create unique and highly heterogeneous wetland and stream habitats within landscapes that enhances richness and diversity for multiple species groups. This thesis also supports part of the rationale for the trial reintroduction of beaver to Scotland that beavers can restore degraded habitats.

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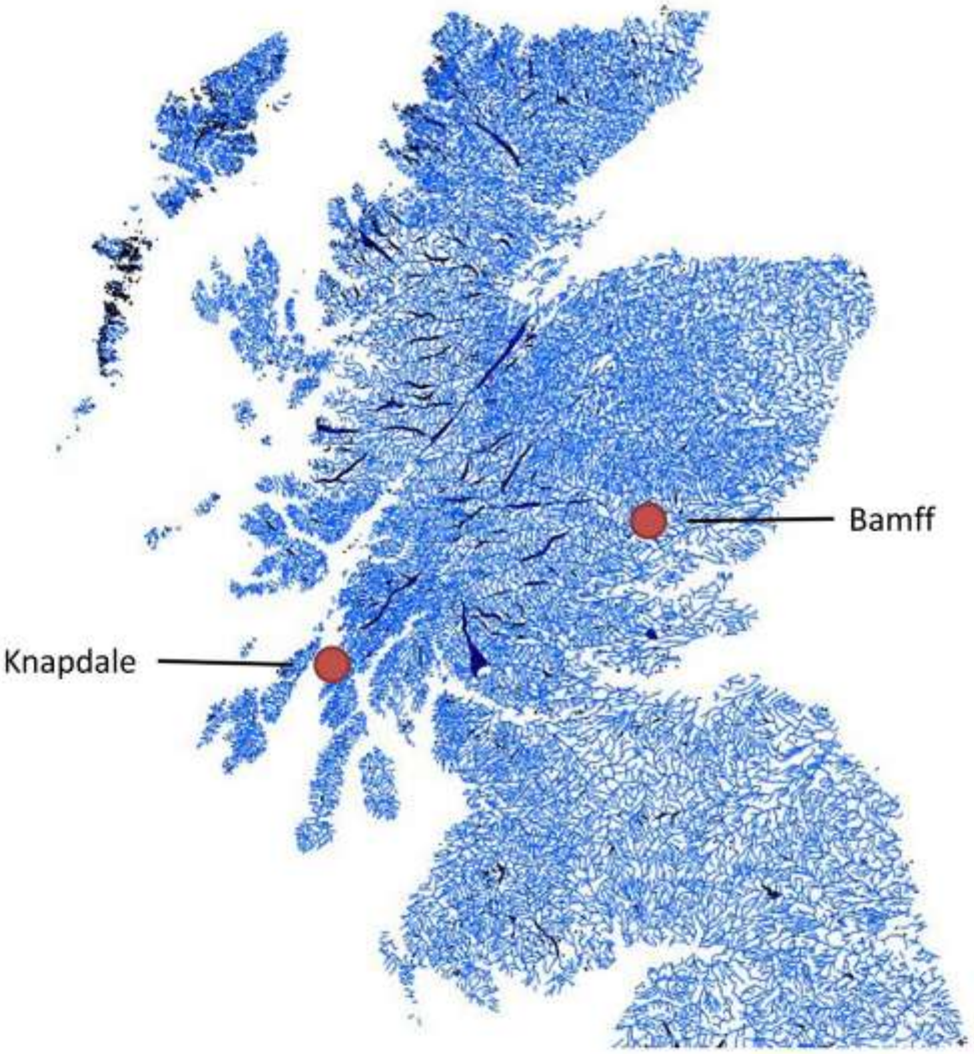
CHAPTER 1 – General introduction

1.1 Scientific background

Freshwaters are tremendously important and diverse habitats: they cover less than 1% of the Earth's surface yet are home to 12% of the world's known plant and animal species, estimated to be around 126,000 species (Collen et al., 2014). However, throughout human history freshwater habitats have been misused and overexploited, in a variety of ways including the creation of large hydro-power dams, withdrawal of water, diversions, pollution by agricultural runoff or sewage effluent, river engineering, draining of wetlands for development, in addition to multiple invasions by non-native species. All of these pressures have been applied over the last century against a backdrop of accelerating global climate change and increasing human population. As such, pristine systems are almost universally rare with demand on existing systems unlikely to abate. There is not only a concern for the economic and altruistic value of their biodiversity, but as freshwaters are directly or indirectly essential to the functioning of all global biomes and therefore human populations, knowledge of how freshwater ecosystems function is crucial in order to predict or explain perceived or real impacts.

The use and demands placed on freshwater systems vary globally, depending on availability of water resources, but are most commonly related to agriculture (70%), industry (20%) and domestic (10%) uses (Collen et al., 2014). From the national perspective, Scotland is not a country that is short of freshwater. Some 2% of the land area is covered by freshwater systems (0.6% in England and 0.52% in Wales), with 50,000 km of running waters interconnected by 27,000 lakes (Maitland, 2007), and numerous ponds and wetland habitats spread almost continuously throughout the country (Fig. 1.1). These systems are important as they provide cultural, aesthetic, symbolic and mythical values; but they are also of major economic importance and value due to the ecosystem services they provide e.g. hydropower, irrigation, recreation and sustenance, that are ultimately beneficial to mankind. For example, conservation of endangered species such as the freshwater pearl mussel (*Margaritifera margaritifera*), may have cumulative, positive effects on water quality through increased filtration of fine particles, which may in turn may benefit salmon populations as spawning grounds are exposed to less siltation. This may then benefit fisheries, through recreation and food export, thereby contributing to the local economy.



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Although in Scotland, and undoubtedly globally, hundreds of years of straightening, diverting, canalising, pollution, removal, dredging, draining and fragmenting have transformed the catchments into what they are today; generally functioning, but not pristine. The conservation of, reliance on and importance of these systems is recognised by both governmental and non-governmental organisations, and as a result, activities that may impact or influence water courses must conform to strict continental and national guidelines e.g. the Water Framework Directive (2000) and Flood Risk Management Act (2010). This legislation also extends to species management e.g. European Habitats Directive (1992), Birds Directive (2009) and Marine Strategy Framework Directive (2008). Therefore if species are going to be conserved, culled, controlled, translocated or reintroduced it is important that this is based on good scientific reasoning.

1.2 The return of the beaver

1.2.1 *Biology, trials and tribulations*

As a species that has been reintroduced, introduced and translocated, global populations of beavers (*Castor* spp.) have expanded through both legal and illegal means. The reason for human-mediated population growth is often holistic. As humans over-hunted beavers to near extinction in North America, but especially Eurasia, there was a strong desire to return this species to their native habitats, in particular where dispersion would be limited by geographic barriers. Though this sounds honourable it has led to multiple, short-sighted beaver introductions with little responsibility taken by the parties involved after populations have become established. This includes the North American beaver (*Castor canadensis*) being released in Finland, Austria, France, Poland, Russia and Luxembourg. The spread of these non-natives throughout Europe is unknown as they are visually identical to Eurasian beaver (*Castor fiber*), with chemical or morphological differences the most reliable way to tell them apart (although researchers in Norway are currently training dogs to detect differences between the two beavers scent marks (F. Rosell, *pers. comms*. May 2014). Fortunately both species cannot successfully interbreed. The N. American beaver has also been introduced to the Tierra del Fuego region of South America to “economically enhance” the area, but their tree felling and habitat alterations has resulted in increased invasion pathways for exotic plants and caused destruction of the most southerly temperate forest ecosystems in the world (Anderson et al., 2006). Whether growth in global beaver populations has been human-mediated or occurred through natural dispersal (i.e. in continental Europe or parts of N. America), it is the robustness and adaptability of the beavers themselves that has undoubtedly led to the ‘success’ of most (re-)introductions. As even when only a handful are released, escape or disperse into a new area, they possess unique abilities to modify their habitat and have a broad, yet specific, diet that allows them to thrive in a variety of freshwater habitats.

Both beaver species are typically monogamous throughout their lifetime (living 8-10 years in the wild) producing 2-3 kits per year, though *C. canadensis* has a higher fertility rate with a greater percentage of females, both sub-adult and adult, reproducing per year (Müller-Schwarze and Sun, 2003). Beavers occupy freshwater habitats (e.g. streams, rivers, lakes, ditches and ponds) as family groups consisting of a breeding pair, young of the year (kits), yearlings and occasionally sub-adults. Sub-adults will disperse or be expelled usually after 2 years, with a family group typically then numbering 6 individuals (Müller-Schwarze and Sun, 2003). During the occupation of a site, which may last from 5-50 years depending on resource availability, beavers will forage on a vast range of terrestrial and aquatic vegetation with riparian feeding initially concentrated close to the water’s edge. The bark from trees is their primary source of nutrition and in order to obtain this resource they will fell trees. As the distance from the water’s edge increases beavers will become choosier, selecting for specific species, particularly aspen (*Poplar* spp.), willow (*Salix* spp.) and birch (*Betula* spp.), and sizes (a lower probability of selection of smaller saplings) (Haarberg and Rosell, 2006). When and where available, beavers will also consume a variety of aquatic plants, that are supplementary to their woody diet and may allow beavers to subside in marginal habitats (Milligan and Humphries, 2010). In areas with high seasonal variation, e.g. high latitudes that experience long, cold winters, beavers will be more obliged to cache spare foraged branches and twigs at the water’s edge or underwater, as these can be consumed throughout the winter with the latter accessible underwater during ice cover. This input of woody debris can affect local physical habitat structure and benefit macroinvertebrates, but the impact of woody debris caches are minor in comparison to the structures beavers are most often associated with; woody debris dams (Fig. 1.2).

Fig. 1.2 An example of one of a series of beaver-constructed dams on an agricultural ditch through the Bamff estate, Perthshire, raising the water table, altering water flow and creating a series of step-pool profiles (© Alan Law, March 2012).

Using stripped branches, rocks and mud beavers create one or more of these dams on small streams to stabilise water levels, therefore their lodge entrance remains consistently under water and terrestrial predators, such as bears, wolves, lynx or badgers, have a reduced chance of accessing the lodge. Dams can be constructed on ponds and lake outflows, but are generally not as well maintained or necessary as water levels are already relatively stable. By increasing the water levels, particularly in low gradient areas, the surrounding habitat becomes flooded. Beavers are then able to float felled tree branches to feeding sites or caches with ease. Dams need to be regularly maintained if they are to withstand seasonal rainfalls and may be extended and enlarged by one or many beaver families. Poorly built dams may be demolished within one season, but as dams can be continuously re-worked they may persist for decades and have potentially shaped the physical and biological landscape throughout historical beaver ranges. Stripped tree branches packed with mud are used in the construction of a beavers' lodge, where a beaver family resides. Lodges may start small (1 m^2), but can reach large sizes if an area is consistently occupied (Fig 1.3). The changes in physical habitat and biological composition through the input of woody debris, alteration of local hydrology and selective terrestrial and aquatic foraging creates a highly heterogeneous environment that affects multiple flora and fauna assemblages. This ability to modify ecosystems is recognised as a natural disturbance that has been missing from many temperate freshwater environments and one the main scientific reasons for the reintroduction of beaver in Europe and N. America.

Fig 1.3 A beaver lodge in Pershyttan, Sweden, constructed from beaver-stripped branches and packed with mud. Over time plant propagules from the beaver-disturbed sediment will develop on the lodge further solidifying the structure (© Alan Law, July 2012).

1.2.2 *The reintroductions of beaver to Scotland*

Beavers were extinct in Scotland by the 16th century, primarily due to overhunting. However, there has been a strong desire to restore them since the 19th century, with several attempted private reintroductions of both Eurasian (*Castor fiber*) and North America beaver (*Castor canadensis*) (Kitchener, 2001). These efforts did not succeed, either due to low survivability, project abandonment or because, in one case “the lordship [of Rothsay, Isle of Bute] wished to send the fisheries exhibition specimens of the beaver and so ransacked the enclosure” (Lever, 1977).

A more practical and legally thorough process of reintroduction was first mooted in the early 1990’s by informal discussions between scientists and practitioners (D. Halley, pers.

comms.), with literature emerging by the mid-90's further encouraging reintroductions (MacDonald, 1995). Over the next decade, a detailed process of reviews, recommendations and criteria were compiled, in line with obligations on the UK Government under Article 22 of the European Council Directive 92/43/EEC (the 'Habitats Directive'), to consider the desirability of reintroducing certain species (listed on Annex IV), including Eurasian beaver (Conroy and Kitchener, 1996; Daniels et al., 2000; MacDonald et al., 1997; Rushton et al., 2002; Webb et al., 1997). Despite these efforts, the application for a licence to permit reintroduction was rejected in 2005, as there was no clear exit strategy in the face of perceived threats to native species from a full-scale reintroduction.

The reintroduction of beaver to Britain was therefore amended to a trial basis (over 5 years), and allowed animals to be re-housed in captive locations in Britain in the event of significant and unsustainable damage, economic loss in the trial area or if project/damage/management costs significantly exceeded expectations. The re-evaluated reintroduction project was received in May 2008 and accepted by the Scottish government. A reintroduction licence was granted to the Scottish Wildlife Trust and the Royal Zoological Society of Scotland with Scottish Natural Heritage coordinating the independent, scientific monitoring that was a condition of the licence. In May 2009, the Scottish beaver trial commenced when beavers, imported from Norway and quarantined in England, were officially released to areas within Knapdale Forest, mid-Argyll, with 4 family groups (2-4 individuals) occupying 4 lakes by summer 2010 (Fig. 1.4).

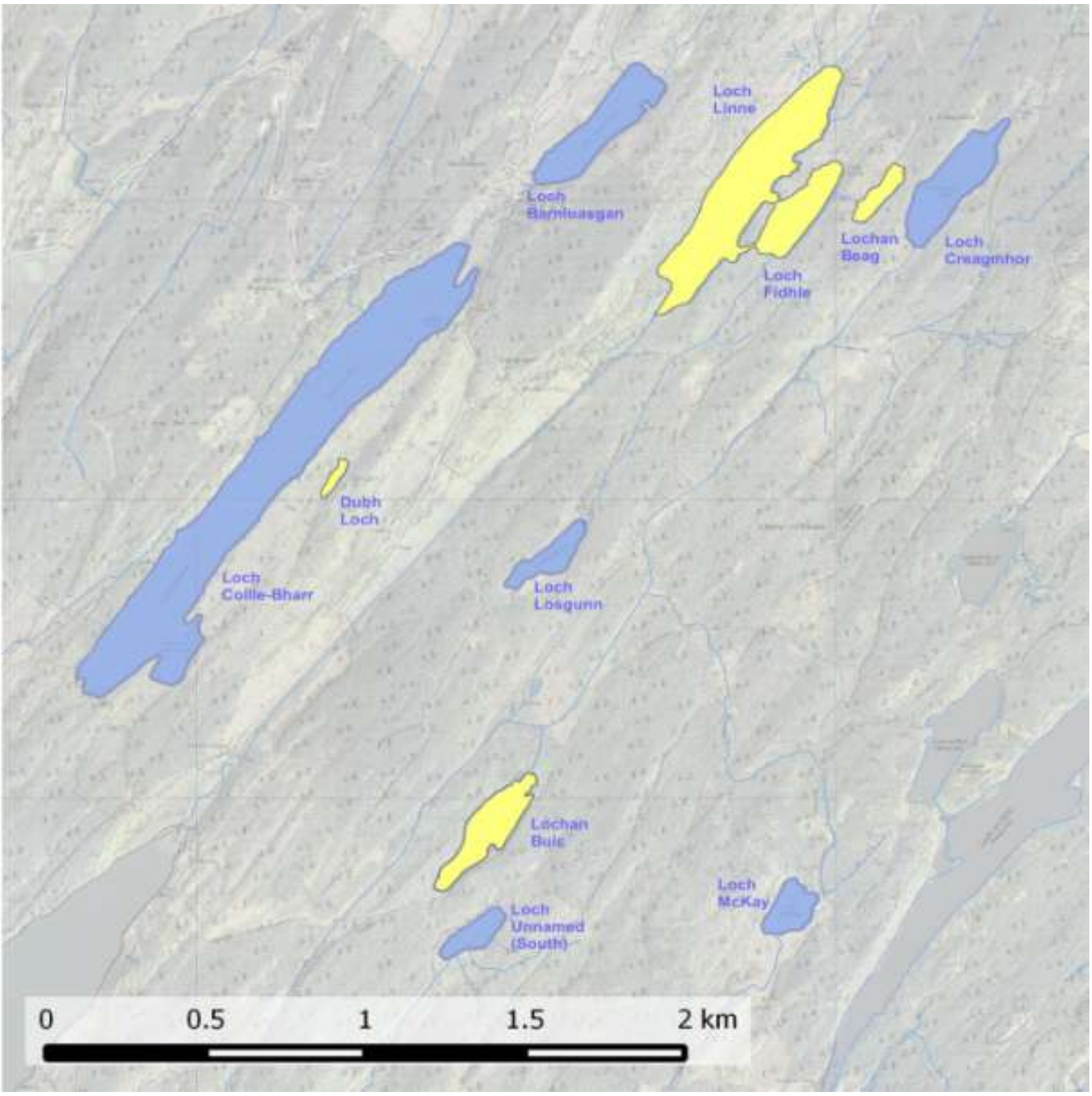

Fig. 1.4 Location of the lochs occupied (yellow) and unoccupied (blue) by beavers during 2011-12 at the official Scottish Beaver Trial, Knapdale. Background OS tiles reproduced from Ordnance Survey map data by permission of Ordnance Survey, © Crown copyright.

However, this process was not quick enough for some beaver enthusiasts, with private estates in the Perthshire e.g. the Bamff estate (Fig. 1.5) and Beauly regions embarking on independent beaver demonstration/education projects as early as 2001 using beavers privately obtained from Bavaria or captive populations in England. The subsequent escape of animals from these and other private collections, perhaps supplemented by deliberate release, has resulted in a feral population of ~150 beaver now present on Tayside (Campbell et al., 2012). The legislative and practical implications of these 'unofficial reintroductions' has been covered in numerous articles and reports (e.g. Jones 2006, Gaywood *et al.* 2008, Jones *et al.* 2013), and have understandably caused some tension, albeit temporally, between the public and governmental organisations. Further information on the politics of this situation is not integral to this thesis.

Fig. 1.5 The location of the pond (purple) and stream (blue) sites at the Bamff estate, Perthshire, Scotland used in chapters 4 and 6 respectively. Background OS tiles reproduced from Ordnance Survey map data by permission of Ordnance Survey, © Crown copyright.

The reintroduction of beavers is particularly interesting as they possess a unique ability to modify ecosystems through dam building (Fig. 1.2) and selectively felling trees (Fig. 1.6), although this also makes their reintroduction potentially controversial. Ecosystem engineering by beavers has been widely recognised as providing local and landscape benefits to multiple and diverse taxon groups through habitat modification and creation, therefore restoring natural discontinuity and heterogeneity to landscapes (Rosell et al., 2005). Yet, objections are raised, in particular from fisherman and riparian landowners, as dams may impede fish migration, especially salmonids, destroy spawning habitat, flood arable land or block culverts, and tree felling can be viewed as destructive. Unfortunately, the answers to these problems will not be fully resolved by the Scottish Beaver Trial, or indeed by subsequent research. For example, the beaver-salmonid debate has rumbled on throughout Europe and North America since the 1930's, with no general globally applicable, conclusive results (Kemp, 2010). However, being pro-active with research whilst identifying and mitigating anthropogenic pressure on wildlife is crucial to alleviate concerns and an essential component of species management. Therefore as a trial reintroduction, partly based on the ability of beavers to restore habitats, assessing the effects of 'ecosystem engineering' is crucial from both a legislative and holistic perspective.

Fig. 1.6 A series of willow (*Salix* spp.) stumps exhibiting unmistakable signs of selective felling by beaver at the Bamff estate, Perthshire (© Nigel Willby, December 2002).

1.3 Overview of research aims and hypotheses tested

The work carried out for this thesis may aid the decision in 2015 as to whether beavers will be formally, fully reintroduced to Scotland, since evaluation of their effects has been carried out within several geographical areas and at different scales. These included the official trial area at Knapdale where beavers were introduced in 2009, a private estate in upper Perthshire where beavers have been present since 2002, and central Sweden, where beavers were reintroduced almost 100 years ago (detailed site descriptions are given in each specific chapter).

Both aquatic plants and macroinvertebrates are particularly responsive to hydrological and physical habitat changes generated by beaver dams, whilst aquatic plants, which are important agents of habitat diversity in ponds and wetlands, are selectivity foraged by beavers. Therefore the data presented allows for comparisons and contrasts to be made of the effects of beavers on aquatic plant and macroinvertebrate biodiversity and composition at contrasting spatial and temporal scales.

The data gathered for this thesis are written up as 5 chapters, consisting of a literature review on direct and indirect effects of beavers on aquatic plants (Chapter 2), followed by a series of four research manuscripts. Chapter 3 documents the selectivity and impact of beaver foraging on water lilies by quantifying biometric relationships between lily organs and predicting the size of lily pads removed from leftover plant stems (petioles). Chapter 4 documents medium (9 years) vs. short-term (1 year) effects of beaver herbivory on aquatic plants using repeat surveys, exclosures, and cafeteria style experiments. Chapter 5 evaluates differences in aquatic plant and beetle assemblages between beaver-created and permanent wetlands (unformed by beavers). Chapter 6 documents changes in aquatic macroinvertebrate richness and composition as a result of beaver dams modifying stream hydrology. The final chapter (Chapter 7) discusses the implications of research conducted in this thesis whilst predicting future research and areas of conflict.

CHAPTER 2 – Indirect and direct effects of beavers alter richness, composition and diversity of aquatic plants

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2.1 Introduction

The impact of animal foraging on biomass and composition of aquatic plants was traditionally considered benign in the functioning of aquatic food webs. This was until a seminal paper by Lodge (1991), concluded that “aquatic plant biomass, productivity, and relative species abundance is dramatically changed by grazing” with large effects on the ecosystem. Subsequently, it has been estimated that approximately 51% of annual primary productivity is removed by aquatic herbivores; three times more than terrestrial herbivores (Cyr and Face, 1993). Numerous studies have since been conducted, detailing the foraging patterns, preferences and impacts across several faunal groups, e.g. mammals (Guichon et al., 2003; Smirnov and Tretyakov, 1998), fish (Søndergaard et al., 2008), crustaceans (Momot, 1995), insects (Cronin et al., 1998; Pieczynska, 2003), birds (Tatu and Anderson, 2007), on both native and introduced plant species. In addition to documented abiotic controls e.g. riparian shading, water temperature, light, nutrient availability, water movement (Bornette and Puijalon, 2011), top-down effects of grazers are thus increasingly recognised as an important controlling influence on aquatic plants in freshwater systems (Parker, Caudill & Hay 2007; Wood *et al.* 2012; Law, Jones & Willby 2014). Therefore, plant-herbivore interactions, both direct and indirect, should be considered integral to normal ecosystem functioning.

Both extant species of beaver (Eurasian *Castor fiber* and North American *Castor canadensis*) are an exceptional example of how a species can influence aquatic plant biomass and community structure. As a keystone organism and ecosystem engineer (Jones et al., 1994), beavers possess the unique ability to build woody debris dams on small-to-medium rivers, thereby increasing, and stabilising water levels, and creating areas of open water that may be colonised by a range of aquatic plants, invertebrates and vertebrates (McDowell and Naiman, 1986; Nummi and Holopainen, 2014; Ray et al., 2001). Rosell *et al.* (2005) briefly summarised the indirect effects of beavers on aquatic plants in relation to the effects of damming and subsequent succession, although multiple studies have since document the alteration of aquatic plant diversity and composition through direct, selective foraging by beavers (e.g. Parker *et al.* (2007); Law, Jones & Willby (2014)), it is timely to review both the direct and indirect impact of beavers with respect to aquatic vegetation. Additionally, beaver populations continue to expand to their former and new ranges due to low hunting pressure, legal protection, low demand for derived resources (i.e. castoreum and fur) and continued reintroductions (Halley and Rosell, 2002). This paper aims to evaluate the findings of previous studies in terms of both direct and indirect effects of beavers (*Castor* spp.) on aquatic vegetation in order to document, contrast and predict potential effects.

2.2 Methods

A literature search using Google Scholar and Web of Science was conducted to find all data-derived, peer-reviewed and ‘grey’ literature (e.g. Ph.D. and Master theses) that explicitly refers to the direct or indirect effect of beaver on aquatic vegetation. The search terms used were: beaver AND aquatic plants, beaver AND aquatic vegetation, beaver AND macrophyte, *Castor fiber* AND aquatic plants, *Castor fiber* AND aquatic vegetation, *Castor fiber* AND macrophyte, *Castor canadensis* AND aquatic plants, *Castor canadensis* AND aquatic vegetation, *Castor canadensis* AND macrophyte and beaver aquatic forage.

A database was compiled with the authors, article title, year, journal, location, type of beaver effect (direct or indirect) recorded and the strength of effect based on categories; 0 = no effect, observation or N/A, effect of beaver activities were not quantified or not applicable (e.g. cafeteria experiment); 1 = local effect, biomass of plant/s effected within the study patch or site and; 2 = landscape level effect, with both the physical and biological habitat and surrounding area significantly modified (Appendix 2.1). Articles citing retrieved literature and references within were thoroughly searched for additional, relevant material and incorporated into the database. Only original research articles or field observations were included in the database, thereby excluding literature reviews and secondary literature i.e. textbooks.

2.3 Results

A total of 46 articles documenting the effects of beaver foraging or engineering on aquatic vegetation were published between 1938 and 2014 (Fig. 2.1). Of these studies, 32 have been conducted in North America and 14 in Europe, with half having been published since 2000. 42 studies were peer-reviewed and published with only 4 being grey.

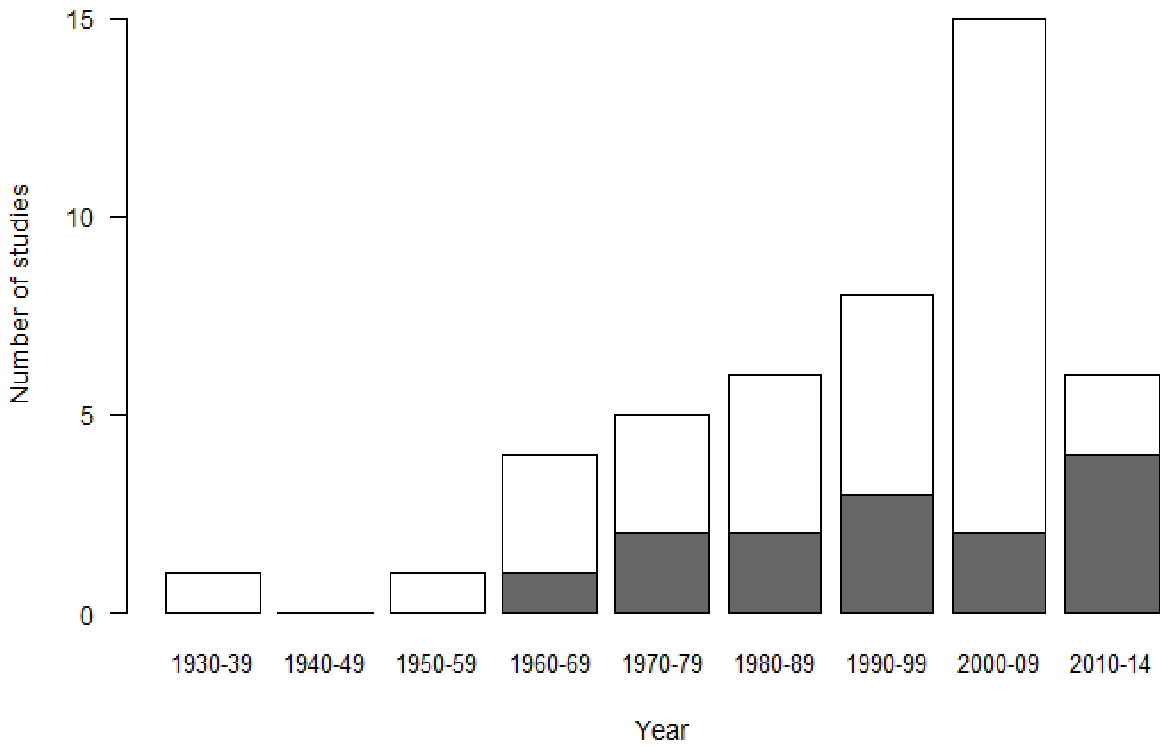

Fig. 2.1 The number of studies considering beaver effects on aquatic vegetation in North America (white bars) and Europe (grey bars) as published since 1930.

The effect of beavers on the environment inhabited was closely associated with disturbance type (Fig. 2.2). For example, direct effects were low or negligible from both N. America and Europe, as many studies used aquatic plants as part of cafeteria experiments e.g. Doucet and Fryxell (1993) used white water lilies (*Nymphaea odorata*) in addition to several tree species to document nutritional quality of foraged species. Indirect effects were mostly reported at the landscape scale and were described more commonly in North American studies (n = 16).

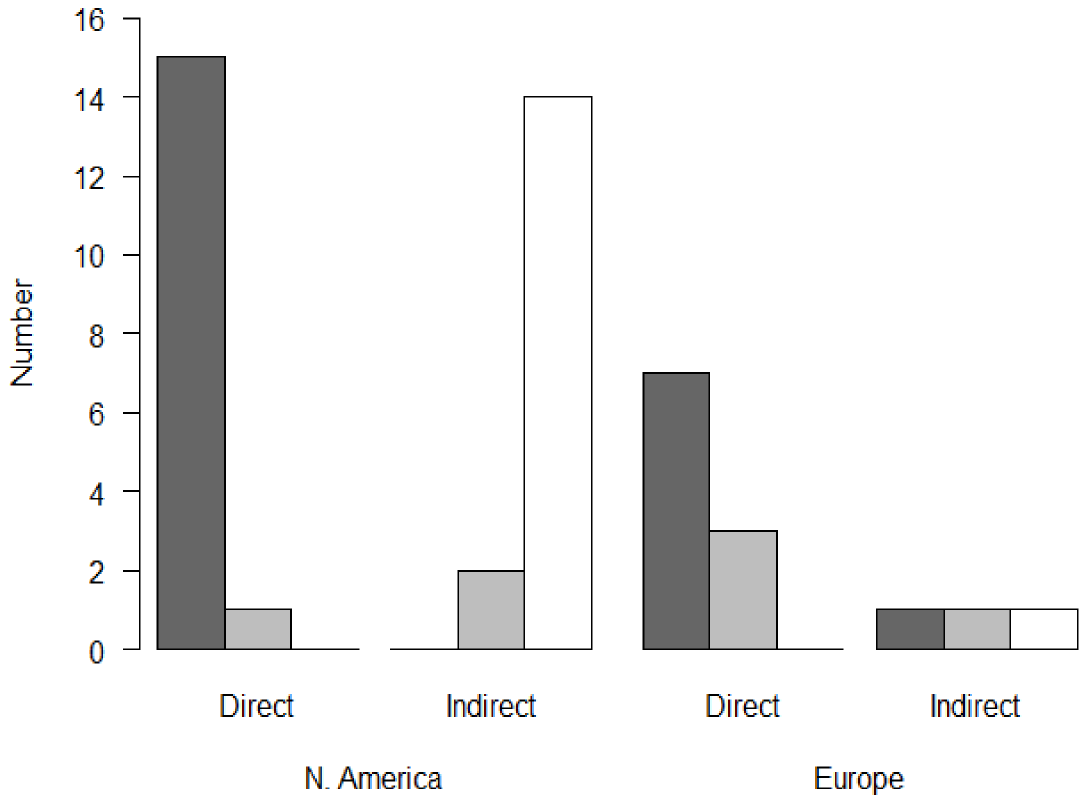

Fig. 2.2 The number of studies reporting not applicable/negligible (grey), local (light grey) and landscape (white) changes per effect type and geographic area.

2.5 Discussion

2.5.1 *Indirect effects*

It has been previously suggested that *C. canadensis* exhibits more building activity (larger or higher density of dams) than *C. fiber* (Danilov and Kan'shiev, 1983). Though this is not substantiated where both beaver species co-occur i.e. Finland, where North American beavers were accidently introduced before the confirmation that there were two different species (MacDonald, 1995; Rosell et al., 2005). The idea of more substantial building activity may be perpetuated by the bias of research towards N. America that describes landscape-wide effects from beaver constructions. The strength of beaver impact could be associated with the desire to study it, but as the majority (94%) of studies conducted in N. America make effective use of historical aerial photography and maps, they are based on an excellent knowledge of land usage in comparison to other geographic regions (e.g. Johnston & Naiman (1990); Bonner *et al.* (2009)). Landscape scale, indirect studies often report both spatial and temporal effects, but the resolution, in terms of changes at the plot scale, is low in comparison to semi-quantitative studies at a few sites e.g. North America (Ray *et al.* 2001) and Scotland (Law, Jones & Willby 2014), which may explain the lack of beaver effects reported at a local scale.

Studies documenting the indirect effect of beavers on aquatic vegetation attribute changes to a number of activities. For example, selective felling of trees may trap water-borne propagules thereby promoting plant establishment (Johansson and Nilsson, 1993), while canopy gaps created by felling may increase abundance and diversity of aquatic plants due to reduced shading and greater light penetration to the water column (Elmeros et al., 2003). But the majority of studies documenting effects of beaver on aquatic vegetation attribute changes to the indirect effects of beaver-constructed dams (e.g. Remillard *et al.* (1987); Little *et al.* (2012)). Damming of streams and rivers is essential for beavers to ensure that the entrance to the lodge remains underwater, therefore the newly-created ponds behind dams will provide beavers with greater protection from terrestrial predators, ease travel and food transport and food caches may be stored underwater (Jones et al., 2009). A predictable sequence of environmental changes and vegetation succession will then occur within the newly-created beaver ponds, regardless of study area (Nolet, 1997; Rosell et al., 2005).

The construction of a dam will almost immediately raise and stabilise water levels, creating lentic conditions, flooding the surrounding forest which leads to tree death and eventual toppling (Johnston, 2012). In ponds or peatlands, raising of water levels may temporarily remove mat vegetation by straining the attached roots and petioles which may break leading to new patches of open water (Ray et al., 2001). In flooded terrestrial areas, the initial establishment of aquatic plants will be dependent on dam stability or the substrate quality. Sediments may be anoxic, with high concentrations of dissolved organic carbon and high volumes of detritus associated with decaying terrestrial vegetation (allochorus), and therefore may not be initially ideal for aquatic plant growth (Elmeros et al., 2003). But over time and without further, major changes in the water level, newly inundated terrestrial vegetation will be replaced by primary aquatic colonists with the exact species dependent on the composition of the regional species pool and its inter-habitat connectivity. This colonisation occurs via indirect dispersal (e.g. beavers or wildfowl), dormant wetland seed banks (Brzyski & Schulte 2009) and direct hydrochory from upstream and is regulated by individual plant characteristics (e.g. easily uprooted, buoyant or no roots). Thus pond proximity to neighbouring freshwater systems is of major importance (Ray et al., 2001). Primary colonists are often free-floating macrophytes (e.g. Lemnaceae, *Utricularia* spp. (Ray et al., 2001)) and pondweeds (e.g. *Potamogeton natans* and *P. obtusifolius*) which form large and long-lived seed banks (Willby, Perfect & Law, 2014). The rate of succession will also depend on the productivity of the system, with establishment likely to be faster in highly productive systems as nutrient limitation of pioneer species will be reduced (Ray et al., 2001).

If beaver ponds remain stable, submerged, floating-leaved and emergent plants will start to colonise, with shade-tolerant species also present beneath the floating canopy (McMaster and McMaster, 2001). Composition now depends on species interactions, e.g. adaptations to efficiently capture light, or expansive rhizomes that exploit nutrients within sediments (Ray et al., 2001). Continued disturbance by beavers, e.g. foraging, felling, water level changes and sediment movement, may selectively inhibit species indicative of mature, pristine ponds e.g. Ray et al. (2001) noted the complete absence of *Nuphar luteum variegatum* from mature beaver ponds, most likely related to foraging (by beaver and deer) and continued physical disturbance. However, structures unique to beaver ponds may also become colonised e.g. canals used for forage transport, or submerged wood caches d (A. Law, pers. obs.). In relation to unmodified streams these lentic aquatic environments support a greater biomass and diversity of aquatic plant species, whilst altering landscape composition and increasing species richness (Wright et al., 2002). Further succession may occur if resources become scarce and beavers vacate an area, leading to full or partial dam collapse and the exposure of sediments. These typically become vegetated by sedges and rushes, a successional stage known as a beaver meadow (Snodgrass, 1997; Wright et al., 2003). Indirect effects of beaver will therefore alter the spatial structure of occupied sites and landscapes, but as these modified or created wetlands may persist for many decades (Bonner et al., 2009), their effects could have been sculpting aquatic plant composition for hundreds of years.

2.5.2 *Direct effects*

In lakes, water levels are relatively stable compared to river systems where seasonal, heavy rainfalls may lead to large variations in water level and flow, therefore the creation of habitat transforming dams by beavers is rarely necessary (Müller-Schwarze & Sun 2003; Law, Jones & Willby 2014). It is within such systems that the effects of direct beaver foraging on aquatic plant communities will be most apparent. In the majority of beaver-based foraging studies direct effects and behaviours are predominantly inferred from conspicuous gnawing of terrestrial wood (e.g. Haarberg & Rosell (2006) and Raffel *et al.* (2009)). This is most likely due to the ease of identifying beaver foraged wood or stumps, relative to broken aquatic plant fragments that may leave little trace. However, as woody plants are the main staple of beaver diets year round, with aquatic plants being consumed only when available (Svendsen 1980; Müller-Schwarze & Sun 2003), their dietary contribution may be underestimated. Relative to indirect impacts, the effect of direct foraging on aquatic plants appears to be minor (Fig. 2.2), yet standing water systems present an opportunity to observe selectivity, behavioural adaptations and interactions between plants, all of which may contribute to temporal biodiversity. The importance of aquatic plants to beaver should not be underestimated, as they are reported to comprise 60 to 90% of summer nutrition (Milligan and Humphries, 2010) with animals spending 40-90% of their time consuming them during the growing season (Svendsen 1980; Gurnell 1998; Müller-Schwarze & Sun 2003). Beavers may even consume aquatic plants in preference to woody material if available (Doucet and Fryxell, 1993; Jenkins, 1979; Northcott, 1971). Therefore supplementing their diet with aquatic plants may be beneficial as it increases habitat flexibility and reduces strict dependency on an optimal supply of riparian woody material.

As foraging generalists, beavers consume multiple food types, in particular aquatic plants, since these are easily accessible and often abundant. But preferences will vary seasonally and between individual animals and families. For example, Shelton (1966) observed beavers from different families choosing plant species that naturally grew at their site of origin over the species that were absent and offered by researchers. Therefore, choice will be related to recognition and local availability, but may also be dependent on minimising intake of potentially harmful compounds that plants have evolved to act as grazing deterrents. For example, willow was selected in favour of other deciduous trees to avoid resins (Bryant and Kuropat, 1980), and younger lily pads, which are rich in anthocyanins, were avoided in favour of large pads (Law, Bunnefeld & Willby 2014). Differentiation will also occur within aquatic plant species according to organs, e.g. lily (Nymphaeaceae spp.) flowers and pads may be directly consumed (Histol, 1989), whereas rhizomes may be cached for later consumption (Milligan and Humphries, 2010). However, above-ground biomass may be discarded in favour of rhizomes in *Schoenoplectus lacustris* and *Cladium mariscus* (Willby, Perfect & Law, 2014). As cut plant biomass may spoil in comparison to woody vegetation, most species are not cached, but consumed *in situ* (Svendsen 1980), rather than being returned to a central place for consumption, as documented for woody material in terrestrial environments (Haarberg and Rosell, 2006; Raffel et al., 2009).

The cumulative effect of selective browsing is likely to significantly reduce plant biomass whilst altering communities, due to localised reductions in preferred potentially dominant rhizomatous species which increases plant diversity and evenness (Law, Jones & Willby, 2014). Desirable plants may also associate with less palatable plants that physically or chemically deter herbivory (Parker et al., 2007) and competitively inferior grazer-resistant species may increase in response to grazing (Law, Jones & Willby, 2014). Foraged plants may also alter growth form or reproductive strategy, e.g. normally clonal species may be stimulated to divert resources to reproduction rather than biomass accumulation (Brzyski and Schulte, 2009). The volume of aquatic plants consumed by individual animals will be dependent on the type of freshwater system occupied. Aquatic vegetation is typically less developed, with lower abundance, in river systems compared to ponds and lakes (Milligan and Humphries, 2010), therefore beaver foraging effects may be less apparent (e.g. Elmeros *et al.* (2003)). Aquatic foraging is likely to be greater if riparian access is limited (e.g. during ice cover) or when preferred tree species are scarce

(Müller-Schwarze and Sun, 2003). Quantitative studies, based on histological analysis, of beaver diet are rare. Krojerová-Prokešová *et al.* (2010) found low volumes of aquatic vegetation in the diet of a population of riverine beavers which was assumed to reflect the limited availability of aquatic vegetation in the studied lotic habitats. Comparable histological studies in lentic habitats, or lotic habitats with greater volumes of aquatic plant biomass, may reveal contrasting patterns.

Aquatic plant consumption will also be subject to local climatic influences. For example, where climatic variation is low foraging on aquatic plants may occur throughout the year and, as a result, beavers may cache food only rarely (Brzyski and Schulte, 2009; Hartman and Axelsson, 2004). By contrast, in highly seasonal, sub-arctic boreal forests, above-ground biomass may only be available in summer months (Milligan and Humphries, 2010). Therefore, highly organised food caches are necessary for winter survival (Hartman and Axelsson, 2004). The presence of kits may also influence time and volume of aquatic plants consumed. For example, Svendsen (1980) noted sub-adults and kits spending more time feeding on aquatic and emergent plants than adults. This could be because kits rarely venture onto land, instead relying on parents and older siblings to supply food until they are able to forage themselves (Müller-Schwarze and Sun, 2003). However, Roberts & Arner (1984) found no difference in food utilisation between either sex or age from histological analysis of captured beavers.

Although foraging effects on aquatic plants are variable, they have clear importance as a food resource to beavers, even as a substitutable part of the diet (Law, Bunnefeld & Willby 2014). Of the literature reviewed in this study, low impacts of direct grazing were observed as aquatic plants were often used as part of cafeteria experiments; therefore beaver effects on assemblages and biomass at a larger scale were not determined in many studies. General effects of beaver foraging depend mostly on the type of system occupied and the species present at the site. However, the productivity of these systems is rarely taken into consideration, which may offset foraging rates and impacts (Danell 1996; Law, Jones & Willby 2014).

2.6 Conclusion

The combined, and potentially cumulative, effects of both indirect and direct impacts on aquatic plants are often stated to increase species richness, diversity and evenness, whilst modifying composition, temporally and spatially, at the local and landscape scale. Further, research may be useful in determining inter-species forage preference and impact at a range of latitudes, habitat types and site fertility. This should include the use of histological and stable isotope analysis for multiple individuals through time. Future studies may also consider the indirect or direct impacts of an altered aquatic plant assemblage on lower biological orders e.g. micro-invertebrates.

CHAPTER 3 – Beavers and lilies: selective herbivory and adaptive foraging behaviour

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Author comments: AL and NW jointly developed the project concept. Field data collection was carried out by AL and NW with lab work carried out by AL. The manuscript was prepared by AL with comments from NW and statistical guidance from NB. When published in the journal *Freshwater Biology*, it carried a picture on the journal front cover of a beaver consuming lily pads. Subsequently, the paper won 1st prize of PhD papers within the departmental internal symposium, and the data/statistical techniques are also being used as a teaching resource by Alain Zuur (Highland Statistics). The results were also presented at the 6th International Beaver Symposium in Croatia (September 2012).

3.1 Abstract

With the global population of beavers (*Castor* spp.) increasing, and reintroductions widespread, it is crucial to be able to predict potential impacts on flora and fauna based on defined foraging behaviours. *Nymphaea alba* (white water lily) is regularly consumed by beavers and provides a model system to test selective foraging behaviour and quantify potential impacts on aquatic resources in standing water habitats. Using biometric relationships within *N. alba* pads we accurately reconstructed the size and weight of consumed pads, demonstrating that Eurasian beavers (*Castor fiber*) selected pads that were significantly larger and heavier than unselected pads. By selecting larger leaves beavers may also avoid chemical defences associated with anthocyanin pigments that dominate in smaller leaves. Grazing was concentrated in shallow depths (55.7 ± 10.7cm) close to the shore (2.95 ± 0.62m) relative to un-grazed plots (100.5 ± 9.2cm; 4.79 ± 0.68m). The level of selectivity was unchanged with increasing distance from a central feeding place. Beavers removed 24-50% of pads within grazed areas, but relative to the whole *N. alba* leaf pad resource the impact of this foraging was low (0.38-1.23% loss). Plant species diversity was unaffected by foraging and there was no evidence of indirect effects on non-targeted *N. alba* pads or flowers. When foraging in the aquatic environment, beavers are highly selective and can have a minor effect on food resources whilst feeding optimally and opportunistically. Since beavers demonstrate adaptive foraging strategies depending on their foraging environment this knowledge should be incorporated into future decisions on further reintroduction or habitat restoration programmes.

3.2 Introduction

The ability to predict and quantify potential environmental impacts by species based on defined habitat requirements and foraging behaviours should improve judgment when species management decisions need to be made (Caro, 2007). Populations of Eurasian (*Castor fiber*) and North American (*Castor canadensis*) beaver are stable or now increasing as a result of formal and informal introductions, reintroductions and natural dispersal (Naiman, Johnston & Kelley 1988; Halley & Rosell 2003, Linzey, Hammerson & Cannings 2011). Early reintroductions were motivated by fur-harvesting (Halley and Rosell, 2002) but later programmes have sought to exploit the potential of beavers to create or restore habitat heterogeneity in degraded freshwater and riparian habitats, through dam building and selective tree felling (Burchsted et al., 2010; Smith and Mather, 2013). The wider, desired impacts of beaver reintroduction are often to restore natural biodiversity and re-establish their role as a keystone organism, although benefits from ecotourism may also occur (Kemp et al., 2011). As a result of their habitat restoration potential, beavers have received considerable attention in the past 20 years, with many planned reintroduction areas guided by density of preferential forage species (Nolet and Rosell, 1998) (e.g. aspen and willow), interconnectivity of freshwater habitats (South et al., 2000) and physical habitat characteristics (Fustec et al., 2001; Gurnell, 1998; MacDonald et al., 2000; Pinto et al., 2009).

As semi-aquatic herbivores, terrestrial forays are energetically costly for beavers (due to time spent selecting, felling and removing items) and increase vulnerability to predation; efficient use of foraging time on land is therefore essential (Fryxell and Doucet, 1991). Depending on the distance from the water's edge beavers exhibit selectivity for trees based on trunk size, distance from water and species (Gerwing et al., 2013; Jenkins, 1980), transporting selected items back to the water (i.e. central place foraging) (Haarberg and Rosell, 2006; Raffel et al., 2009). Nevertheless, as opportunistic, generalist herbivores beavers also spend significant periods in spring and summer supplementing a woody diet by consuming aquatic vegetation that is typically rich in protein, sodium and iron (Svendsen 1980; Nolet, Veer & Evers 1994; Milligan & Humphries 2010) and has higher digestibility than terrestrial vegetation (Belovsky, 1984; Doucet and Fryxell, 1993). The importance of aquatic vegetation to beavers, and indeed other aquatic rodents, should not be underestimated. Muskrat (*Ondatra zibethicus*), coypu (*Myocastor coypus*) and capybara (*Hydrochoerus hydrochaeris*) all consume significant volumes of preferred aquatic plants, often significantly reducing their abundance (Corriale et al., 2011; Danell, 1996; Johnson and Foote, 1997), though the contribution of woody vegetation to the diet of these species is minimal. Within lentic environments aquatic plants are an easily accessible and reliable food source to mammalian herbivores even outside the growing season. For beavers, this aquatic resource requires less search and handling time than woody material on land since the cost of travel to foraging areas and in conveying selected items are reduced due to their buoyancy in water, whilst predation risk is lowered (Fryxell and Doucet, 1993; Severud et al., 2013). As yet, no beaver reintroduction programmes have formally considered aquatic vegetation as an important resource or studied any associated foraging behaviours. This is perhaps because the aquatic resource can be more difficult to quantify (Howard and Larson, 1985) relative to conspicuous tree coppicing. Therefore population and energetic models are likely to be underestimating the dietary importance of aquatic vegetation when predicting survival and persistence (South et al., 2001; Webb et al., 1997).

The consumption by beavers of water lilies (Nymphaeaceae spp.), particularly *Nymphaea alba* or its North American equivalent *Nymphaea odorata*, provides a model system in which to study aquatic foraging behaviour and associated impacts. Lilies are a major component of the vegetation of shallow lakes and ponds in temperate and boreal regions, with leaves, rhizomes and flowers all frequently mentioned in accounts of the diet of beaver (Doucet and Fryxell, 1993; Jenkins, 1980; Nolet et al., 1994; Northcott, 1972; Roberts and Arner, 1984; Severud et al., 2013). The floating blades (henceforth referred to as pads) are typically severed by beaver and then transported to a central place (e.g. shoreline or lodge) for consumption, leaving the petiole projecting above the water surface and still attached to the buried rhizome. These petioles are easily recognised and, through simple biometric relationships, provide a means to reconstruct the size of pads removed by beavers.

We tested the following hypotheses: (1) beaver forage selectively on *N. alba* pads based on their size and weight, (2) pad selection is based on depth and distance, (3) the impact of foraging on the *N. alba* resource occurs at different scales and (4) aquatic foraging behaviour of beavers is different to accepted foraging models developed for terrestrial environments.

3.3 Methods

3.3.1 *Site*

The study took place in the Taynish and Knapdale Woods, on the west coast of Scotland (Lat: 56° 2'32.06"N, Long: 5°33'22.21"W) during 2011 and 2012. This is a designated Special Area of Conservation due to the occurrence of western acidic oak woodland (*Quercus petraea*) and clear-water oligotrophic to mesotrophic lakes with aquatic vegetation. The site receives approximately 1787mm of rainfall annually, with a mean maximum temperature of 11.3°C and mean minimum temperature of 4.8°C from 1981-2010 (Meteorological Office UK, 2012). In spring 2009, Eurasian beaver families were released as part of a trial reintroduction and by summer 2010 family groups (2-4 individuals) occupied four lakes ranging in size from 0.4 to 16.5ha (Fig. 1.2). Subsequently animals have become established within these or surrounding lakes, exhibiting typical foraging and engineering activities (e.g. felling trees and constructing lodges). To date, incidences of large scale dam building have been rare. The surrounding riparian forest is composed of mixed deciduous species (mainly *Betula pubescens* and *Salix* spp., plus *Sorbus aucuparia* and *Corylus avellana*) backed by *Quercus petraea* or commercially planted conifers (*Picea* spp. and *Larix* spp.). The aquatic vegetation of these lakes comprises substantial stands of emergent (e.g. *Cladium mariscus*, *Schoenoplectus lacustris*, *Phragmites australis*, *Equisetum fluviatile* and *Carex rostrata*) and floating-leaved species (mainly *N. alba* and *Potamogeton natans*) plus a range of submerged plants, in particular the isoetids *Littorella uniflora* and *Lobelia dortmanna* (Willby & Mulet 2010).

3.3.2 *Survey*

In order to document selectivity and impacts of beaver foraging, stands of *N. alba* in the 11 lakes of the Knapdale forest were surveyed in late summer for two consecutive years (Autumn 2011 and 2012) using a 2x2m floating quadrat. Beavers were regularly present in five of these lakes throughout the study period and absent from or only intermittently present in the remaining lakes. In each lake 20 healthy and ungrazed *N. alba* pads of a range of sizes were removed and the mid-line distance (petiole junction to pad tip) and petiole diameter of each pad was measured to the nearest mm and nearest 0.01mm respectively using digital callipers (Fig. 3.1). Petiole diameter of these pads was measured 5-10cm from the base of the pad in accordance with the position at which beavers typically sever the pad. The change in petiole diameter over this length range was negligible (<0.05mm). The remaining sections of petiole were then removed from these pads with a scalpel prior to measuring the wet weight of the pad. Pads were then dried at 60°C for 48 hours and re-weighed. All weights were determined to the nearest 0.01g.

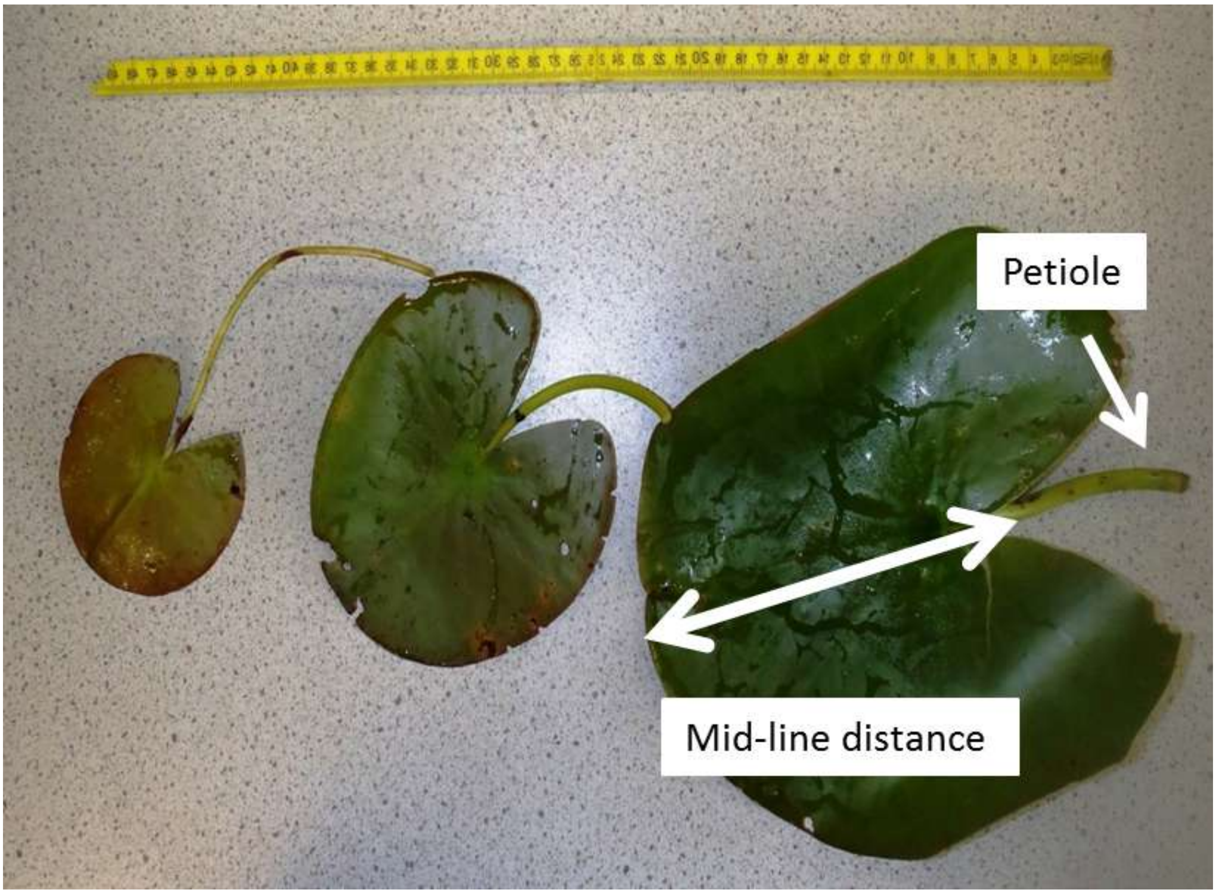

Fig. 3.1 An example of the three pad size categories from *Nymphaea alba* used in this study. Note the greater proportion of green: red pigmentation as the pad size increases (© Alan Law).

Beaver-grazed patches of *N. alba* only became apparent in mid-summer (late July to August) in two lakes (Buic and Beag), with no evidence of prior feeding. Within those patches of *N. alba* where beaver had been actively grazing (principally on the lakes Buic (2011) and Beag (2011-12), between 10 and 20 2 x 2 m quadrats were placed depending on the size of the foraged area. The petiole diameter of each beaver-cut *N. alba* stem in the quadrat was measured. There was no sign of senescence or shrinkage of the remaining petiole, confirming that all leaves had been recently grazed. In addition the water depth, distance from shore, number of *N. alba* flowers, presence of other aquatic macrophyte species and number of surviving *N. alba* pads based on three size categories of mid-line distance; large (>100mm), medium (50-100mm) and small (<50mm), were recorded per quadrat. To predict the dry weight of ungrazed pads ten *N. alba* pads were randomly selected within each quadrat for measurement of midline distance. In each lake a further 20 quadrats were randomly placed within ungrazed *N. alba* stands with the aforementioned variables measured. The mid-line distance of a further 120 pads was measured and the colour, expressed in terms of percentage green vs. red pigmentation (to the nearest 5%), of the dorsal side of each pad was independently visually estimated by three surveyors.

3.3.3 *Statistical analyses*

Relationships between petiole diameter, mid-line distance and dry weight of ungrazed pads were constructed using generalised mixed effect models (GLMM) with a log-link and Poisson error distribution (Winkelmann, 2008) to account for underlying heteroscedasticity of the data (Zuur et al., 2009). Using these models we could predict, with high precision (mean ± 11.5%), the mid-line distance and dry weight of pads removed by beaver, based on the diameter of the projecting petiole from which the pad had been removed. Pad selection was analysed using a GLMM with binomial error distribution and logit-link. Quasibinomial distributions were used to correct for over-dispersion within predicted pad selection models. The relationship between mid-line distance and the mean proportion of pad area pigmented green was derived using a logistic regression.

A weighted mean of pad size and biomass per quadrat was calculated using the number of pads in each size category and the mid value of each size class. These values were then log transformed to meet linear requirements of general linear and linear mixed effect models to assess possible relationships between estimated mean pad size, water depth and grazing impact. Predicted pad sizes or biomass from model outputs were then exponentially back-transformed. Count data of species number and *N. alba* flower density were analysed using

GLMM with Poisson error distribution and log-link. Within all mixed models, lake identity and year sampled were treated as random effects to control for pseudoreplication in the data (Zuur *et al.* 2009). The best performing models were selected using an information theoretic approach (Akaike Information Criterion) (Burnham and Anderson, 2002). Where model explanatory factors were correlated ($P < 0.05$) (e.g. pad mid-line distance with dry weight and depth with distance) one factor was removed from the model (i.e. dry weight and distance). Significance in all models was taken to be $P < 0.05$. Statistical analyses and graphics were produced using R Studio version 0.97 (R Development Core Team, 2013) using the packages lme4 (Bates, Maechler & Bolker 2012), AED (Zuur 2010) and languageR (Baayen 2011).

3.4 Results

3.4.1 N. alba *biometric relationships*

Based on *N. alba* pads collected from lakes where beavers are absent or where there was no evidence of grazing on *N. alba* there was a strong positive relationship between the petiole diameter and mid-line distance of *N. alba* pads ($Z_4 = 647.8$, $P < 0.001$) (Fig. 3.2). The model predicted that mid-line distance was on average within 11.5% of the observed values. There was also a significant positive relationship between *N. alba* petiole diameter and dry weight ($Z_3 = 123.9$, $P < 0.001$), and between pad mid-line distance and dry weight ($Z_3 = 125.6$, $P < 0.001$) (see appendix 3.2.1 and 3.2.2).

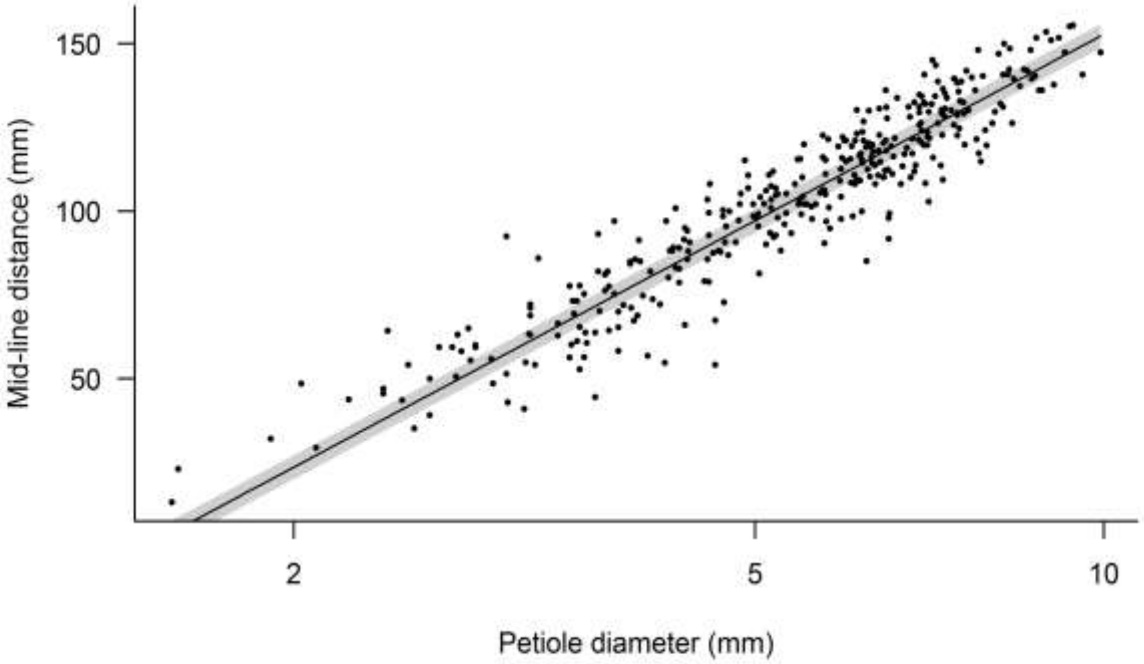

Fig. 3.2 The relationship between *N. alba* petiole diameter and mid-line distance (solid line with 95% confidence intervals, on a log scale) based on pads collected from lakes where beavers are absent or where there is no evidence of grazing.

3.4.2 *Selection* of N. alba *pads by beavers*

When a pad is encountered, the probability of it being grazed increased significantly as pad mid-line distance increased (Z_{480} = 7.12, $P < 0.001$) (Fig. 3.3). From field measurements, pads removed by beaver were of a significantly larger size (114.2 ± 1.6mm) (mean ± SE) relative to unselected pads (92.4 ± 2.0mm). Predicted biomass of selected pads (2.77 ± 0.09g) was also greater than unselected pads (1.75 ± 0.09g). Selected pads were also larger relative to the measured global mean pad size available (106.1 ± 2.7mm, 2.29 ± 0.12g), and larger pads also had significantly more extensive green pigmentation (Z_{115} = 4.627, $P < 0.001$) (Fig. 3.4).

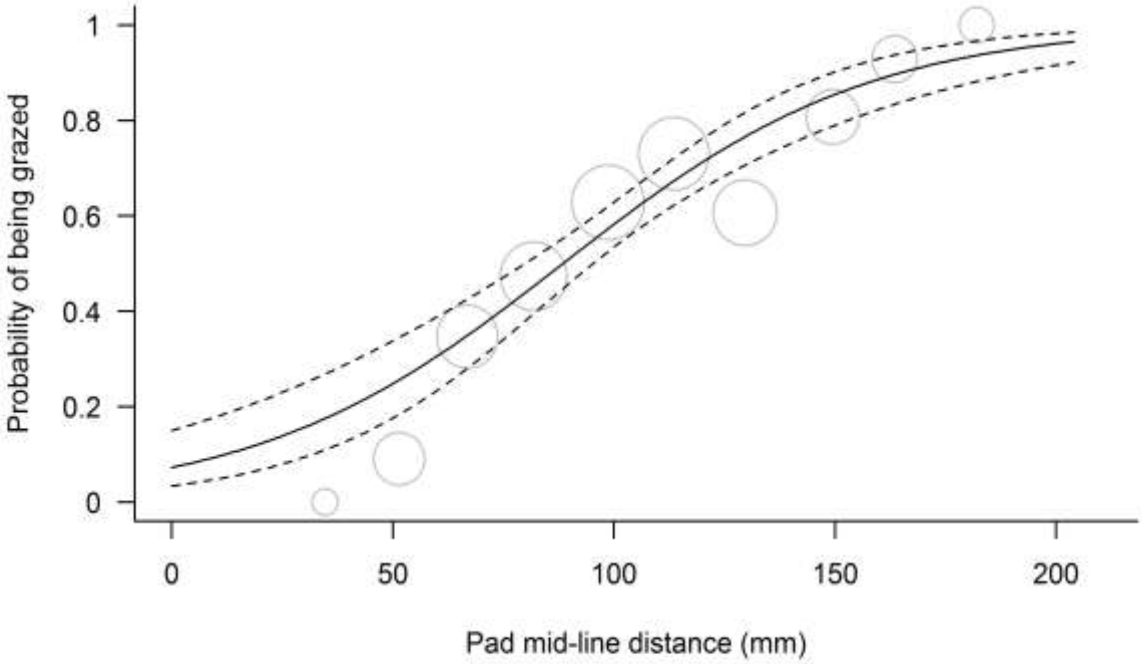

Fig. 3.3 Estimated probability of grazing based on unselected and reconstructed *N. alba* pad mid-line distances. Dashed lines indicate 95% confidence intervals. Original data on the proportion of grazed pads are superimposed as grey circles with diameter proportional to the total number of pads.

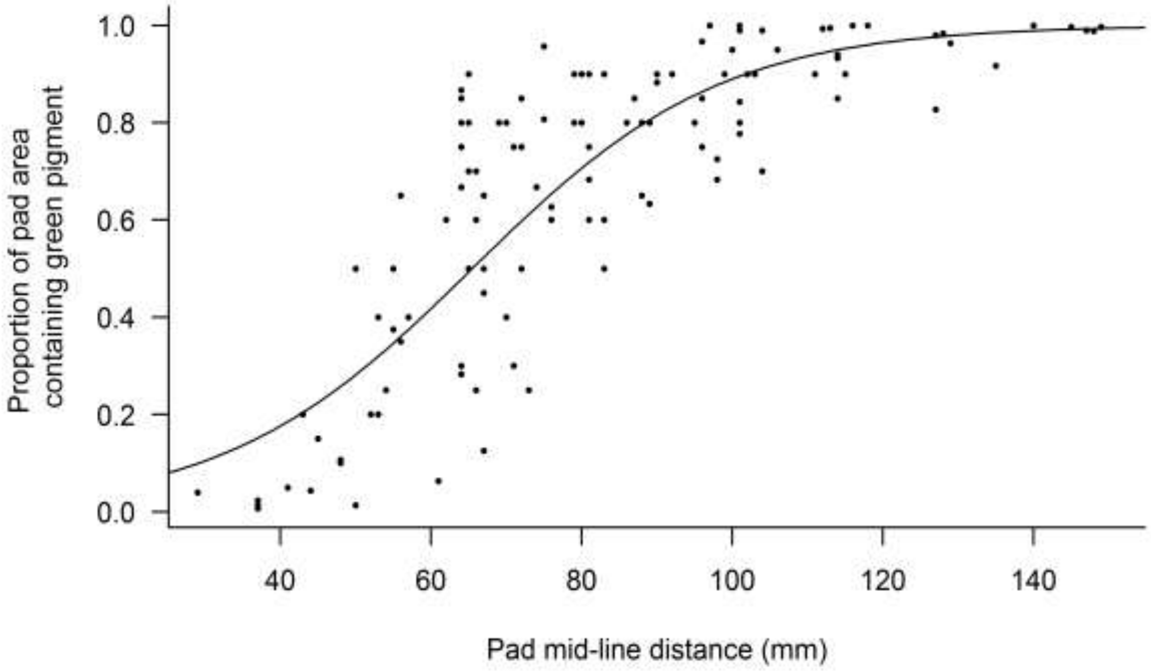

Fig. 3.4 The observed (solid circles) and modelled (solid line) relationship between *N. alba* mid-line distance and visually assessed proportion of pad area containing green pigment.

The observed mean percentage of pads per size category varied within plots, with medium sized pads being the most dominant size class; > 100mm = 40.2%, 50-100mm = 52.9% and < 50mm = 6.9%. Regardless of the proportion of available pads in each size category, beaver selected a significantly greater number of large pads compared to medium (t_{57} = -7.35, *P* <0.001) and small pads (t_{57} = -2.71, *P* = 0.008). The observed percentage of consumed pads were large 58.4 ± 5.5%, medium 12.5 ± 2.2% and small 0.7 ± 0.7%.

3.4.3 *Factors influencing pad selection*

As water depth increased, mean pad size increased significantly (t_7 = 2.3, *P* = 0.025), despite large variation in mean pad size at water depths less than 150cm (Fig. 3.5). However, beaver grazing was concentrated at shallower depths (55.7 ± 10.7cm) and closer to the shore (2.95 ± 0.62m) relative to un-grazed areas (100.5 ± 9.2cm; 4.79 ± 0.68m). The difference in depth between grazed and ungrazed plots was significant (Z_{72} = -3.03, P = 0.002), but weighted mean pad size had no effect on selectivity (Z_{72} = 0.03, P = 0.974). Thus, as depth increased there was no increase in pad size selectivity (t_{36} = -0.26, P = 0.80) and no interaction between pad size x depth and the proportion of pads grazed (t_{36} = 0.65, P = 0.52).

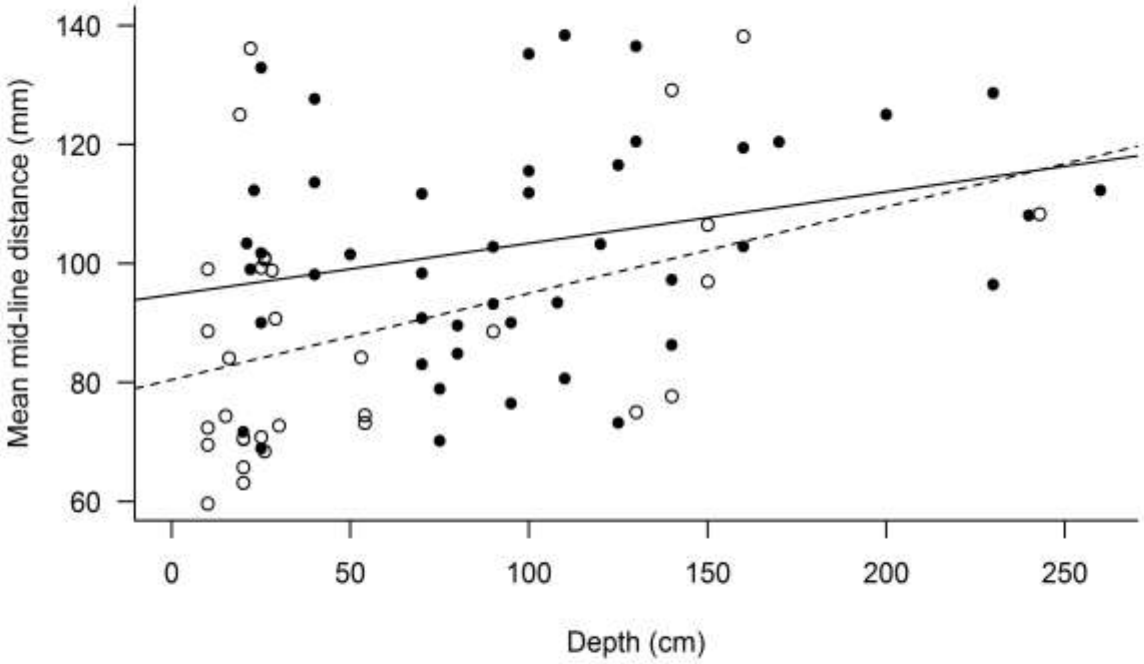

Fig. 3.5 The relationship between *N. alba* pad mean mid-line distance and water depth between grazed (open circles, dashed line) and ungrazed quadrats (solid circles, solid line) within lakes with active beaver foraging on pads.

3.4.4 *Scale and impact of feeding on* N. alba *by beavers*

Preference for grazing on large pads in shallower waters led to a reduced mean pad size within grazed quadrats (t_7 = -2.28, P = 0.028) (Fig. 3.5), but not sufficiently to produce a significant interaction effect between grazing and depth (t_7 = 0.63, P = 0.534). At the quadrat scale beavers removed between a quarter and a half of *N. alba* pads (Table 3.1), but impacts were barely evident at a coarser scale (lake level). The total grazed area per lake was small relative to resource size and hence there were no significant differences in total pad density per meter square between lakes with beavers present and grazing *N. alba,* and lakes where beavers were present but did not feed on *N. alba* (Z_5 = 0.72, P = 0.47), or lakes with no beavers present at all (Z_5 = 1.45, P = 0.15).

Table 3.1 Summary of foraging impacts by beaver on *N. alba* pads where beavers were observed foraging (n.b. *N. alba* pad grazing did not occur in Buic during 2012).

Year	Lake	Area of *N. alba* (ha)	*N. alba* pads removed per grazed quadrat (%)	Estimated total *N. alba* pad biomass removed (dw/g)	Grazed area (% of total resource)
2011	Buic	0.329	50.4	419.1	0.38
	Beag	0.224	24.4	461.3	0.54
2012	Beag	0.224	39.3	752.2	1.23

Excluding *N. alba,* the total number of aquatic plant species present per quadrat did not differ between lakes with and without beaver present (Z_3 = -1.22, P = 0.221). Within lakes with active feeding there was also no difference in species number between grazed and ungrazed plots (Z_3 = 0.22, P = 0.824). In lakes where beaver actively grazed on *N. alba* there was no significant impact on *Nymphaea* flower density (Z_4 = -1.33, P = 0.184). Also, in lakes where beaver were present there was a higher flower density per square meter than sites without beaver, but not significantly so (Z_4 = 1.09, P = 0.28).

3.5 Discussion

In comparison to terrestrial feeding, foraging on aquatic vegetation by beavers is understudied yet can be equally pronounced (Parker et al., 2007). In the present study beavers selectively fed on larger and heavier pads but there was no evidence that this selectivity changed with distance from shore or foraging depth. The availability of edible and palatable organs of *N. alba* will vary seasonally, thus contributing to selection by beavers (e.g. switching to plant rhizomes in winter in the absence of above-ground biomass). Temperate species of Nymphaeaceae peak in biomass and standing crop during August with pads then containing significantly more phosphorus and nitrogen per unit dry weight than the rhizome (Smart, 1980). This timing coincides with observations in this study whereby beaver grazed larger *N. alba* pads predominantly in late summer, with no evidence (from senescence or shrinkage of cut petioles) of pad removal earlier in the season, despite pads being available. During the early developmental stage, pads are red in colour due to cell pigments, notably anthocyanins (Bendz and Jönsson, 1971), that share the same phenylpropanoid biosynthetic pathway as many defensive phenolic compounds (e.g. tannins, terpenoids, alkaloids and flavonoids). The extensive red pigmentation observed only in smaller pads in this study could provide both direct (internal chemical repellents) (Lev-Yadun and Gould, 2009) and indirect defences against foraging by beavers (e.g. visual aposematic stimuli) as beavers demonstrate selection of food items of higher contrast to their background (Richard, 1979). *N. alba* delays greening until full leaf expansion due to delayed chlorophyll synthesis or chloroplast development (Coley and Kursar, 1996). As the expression and importance of anthocynanin pigments, and associated secondary compounds, declines during pad maturation this could be contributing to selection of larger, more visible or more palatable pads by beavers.

Aquatic plants will provide complementary nutrients to herbivorous mammals, particularly to gestating females; for example, moose consume aquatic plants rich in sodium and iron during the summer to correct an accumulated deficiency during winter and spring (Belovsky, 1978; Fraser, 1984). Yet without water lily in their diet Nolet *et al.* (1994) found that beavers had sufficient concentrations of sodium for nutritional needs, and in the present study lilies were utilised to a similar degree by both sexes (A. Law, *pers. obs.*). Some studies have noted that water lilies are grazed infrequently by beavers (Krojerová-Prokešová et al., 2010; Roberts and Arner, 1984), and since other family groups within the present study area have successfully bred annually without utilising the lily resource it is most likely that water lilies are a substitutable food source.

According to central place foraging theory, beavers should become more selective as the distance from the central place increases (Haarberg and Rosell, 2006; McGinley and Whitham, 1985). Our results are contrary to this expectation. Beaver were consistently highly selective regardless of distance from the central place (shoreline or lodge). Pad size was not uniformly distributed, with the density of pads of the preferred size increasing with depth, but the large variance in pad size at all depths ensured that the encounter rate with large pads in shallow water was sufficiently high that beavers did not need to forage far from a central place. Transportation costs of removed pads are assumed to be minimal due to buoyancy and, consequently, the longer handling and digestion times associated with selection of larger and heavier pads are presumably outweighed by greater nutritional value and/or palatability compared to smaller pads. By selecting relatively larger and heavier pads we speculate that beavers maximise energy gain and, whilst foraging at shallower depths and travelling minimal distances to obtain preferred food items, also minimise energy expenditure. Also, as beavers are often observed consuming the pads of Nymphaeaceae *in situ* rather than severing the whole pad from the petiole (P. Busher, pers comm.) an individual does not need to return to a central place to feed. These feeding constraints are more closely associated with optimal foraging theory (Belovsky, 1986; Schoener, 1979) than central place foraging, a special case of optimal foraging theory (Orians and Pearson, 1979), as described for terrestrial habitats. Observations of beavers returning with harvested *N. alba* pads to feed at a central place are likely to be associated with the ease of feeding on preferred pads close to the shore in a stationary position, further maximising net energy gain. Similar optimal feeding behaviour occurs in other semi-aquatic rodents whilst consuming aquatic plants, including muskrat (Connors and Kiviat, 1999; Lacki et al., 1990), coypu (Guichon et al., 2003) and capybara (Corriale et al., 2011), where individuals consume a greater volume of material in close proximity to the shoreline, lodge or burrow.

Removal of plants or specific plant organs has the potential to alter the composition and richness of surrounding vegetation (Northcott 1971; Lodge 1991; Ray *et al.* 2001). Beaver foraging did significantly reduce lily pad density in areas of feeding, but this effect was negligible at the scale of the water body. Beavers fed at low average intensity despite the ready availability of *N. alba* pads. With no differences in patch scale species richness between grazed and ungrazed areas there was no evidence for colonisation by other species following selective removal of larger *N. alba* pads by beavers. This may reflect the low number of available species within a site that could quickly colonise such gaps since oligotrophic lakes tend to support stress-tolerant rather than ruderal species. However, it is more probable that beaver foraging did not create large enough gaps for other species to colonise and that lily rhizomes that remain in place further preclude establishment of other species or the short period of this study. Floating leaves are essential to the functioning of the internal ventilation system of lilies, with stomata on the upper side of the pad supplying the buried rhizomes with oxygen, as well as providing access to atmospheric carbon dioxide. However, there was no evidence of compensatory growth by smaller pads following the removal of larger pads, as might have been expected to meet physiological requirements. Prior to winter, assimilated compounds in lily pads are translocated to the rhizome; investing energy into new growth after the peak of the growing season is therefore neither essential nor efficient. These findings are in accordance with Kouki (1991), who found that *Nuphar lutea* (Nymphaeaceae) also did not exhibit a compensatory regrowth response in relation to herbivory by water-lily beetles (*Galerucella nymphaeae*) during the peak of growth.

In the terrestrial environment felling and transportation of trees by beavers may be detrimental to other vegetation as this action creates patches of trampling and disturbance. When selectively removing and transporting pads in the water, there was no visible evidence of collateral damage to unselected pads or flowers. On the contrary, those sites where beavers consumed *N. alba* pads had a greater density of flowers, although this is more likely related to the slightly higher productivity of the lakes occupied by beavers. Various authors refer to feeding by beavers on the flowers of Nymphaeaceae species (e.g. Histol 1989), but no evidence of consumption of the flowers of *N. alba* was found in any of the lakes in this study. Anecdotal reports and photographs suggest that this habit may be commoner in *Nuphar*-dominated lakes where flowers are smaller and perhaps easier to handle and therefore more profitable as food items than those of *Nymphaea*. As the impacts of beaver feeding were low, feeding occurs over short periods and the resource is diet-complementary we conclude that increasing numbers of beavers will probably not severely alter the abundance of Nymphaeaceae species through direct foraging; attendant effects on associated species are also unlikely at the lake scale. However, as beavers are territorial, generalist herbivores it is likely that they exhibit subtle selection behaviour when feeding on other aquatic plants, the effects of which have not yet been documented.

3.6 Conclusion

Planned reintroductions of beavers often base the predictions of survival models on population dynamics and terrestrial foraging behaviour. Impacts on other flora and fauna should, however, be fully considered pre-release if reintroductions are to be classed as ‘successful’ from a more holistic conservation perspective. The highly selective, optimal foraging behaviour on *N. alba* observed in this study has not been previously described in freshwater systems for beavers. This differs from accepted principles of central place foraging behaviour in the terrestrial environment and may also apply to foraging on other aquatic plant species. Since beavers evidently demonstrate adaptive foraging strategies depending on their foraging environment this knowledge should be incorporated into future decisions on reintroduction or habitat restoration programmes.

CHAPTER 4 – Medium vs. short-term effects of herbivory by Eurasian beaver on aquatic vegetation

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Author comments: Initial project concept was designed by NW and KJ, where permanent survey plots were established and surveyed in 2003 by KJ and NW as part of KJ's PhD thesis (completed in 2006). In light of observed changes in structure of plants and continued beaver occupancy these plots were further surveyed by NW and AL, whilst exclosure and cafeteria experiments were carried out in 2012 by AL. Data was analysed and manuscript prepared by AL with input from NW.

4.1 Abstract

It is important to disentangle the effects of physical ecosystem modifications from plant-herbivore interactions to understand how keystone species, such as beavers, influence aquatic ecosystems, especially when populations are reintroduced or non-native. Through dam building beavers have the potential to influence macrophytes indirectly by altering the hydrological regime, but macrophytes also comprise a major component of beaver diet. In water bodies uninfluenced by dams, direct grazing will therefore be the primary basis of beaver-induced effects on macrophytes. Temporal change in macrophyte height, abundance and composition from three habitats within a pond system in Scotland were measured non-continuously over a nine year period following beaver introduction. From 2003 to 2012, persistent, selective grazing by beaver led to three fold increases in macrophyte richness and significant turnover in composition, reflecting overall reductions in abundance of the preferred dominant species (e.g. *Iris pseudacorus*). Within-season herbivory effects were quantified in 2011-12 using exclosures and by conducting cafeteria-style choice experiments. Significant volumes of macrophyte biomass (mostly rhizomes of *Menyanthes trifoliata*) were removed at constant rates throughout the growing season. Feeding was highly selective whilst effects on diversity were negligible in the short term. In the medium term, selective foraging by beavers significantly increased alpha and beta diversity of macrophytes. Macrophytes in temperate and boreal regions are potentially widely influenced by beaver grazing, although the positive effects we observed are not necessarily universal and are unlikely to persist within individual sites indefinitely.

4.2 Introduction

Freshwater systems support various large rodents including capybara (*Hydrochoerus hydrochaeris* L.), beaver (*Castor canadensis* Kuhl and *Castor fiber* L.), coypu (*Myocastor coypus* Molina) and muskrat (*Ondatra zibethicus* L.). One or more of these aquatic rodents are native across most of mainland Europe, Asia and the Americas. But also, with the exception of capybara, they have been reintroduced to their former native range or occur as non-native invasive species due to deliberate release or escape from fur farms (Johnson and Foote, 1997; Halley and Rosell, 2002). Within freshwater environments large rodents benefit through protection from land-based predators (e.g. wolves, lynx, badgers or bear) and access to suitable habitats for lodge or burrow construction, with populations often remaining in residence for multiple generations. Most lentic freshwaters also provide an abundance of accessible and reliable food resources year-round relative to rivers, with several studies having therefore focussed on the direct impacts of herbivory by aquatic rodents on macrophytes. Yet the impacts of large herbivores on native flora are still poorly understood in comparison to well-studied aquatic invertebrate herbivores. This is partly due to the low amenability of mammalian herbivores to mesocosm-style investigations and their generalist diet. But also, changes in their forage preferences according to supply and productivity of the ecosystem (Milligan and Humphries, 2010).

The most detailed and numerous studies of herbivory by aquatic rodents concern native muskrat in North America or non-native animals in Europe. Muskrats selectively reduce the density of macrophytes through direct feeding, establishing openings in dense vegetation that creates patches at different successional stages (Danell, 1977). The impact on specific vegetation is variable and dependent on the productivity of the system (Toivonen and Meriläinen; 1980, Danell, 1996), but selective grazing by muskrats generally increases heterogeneity of wetlands, both structurally and functionally, with an increase in species richness reported at intermediate disturbance intensity (Smirnov and Tretyakov, 1998; Bhattacharjee *et al*., 2007). However, with the exception of muskrat, long-term impacts of direct herbivory by aquatic rodents on aquatic vegetation are rarely studied and short-term studies may not be indicative of future trends. Therefore predicting temporal changes in aquatic vegetation or wider ecosystem effects in response to the gain or loss of aquatic rodents is difficult. In particular, since some of these animals, most notably Eurasian and North American beavers, are being actively introduced, reintroduced or dispersing to their former range. Also, the impacts of aquatic herbivores can be perceived positively or negatively by the public and site managers depending on whether these organisms are native or not (Schüttler et al., 2011). Or according to perceptions of the ecosystem services they provide e.g. muskrat foraging prevents lakes becoming overgrown by vegetation (Danell, 1996). The strength of any impacts often provides the motivation for study.

As a commonly introduced, reintroduced or non-native species, beavers present an interesting case study. They have the capacity to alter freshwater habitats through dam building, thereby directly or indirectly changing the availability of resources to other organisms (Jones et al., 1994). Building dams maintains a submerged lodge entrance and consequently decreases the risk of predation by land-based predators, whilst the cost of travel to foraging areas and in conveying selected items is reduced due to their buoyancy in water (Law, Bunnefeld & Willby 2014). The modification or creation of habitats through dam building by beavers (ecosystem engineering) is often reported to enhance landscape diversity for various groups of organisms e.g. macrophytes (McMaster and McMaster, 2001), herbaceous plants (Wright et al., 2002), invertebrates (Rolauffs et al., 2001), fish (Kemp et al., 2011), amphibians (Dalbeck et al., 2007), bats (Nummi et al., 2011), and birds (Nummi, 1992). However, when beavers inhabit medium to large, lentic systems the occurrence and impacts of well-maintained, habitat-transforming dams are often negligible as elevation of water levels is unnecessary (Gurnell, 1998; Wright et al., 2004). Nevertheless, significant impacts on macrophytes still occur, primarily through direct, selective grazing (Parker et al., 2007), since macrophytes are a major component of beaver diets (Svendsen 1980; Elmeros *et al.,* 2003; Milligan and Humphries, 2010). Lentic environments thus present an opportunity to study direct impacts of herbivory by beaver on aquatic vegetation. These are liable to be overlooked or underestimated due to the traditional preoccupation with the effects of dam building or the succession that occurs following abandonment of beaver-generated wetlands.

Both species of beaver, *C. fiber* and *C. canadensis*, now occupy much of their former range throughout Europe and North America respectively, with further expansion expected, especially in western Europe and the lower Danube basin (Halley and Rosell, 2002). Furthermore, *C. canadensis* has also been introduced to Europe (Finland and Russian Karelia) and South America (Tierra del Fuego) (Halley and Rosell, 2002; Lizurralde et al., 2004). With the range and density of animals increasing globally and with populations now present outside their native range a better understanding of the impacts of direct herbivory by beavers on aquatic vegetation is timely. We therefore tested the following hypotheses: (1) foraging by beaver influences macrophyte composition and abundance over medium time scales (nine years in this study), (2) beaver selectively forage on macrophytes and their organs and (3) beaver foraging will influence macrophyte richness and biomass over seasonal time scales.

4.3 Methods

4.3.1 *Study area*

The study took place on a private estate situated near Blairgowrie, Perth in east Scotland (56º64’42.91” N, 3º27’34.99” W) which receives approximately 1400 mm of rain annually, with a mean maximum temperature of 12 °C and mean minimum temperature of 5 °C from 1981-2010 (Meteorological Office UK, 2013). Two Eurasian beavers were introduced to a 9 ha site in 2002 composed of a mature conifer plantation with areas of willow and birch scrub surrounding a 2 ha mature pond. Subsequently these animals constructed a lodge and a small, poorly maintained dam on the pond outflow resulting in a water level rise of ~ 0.2 m (A. Law, *pers. obs*.). Successful breeding first occurred in 2006 following the introduction of a male in 2004. Since this time up to four animals have been regularly present and commonly observed feeding on aquatic plants.

The pond was characterised by three predominant habitat types: (i) fringing emergent vegetation dominated by *Iris pseudacorus*, *Carex rostrata* and *Equisetum fluviatile* (ii) open water dominated by floating-leaved macrophytes, specifically *Potamogeton natans* and *Potamogeton polygonifolius* and (iii) a homogenous floating mat of *Menyanthes trifoliata* with patchily distributed *C. rostrata*. Water chemistry in the pond averaged 21 µg L^{-1} for orthophosphate (P-PO_4) and 150 µS cm^{-1} for conductivity during 2011 suggesting mesotrophic conditions.

4.3.2 *Methods and statistical analyses*

4.3.2.1 Change in the macrophyte community 2003-2012

In autumn 2003, following the introduction of beavers, but prior to any observable impacts of foraging or dam building, the composition and coverage (%) of macrophytes was surveyed within fixed areas (marked with wooden posts) of each habitat type using a randomly placed 1 m^2 quadrat. Between 8 and 24 quadrats were surveyed per habitat reflecting their uniformity, extent and the rate of accumulation of new species. Maximum vegetation height was measured at six points within each quadrat except those located in open water. The same fixed areas within these three habitats were resurveyed in autumn 2004 and 2012, excluding height measurements in 2004.

Data were analysed to assess the significance of between- relative to within-year differences. Normalised plant height data did not meet assumptions of parametric statistical tests; therefore a non-parametric Mann-Whitney U test was used. Richness was assessed as numbers of species per quadrat and as Shannon's Diversity Index (*H'*). Count data on macrophyte species richness were analysed using generalised linear mixed models with a Poisson error distribution and log-link. Within these mixed models quadrat identity was treated as a random factor. The Bray-Curtis dissimilarity Index (BCI) was used to quantify change in species composition within- and between-years. Total coverage, H' and BCI (mean difference within plots) did not meet parametric test requirements, even after transformation, and so a Kruskal-Wallis one-way analysis of variance with post hoc multiple comparison tests was used. A Mann-Whitney U test was used to test the difference in mean BCI between plots in successive years. Species composition and turnover per habitat and year was compared using non-metric multidimensional scaling (NMDS) based on a BCI matrix.

4.3.2.2 Feeding trials

Cafeteria-style feeding trials were carried out in 2012, from May to September inclusive, using 5 to 7 replicates each comprising two whole plants (stems, leaves, flowers (if present), roots and rhizome) of seven different species found within the study site (Fig. 4.1). These were placed upon saturated, exposed sediment or in shallow water (< 5 cm) close to areas where beavers had been observed to forage i.e. within the mat and emergent habitats. The order of plants within each replicate was randomised with the following species used; *E. fluviatile, C. rostrata, M. trifoliata, I. pseudacorus, P. natans, Juncus effusus* L. and *Hippuris vulgaris* L. The percentage of biomass removed per species in each replicate was estimated visually after 5 days of exposure. To assess the significance of differences in palatability between species and the effect of month on selection a general linear model with post-hoc multiple comparisons using Tukey's Honestly Significant Differences (HSD) test was used.

Fig. 4.1 One replicate from the cafeteria-style feeding trial used in this study. Species used, left to right; *Juncus effusus*, *Carex rostrata*, *Menyanthes trifoliata*, *Potamogeton natans* and *Iris pseudacorus* (© Alan Law, May 2012).

4.3.2.3 Within-season changes in the macrophyte community

Post 2010 evidence of foraging was more apparent within the floating *Menyanthes* mat compared to other areas of the pond. Two 2 m x 2 m (1 m high) exclosures were therefore constructed in this habitat during ice cover in January 2011. Exclosures were constructed from 30mm mesh size chicken wire anchored into the substrate by metal rods and stapled to 2 m long treated pine posts. These exclosures were regularly checked and maintained throughout the study period in order to prevent beaver access. Macrophytes were harvested from within the exclosures down to ground level using a 34 cm x 34 cm quadrat. Outwith the exclosures macrophytes were sampled in the same way within the surrounding habitat. These samples were not taken within one meter of the exclosures to avoid possible effects of human trampling associated with exclosure sampling or construction. Samples were collected approximately every four weeks throughout 2011 from April to October inclusive with three quadrats harvested from each exclosure (ungrazed) and six from the unenclosed (grazed) areas per visit. In March 2012, to investigate possible exclosure artefact effects, the exclosures were halved in size and two separate artefact exclosures were built within the surrounding grazed area. Artefact exclosures were built to the same design but with two sides left open for beaver access by creating an ‘L’ shape. These were designed to test if exclosures could increase biomass production over and above the effects of removing grazing entirely. Macrophytes from ungrazed, grazed and artefact treatments were harvested in November 2012. Motion sensor cameras (ProStalk 2 megapixel Infrared Motion Camera) were placed on each exclosure facing the grazed areas for periods during July and August 2011 to confirm the identity of the herbivores present.

Necromass and sediment were washed from the harvested material which was then dried with paper towels and separated into component species. Material of the main biomass component *M. trifoliata* was separated into (i) rhizome/stolon and roots, (ii) leaves (blade and petiole) and (iii) flowers, so that seasonal changes in biomass of separate tissues could be quantified. Wet weight of each species/organ was measured to two decimal places before samples were dried in an oven for 48 hours at 80 °C and re-weighed.

Macrophyte biomass data were log transformed to meet linear requirements and analysed with general linear models with post hoc multiple comparisons using Tukey’s HSD test. Count data on species richness of harvested material were analysed using a generalised linear mixed models with a log-link and Poisson error distribution. Within these mixed models individual quadrats were treated as random factors. Models were selected with the lowest AIC score with interactions removed when not significant i.e. the interaction for month x area for species richness from samples during 2011.

All statistical analyses and graphics were produced using R Studio version 2.15.0 (R Development Core Team, 2013) using the packages sciplot (Morales & Murdoch 2011), vegan (Oksanen *et al*. 2012), lme4 (Bates, Maechler & Bolker 2012), pgirmess (Giraudoux 2012).

4.4 Results

4.4.1 *Changes in the macrophyte community 2003-2012*

From 2003 to 2012 there was a significant reduction in plant height in both emergent (W = 16279, $P < 0.001$) (Fig. 4.2) and mat (W = 2304, $P < 0.001$) habitats. Height was reduced by 63.5 ± 1.8% (mean ± SE) and 57.8 ± 2.1% in the emergent and mat habitats respectively.

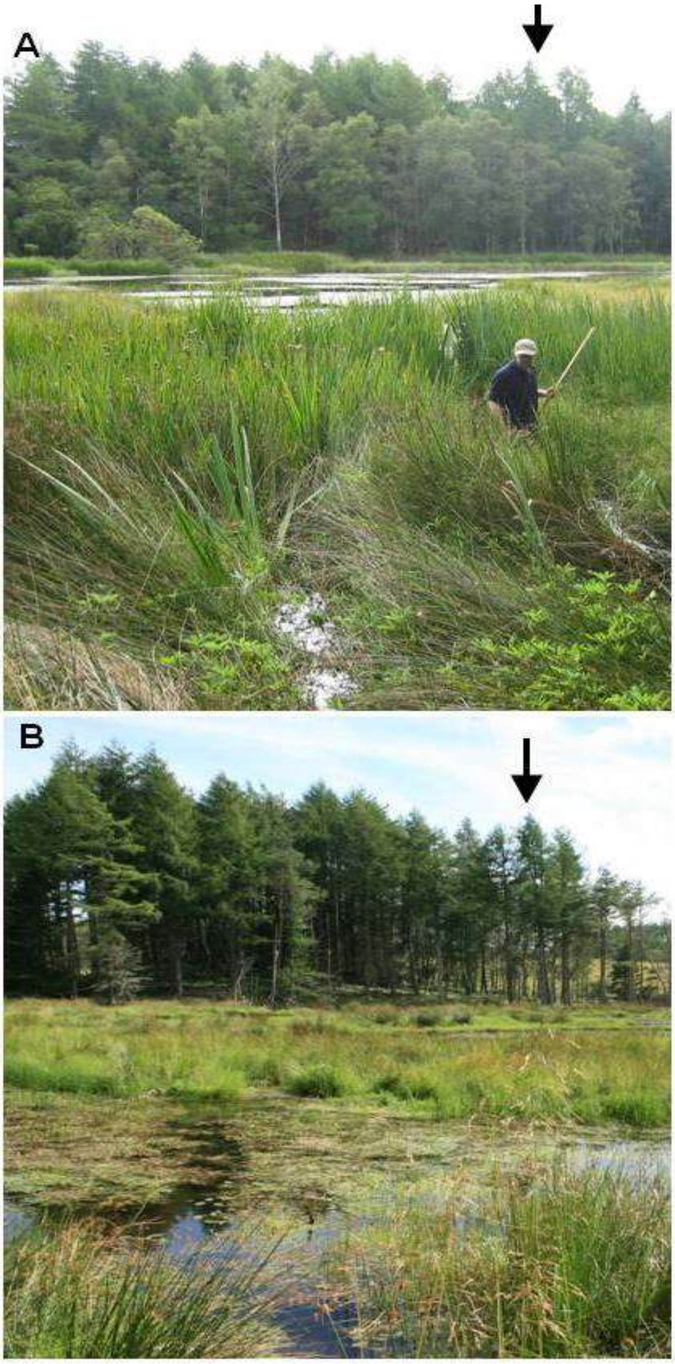

Fig. 4.2 An overview of the western pond area with fringing emergent vegetation in: a – August 2003, and b – August 2012 (© Nigel Willby). Note the decrease in the plant height within emergent vegetation zone in the foreground. The arrows indicate the same group of trees in each photograph with the decrease in tree cover in the background is due to commercial forestry management.

Changes in macrophyte cover (Table 4.1) were mostly consistent between habitats and years, yet cover of *C. rostrata* displayed opposing trends depending on habitat, relating to initial high (55%) and low (5%) densities in 2003 within mat and emergent habitats respectively. Other than the species listed in Table 4.1, the most striking change was the + 10% absolute change in cover of *Galium palustre* in the emergent vegetation habitat. Changes in coverage of all other species within habitats were negligible (< ± 3%). The degree and direction of change in specific cover values over one year (2003-4) gave no strong indication of future trends, as initial increases in coverage (e.g. *P. natans* and *E. fluviatile*) were inconsistent with longer term trends. Total coverage did not change significantly between years within emergent or mat habitats, but did within open habitats (Fig. 4.3a) (see Appendix 4.1), relating to the combined reduction of *E. fluviatile* and *P. natans* from 2004 to 2012. However, between 2003-2012 total coverage in open water habitats did not change significantly.

Table 4.1 Absolute change in percentage species cover from common macrophyte species from 2003 to 2004 and 2003 to 2012 per habitat. Species were assigned to grazed and ungrazed categories based on results from feeding trials.

		Emergent		Open		Mat	
	Species	2004	2012	2004	2012	2004	2012
Grazed Species	*Carex rostrata*	+ 0.1	+ 27.1	-	-	- 26.3	- 30.0
	Equisetum fluviatile	+ 2.4	- 2.9	+ 14.6	- 7.3	+ 1.9	+ 0.4
	Iris pseudacorus	- 6.3	- 57.7	-	-	-	-
	Menyanthes trifoliata	+ 0.5	+ 2.0	-	-	+ 18.8	+ 27.5
Ungrazed Species	*Hippuris vulgaris*	0	+ 6.0	-	-	-	-
	Juncus effusus	0	+ 12.9	-	-	0	+ 1.3
	Potamogeton natans	+ 2.1	- 16.5	+ 4.1	- 13.8	-	-

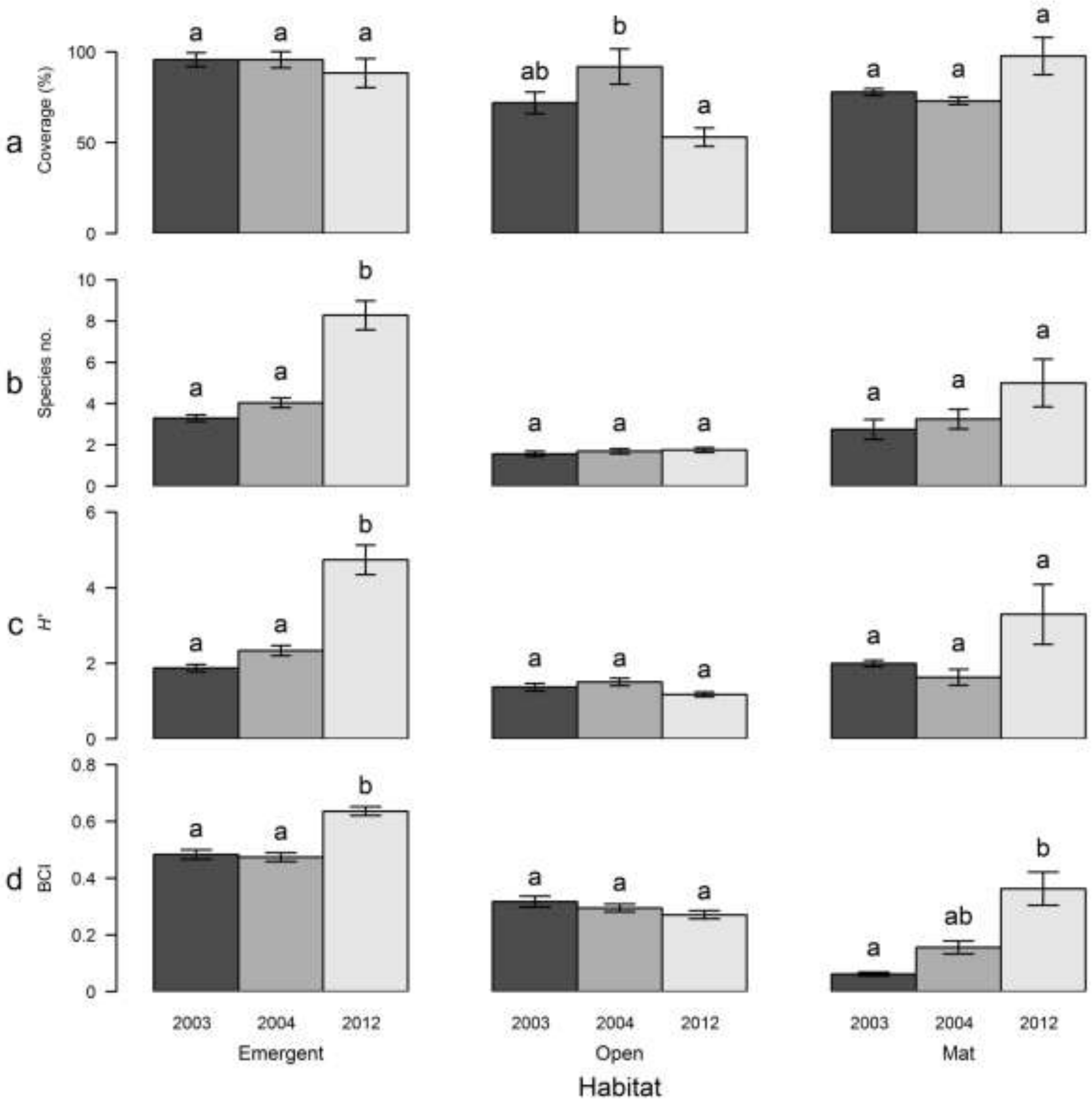

Fig. 4.3 Relationships of a - mean percentage coverage, b - observed mean number of macrophyte species, c- mean Shannon's diversity index (*H'*) and d- mean Bray-Curtis dissimilarity Index per quadrat for habitats and years sampled. Where numbers share a superscript letter they are not significantly different from each other ($P > 0.05$). Error bars indicate standard error. Note that the BCI is bound between 0 (all species shared) and 1 (mutually exclusive composition).

In areas where grazing was prevalent, namely emergent and mat habitats, a greater total number of macrophyte species were recorded in 2012 (31 and 15 species in emergent and mat habitats respectively) compared to 2003 (11 and 5 species) and 2004 (10 and 5 species).

Observed species richness only increased in open water habitats due to the widespread occurrence of *Sparganium natans* by 2012. Despite this only emergent habitats had significantly greater species richness per quadrat ($Z_{72} = 8.012$, $P < 0.001$) (Fig. 4.3b). No significant differences occurred within mat ($Z_{11} = 1.715$, $P = 0.086$) or open water habitats ($Z_{47} = 0.342$, $P = 0.733$) (Appendix 4.2). The increased *H*' for both emergent and mat habitats (Fig. 4.3c) further indicates the reduced dominance by a few species.

Table 4.2 The mean pairwise Bray-Curtis dissimilarity Index ± SE between plots for 2003-2004 and 2003-2012 per habitat. * indicates a significant (P < 0.05) change in BCI.

		2003-2004	2003-2012
BCI	Emergent	0.484 ± 0.01	0.929 ± 0.004*
	Open	0.323 ± 0.01	0.338 ± 0.01
	Mat	0.466 ± 0.02	0.476 ± 0.02

Plots within emergent habitats became more dissimilar to each other throughout the study (Fig. 4.3d), reflecting the greater heterogeneity of vegetation and reduction in dominant species, but the mean pairwise BCI between plots from this habitat also varied strongly from 2003 to 2012, reflecting a significant change in species assemblage ($W = 26429.5$, $P < 0.001$) (Table 4.2) in addition to the changes in diversity and richness reported above. This is displayed in Fig. 4.4 by the change in position of the largest, solid lined ellipses. Plots within mat habitats became more dissimilar from one another (Fig. 4.3d) but the overall species assemblage did not change significantly ($W = 115$, $P = 0.637$) (dotted ellipses Fig. 4.4), whereas similarity remained constant between years within open water habitats ($W = 32188$, $P = 0.729$) (far left ellipses Fig. 4.4).

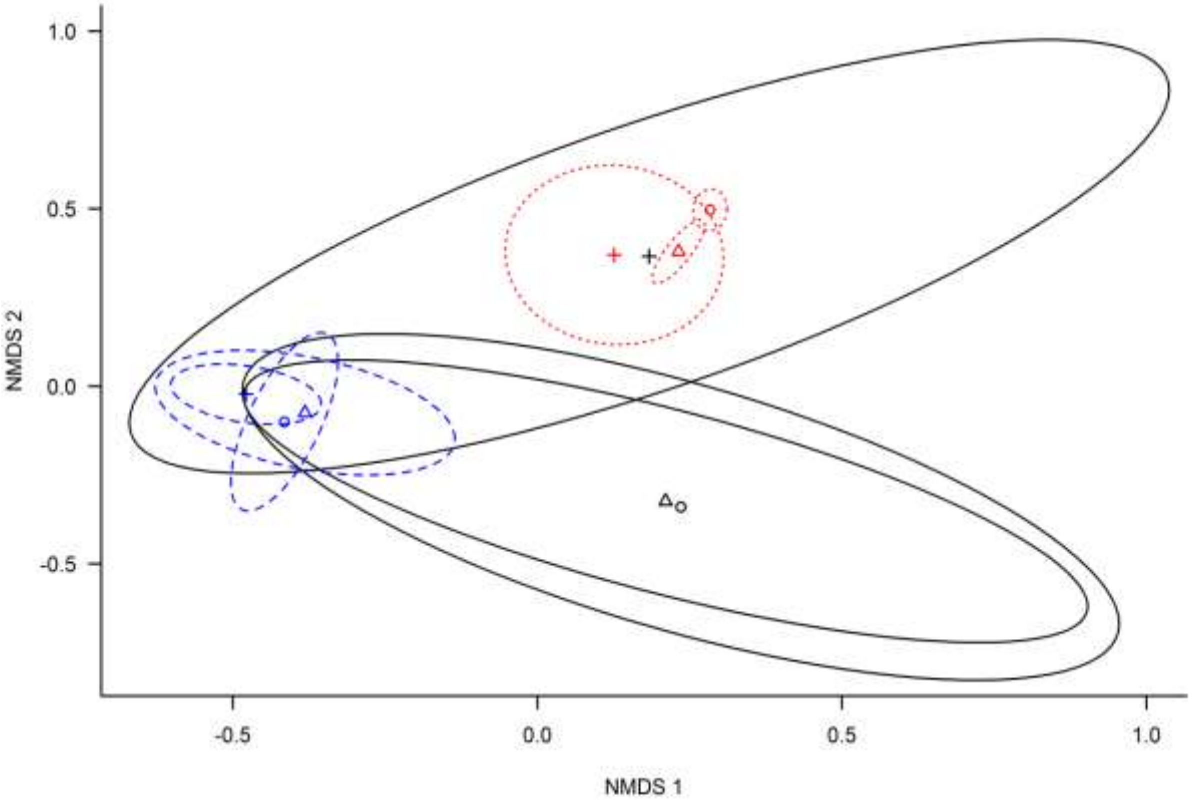

Fig. 4.4 Non-metric multidimensional scaling ordination (NMDS) plot for mean species composition per emergent (solid black ellipses), open (dashed blue ellipses) and mat (dotted red ellipses) habitats per year 2003 (open circles), 2004 (open triangles) and 2012 (crosses). All stress values < 0.1.

4.4.2 *Feeding trials*

Macrophytes that were grazed were consumed disproportionately ($F_{3,112}$ = 10.12, $P <$ 0.001) (Fig. 4.5), with a greater proportion of *I. pseudacorus* consumed compared to all other grazed species ($P < 0.001$). This was consistent with the observed decrease in coverage of this species from 2003 to 2012 (Fig. 4.1). Excluding *I. pseudacorus*, there were no differences in the total biomass consumed between any of the other grazed macrophytes ($P > 0.91$). Total biomass consumed in the feeding trials was constant throughout the trial ($F_{3,112}$ = 1.31, P = 0.28) and between individual monthly comparisons ($P > 0.23$). Similarly, the proportion of biomass consumed per plant species between months was constant throughout the trial ($P > 0.32$). There was no evidence of direct grazing on *H. vulgaris*, *J. effusus* or *P. natans* throughout the feeding trials and no grazing whatsoever occurred in the September trial. Images taken from the motion sensor cameras recorded no above-ground macrofauna foraging on macrophytes other than beavers.

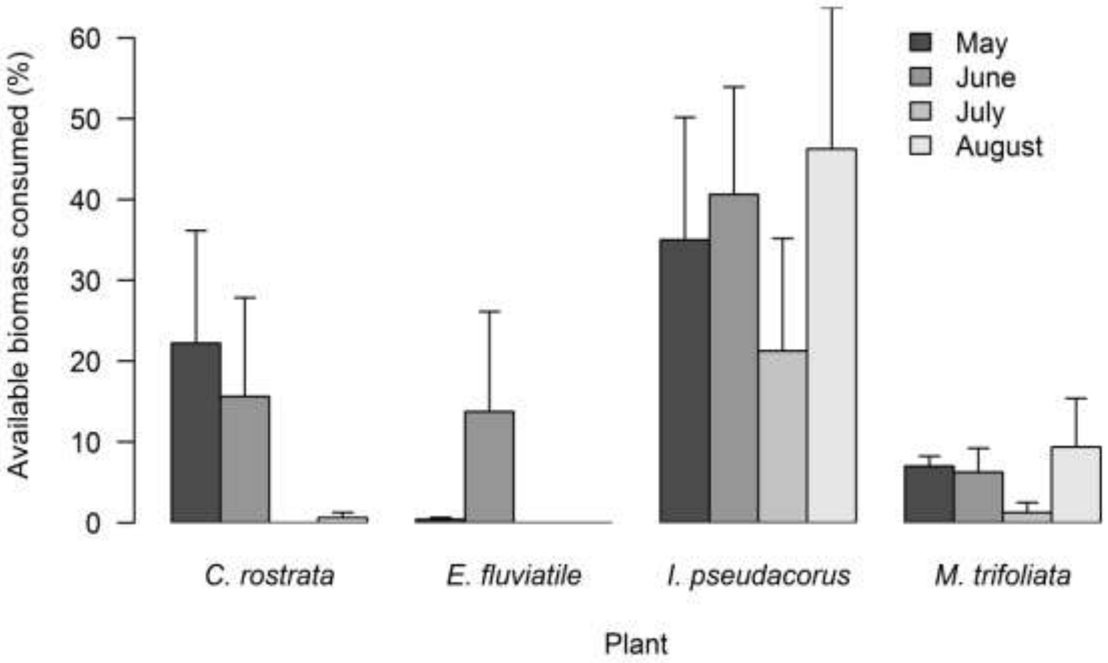

Fig. 4.5 The mean proportion of available biomass consumed in cafeteria-style feedings trials for grazed macrophyte species per month in 2012. Error bars indicate standard error.

The results from the feeding trial in relation to changes in species coverage are most likely habitat-specific i.e. the lack of grazing on *H. vulgaris* and *J. effusus* could explain their increased coverage in the emergent habitat, yet coverage of the grazed *M. trifoliata* increased substantially in the mat habitat. Beavers did not selectively graze *P. natans* but coverage of this species decreased regardless, potentially due to disturbance caused by transport of felled wood by beavers, accumulation of cached woody material or increased, periodic turbidity in the water due to beaver activity.

4.4.3 *Within-season changes in the macrophyte community*

During 2011 grazed areas within the mat habitat supported greater observed mean and total species richness within the majority of months compared to exclosures (Appendix 4.3) although species richness did not significantly differ between grazed and ungrazed areas in general ($Z_9 = 0.84$, $P = 0.401$) or between these treatments in the majority of individual months ($Z_9 > 0.864$, $P > 0.168$). In terms of seasonality, October had a marginally greater species number relative to April ($Z_9 = 1.96$, $P = 0.050$).

Table 4.3 Mean difference in biomass between grazed and exclosed areas from 2011 with general linear model results.

M. trifoliata tissue	Mean biomass difference (g m^{-2}) (%)	Area	Month	Area*Month interaction	Within month biomass differences
Rhizome	147.1 (48.5%)	$F_{1,68} = 37.24$, $P < 0.001$	$F_{6,68} = 2.36$, $P = 0.040$	$F_{6,68} = 0.74$, $P = 0.622$	September ($P = 0.032$)
Leaf	27.1 (29.2%)	$F_{1,52} = 7.06$, $P = 0.01$	$F_{5,52} = 26.66$, $P < 0.001$	$F_{5,52} = 10.53$, P = 0.07	-
Flower	7.9 (90.8%)	$F_{1,17} = 28.44$, $P < 0.001$	$F_{2,17} = 2.12$, $P = 0.150$	$F_{1,17} = 1.38$, $P = 0.257$	May ($P = 0.005$)

The mean macrophyte biomass between grazed (231.5 ± 18.0 g m^{-2}) and ungrazed (418.7 ± 25.6 g m^{-2}) areas was significantly different ($F_{1,70} = 46.7$, $P < 0.001$) with an estimated difference of 45%. Ungrazed areas had a total dry biomass 1.8 times (range: 1.6 - 2.4) greater than grazed areas. Although the total biomass was greater in ungrazed areas in all months, it was only significantly greater in May ($P = 0.011$). The difference in biomass between areas was not enough to affect the overall trend in growth as the biomass in both areas increased from April to July before declining till September, displaying typical significant seasonality ($F_{6,70} = 6.239$, $P < 0.001$) (Fig. 4.5d). Differences in biomass between ungrazed and grazed areas were approximately constant as indicated by the lack of interaction between month x grazing ($F_{6,70} = 0.622$, $P = 0.712$). Similarly, ungrazed areas had significantly higher rhizome, leaf and flower biomass (Table 4.3), with no foraging impact on seasonal biomass growth trends (Fig. 4.6a, b and c respectively). Within-month differences did occur in biomasses between areas but were not consistent. Macrophyte biomass harvested in November 2012 displayed differences between treatments ($F_{3,20} = 15.0$, $P < 0.001$), with ungrazed areas having significantly greater biomass (370.9 ± 46.7 g m^{-2}) than all other areas (all comparisons; $P < 0.001$), including those that were ungrazed in the previous year. No significant differences in biomass occurred between areas open to grazing, and no exclosure artefact effect was found (1 year grazed = 166.8 ± 14.8 g m^{-2}, Artefact = 136.9 ± 8.0 g m^{-2}, Grazed = 174.6 ± 13.6 g m^{-2}) (all comparisons; $P > 0.77$). Figures 4.6a and d indicate that some differences in biomass existed between exclosed and open areas prior to the start of sampling. In fact, these differences arose due to grazing immediately following ice melt but prior to the initial sampling in April 2011. The close similarity in 1 year grazed and grazed mean biomasses in November 2012, and the similarity of these values to those recorded in grazed areas in April 2011 at the beginning of the study, implies that any differences in *Menyanthes* biomass between exclosed and open areas that existed prior to the onset of grazing were trivial.

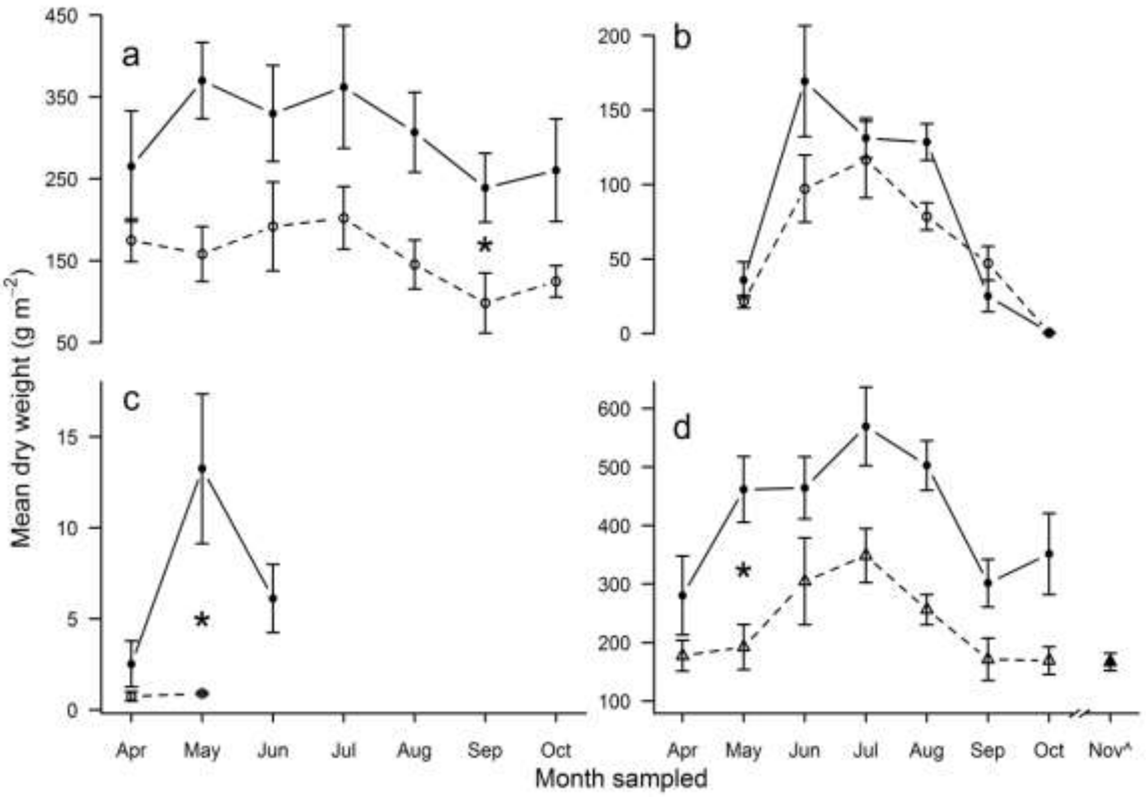

Fig. 4.6 Mean macrophyte biomass for ungrazed (solid circles, solid lines) and grazed (open circles, dashed lines) areas per month during 2011 for: a - *M. trifoliata* rhizome, b - *M. trifoliata* leaves, c - *M. trifoliata* flowers, d - total biomass. Error bars indicate standard error (* denotes a significant difference in biomass between areas within each specific month, ^ denotes the biomass for 1 year grazed and grazed areas from November 2012 only).

4.5 Discussion

4.5.1 *Change in macrophyte community 2003-2012 and selective foraging*

Plant responses to herbivory are complex (Crawley, 1983; Lodge, 1991). Thus, although this study documented evidence of the selective grazing of macrophytes by beavers, without quantitative diet data we cannot conclude that differences in macrophyte coverage, height, species richness and biomass over time are related exclusively to beaver herbivory (i.e.

consumptive losses). Instead the term ‘net grazing impact’ is preferable. This term encompasses direct macrophyte consumption, trampling and associated wastage by beaver.

From 2003 to 2012 there was a significant reduction in macrophyte height and decreased coverage of emergent, tall, dominant species i.e. *I. pseudacorus* (~ 100-150 cm) or *C. rostrata* (~ 60 cm). These changes primarily occurred within emergent and mat habitats respectively and likely contributed to reduced density-dependent competition. This was undoubtedly related to persistent, selective grazing by beavers leading to a greater diversity in terms of mean richness and total number of species at the quadrat and pond scale respectively. There was also general increase in less competitive, grazing-tolerant or less palatable species that were capable of exploiting these gaps i.e. *H. vulgaris*, *J. effusus*, *G. palustre*, *S. natans* and *Sphagnum* spp. The tripling in total species number we observed within grazed habitats was much higher than the 15% (Bartel et al., 2010) and 33% (Wright et al., 2002) increases previously reported. Although these latter studies were cross-sectional at the landscape scale, and attribute increased herbaceous plant richness to beaver modified riparian zones rather than foraging per se. Similar foraging effects have been reported for muskrats e.g. reductions in specific macrophyte densities (Danell, 1977) with increases in heterogeneity and species richness associated with selective grazing (Smirnov and Tretyakov, 1998; Bhattacharjee *et al*., 2007). These results are more comparable to this study as muskrats do not build dams, but macrophytes also comprise a major part of their diet, as well as being utilised in nest construction.

Spatial heterogeneity in aquatic habitats already existed prior to this study, but selective foraging modified this further. Within the mat habitat, plots were extremely homogenous in 2003/4 but became more diverse over time, as reflected by the increase in Bray-Curtis dissimilarity index. Turnover in species assemblage also occurred in grazed habitats, especially within the emergent habitat, during the nine year study period. This was attributed to the recruitment of additional species e.g. *Cardamine pratensis*, *Epilobium montanum* and *G. palustre*, rather than losses. Only one species per grazed habitat was absent in 2012 compared to 2003 i.e. *P. natans* and *Salix* spp., but these were present elsewhere in the site. Therefore, as well as their widely recognised ability to increase course scale habitat heterogeneity through ecosystem engineering

(Wright et al., 2002), beavers can also strongly modify smaller habitats over time through net grazing impacts. There is no consensus across studies of mammalian herbivory relating food selection to either nutritional benefit or behavioural trade-offs. For example, moose selected plants that were higher in sodium, phosphorus and protein (Fraser *et al*. 1984), whereas muskrat selected easily-digested plant tissues based on low lignin and cellulose content (Lacki et al., 1990). Yet, food selection by other herbivores was only partially related to nutritional content. Instead, it was associated with minimising predation risk for coypu (Guichon et al., 2003) or related to physiological mechanisms of the animal i.e. facultative coecotrophy for capybara (Corriale et al., 2011). Food selection is therefore likely to be species- and habitat-specific.

As no comparable, qualitative data exists for all the macrophyte species used in this study, selection has to be measured by the overall contribution to physical and genetic fitness. We speculate that selected plants must be of a greater net quality compared to ungrazed species as beavers at this site have bred successfully for each of the past seven years. Further to this, for *C. rostrata* and *I. pseudacorus,* beavers consumed only the leaf blade, whereas for *M. trifoliata* only the rhizome was consumed with the leaf blades untouched. This species-specific, within-plant tissue selection further indicates the importance of net quality in relation to selection. There is no anecdotal evidence for plant structural defences specifically against beaver foraging. However, as beavers are opportunistic generalists this is not surprising, since selection for defence mechanisms will be weak.

4.5.2 *Within-season changes in macrophyte community*

Foraging impacts on species richness within the 2011 growing season in the mat habitat were low in comparison to those evident across the nine year period. The dominant species in this habitat, *M. trifoliata*, can almost completely exclude other species when dense stands are formed (Hewett, 1964). With clonal, below-ground structures refilling foraging-created gaps more quickly than new species can colonise them (Haraguchi, 1996). Of the ever-present species in this habitat, *C. rostrata,* abundance decreased, in parallel with increased *M. trifoliata* cover since

2003. This may explain initial low species richness in 2011 and the lack of a suitable propagule bank to respond to partial biomass removal. Within this season no significant differences occurred in *M. trifoliata* leaf biomass between grazed and ungrazed areas, and it is therefore unlikely that additional light created by canopy gaps would be available to stimulate growth of opportunistic species. Further to this, half the total species observed were present in October, with only isolated occurrences of additional species in areas open to grazing e.g. the small herb *Cardamine flexuosa*. Therefore it is likely that seasonal recession of *M. trifoliata* foliage has a greater influence on species richness than beaver grazing within this habitat during one growth season.

There was a significantly lower standing crop of macrophytes each month in areas open to grazing (biomass of grazed areas averaging 45% of control). The difference in mean dry weight between areas at the beginning of the study was a result of beavers heavily feeding on *M. trifoliata* rhizomes in the two weeks free of ice cover prior to the start of this study (A. Law, *pers. obs.*). Other exclusion studies involving aquatic rodents foraging on macrophytes report variable extents of biomass removed (all figures are for above-ground macrophyte biomass) e.g. ~ 200% increase in biomass after beaver (*C. canadensis*) exclusion (Parker et al., 2007). In areas of coypu and muskrat feeding the estimated difference in biomass between grazed and control areas were 48% and 62% respectively (Johnson and Foote, 1997; Evers *et al*., 1998; Connors and Kiviat, 1999). Although the amount of biomass removed is variable, and occurs within different habitats, the impacts on macrophyte assemblages are clear; foraging by large rodents strongly affects plant biomass in aquatic systems. Although impacts may be offset by the fertility of the site (Danell, 1996). Throughout the present study variation in total and plant specific biomass removed were low for both the exclosure experiment and feeding trials from 2011 and 2012 respectively. This is despite extensive evidence that the nutritional value of specific plants and their tissues varies predictably through the growing season (Nolet *et al*., 1994; Haraguchi, 1996; Milligan and Humphries, 2010). Also, areas that were exclosed in 2011 and opened for grazing during 2012 displayed a similar mean difference in biomass (45%) compared to the previous year. These results suggest that beaver were consistently utilising specific aquatic vegetation throughout the majority of the growing season and having constant annual impacts.

Growth trends of specific *M. trifoliata* organs differed between grazed and ungrazed areas. This was especially apparent in rhizome biomass from April to June 2011. Within the feeding trials rhizomes were preferentially grazed compared to any other organ of *M. trifoliata*. This selective feeding may coincide with storage of high volumes of mineral nutrients in rhizomes and roots, i.e. magnesium, calcium, manganese and sodium, prior to leaf and petiole expansion (Haraguchi, 2004). Growth trends in *M. trifoliata* leaf biomass were similar between grazing treatments, the only significant difference being a later peak in the most active phase of growth potentially from lower level grazing or indirect disturbance. There was no direct evidence of selective foraging on flowers despite the difference in flower biomass between treatments. Early season foraging on *M. trifolitata* rhizomes and petioles may have impacted floral tissues before buds were formed, thus modifying the development of the plant (Crawley, 1983). Resources may have then been diverted to vegetative processes, such as leaf and rhizome maintenance, rather than flower production (Haraguchi, 1996). Relative to the 2003 survey the coverage of *M. trifoliata* increased, therefore the destruction of floral tissue may have contributed to consolidation of the rhizome mat.

Observations of changes in species richness and diversity in areas occupied by beaver often attribute this to ecosystem engineering associated with dam building that promotes geomorphological and hydrological heterogeneity across the landscape (Jones *et al.*, 1994; Sturtevant, 1998; McMaster and McMaster, 2000; Wright *et al*., 2002, 2003; Rosell *et al.*, 2005). At the present site there has been little change in hydrology over 10 years of beaver occupancy (and estimated 10 cm) and the indirect effects of beaver engineering on macrophyte diversity can therefore be largely discounted. It is important to disentangle the effects of physical ecosystem engineering and plant-herbivore interactions if we are to understand the contribution of each factor to biological changes at the plot, site and landscape scale, especially if the herbivore population is reintroduced or non-native. As beavers were the only significant consumer of macrophytes within this habitat it is clear that, over time, their net foraging impacts significantly increased macrophyte diversity at alpha and beta levels through intra- and inter-specific selection. Within-season foraging impacts on macrophyte diversity were less pronounced, suggesting that changes in macrophyte assemblage due to beaver herbivory are better studied over the medium to long-term.

4.6 Conclusion

Beavers are historically widespread in temperate and boreal regions and are increasingly re-establishing within their original range as well as being introduced outside it. Grazing-related effects on macrophytes are therefore likely to be the historic norm. Although the present work reveals positive effects it is likely that these are mitigated by the higher productivity of the habitat. Studies of muskrats have highlighted greater impacts in lower productivity habitats (Dannell, 1986), consistent with the Dynamic Equilibrium model (Huston, 1994), and the positive effects of beaver grazing are therefore unlikely to prove universal. It is also unlikely that the effects reported here will persist indefinitely as beavers switch to new territories once resources are depleted (e.g. < 10 years (Wright et al., 2002)); yet their effects may persist for decades (Bonner et al., 2009). Consequently, at the landscape scale, herbivory by beavers, or recovery from its effects, is likely to enhance the regional diversity of wetland plants.

CHAPTER 5 – Engineering biodiversity: beavers enrich aquatic plant and beetle assemblages at multiple spatial scales

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Author comments: NW developed the project methodology and obtained principle funding from the Carnegie trust. Data collection was carried out by both NW and AL in Sweden (2012). FE and OL provided information on beaver activity and distribution for central Sweden. Identification of beetle specimens was carried out by AL with the assistance of GF. Data analyses were undertaken by AL with input from NW. Manuscript was prepared by both AL and NW. The data were presented by AL at an invitation only, international symposium of the ecology of inland waters in Donana, Spain, the Scottish Freshwater Group (both during October 2013), and also documented in the Freshwater Biological Associations' quarterly newsletter (FBA 62, Spring, 2014).

5.1 Abstract

The extent and quality of freshwater wetlands is declining globally. The reintroduction and natural re-colonisation of beavers to their former range offers one possible biologically-based solution to the need for wetland restoration or creation. Through dam building beavers have the potential to significantly modify ecosystems, and, coupled with smaller-scale disturbances, can create unique habitats (beaver ponds). By comparing active-phase beaver ponds with adjacent permanent wetlands, unformed by beavers (‘control’ wetlands), we documented the spatial effects of ecosystem engineering by beavers on wetland plants and water beetles at plot/sample, site and landscape scale. Beaver ponds were more diverse and species-rich at both plot and site scales in comparison to control wetlands, for both plants (15% and 33% greater richness at plot and site scales respectively) and beetles (16% and 19% greater richness at sample and site scales respectively), with 30% of the species found in beaver ponds being unique to this habitat. Species assemblages differed between wetland types, more so for plants than beetles, therefore in a simulated wetland landscape incorporating active beaver ponds contained on average 14% more plant species and 24% more beetle species than one without. The benefits to biodiversity that accrue from the coexistence of beaver wetlands in the landscape at different successional states are well documented. Our findings demonstrate that beavers are also architects of heterogeneity at the local scale which is reflected in elevated diversity of disparate wetland-dependent taxa at a hierarchy of scales.

5.2 Introduction

Freshwater habitats are crucial for the conservation of global biodiversity (Gioria et al. 2010) and functioning of ecosystems, but they also contribute ecosystem services that are essential to society (Vigerstol & Aukema 2011). Despite this, most freshwater habitats have been impacted by multiple anthropogenic stressors for many centuries (Burroni et al. 2011). Ponds and wetlands In particular which contribute disproportionally greater biodiversity to the landscape in comparison to lakes, ditches, streams and rivers, have become globally threatened in part due to overexploitation, pollution, drainage and other forms of degradation (Williams et al. 2004; Dudgeon et al. 2006; Gioria et al. 2010). Construction of artificial wetlands and ponds or functional restoration of degraded wetlands in agricultural areas are common methods of compensation (Biggs et al. 2005; Williams, Whitfield & Biggs 2008; Thiere et al. 2009). However, lower cost, 'biotic approaches' that exploit the distribution or behaviour of organisms or trophic interactions, may also be useful to accelerate recovery, promote heterogeneity and restore lost ecosystem services. For example, donor seed banks may be used to re-establish vegetation in areas affected by water level changes or in newly-created wetlands (van der Valk, Pederson & Davis 1992). Sustainable biomanipulation of fish densities in lakes may deter algal growth by restoring top-down control, thereby allowing establishment of submerged aquatic plants that are negatively affected by eutrophication (Søndergaard et al. 2008). Alternatively, introducing keystone species, e.g. muskrat or beaver, may directly or indirectly alter the biological and physical habitat (Danell 1996; Burchsted et al. 2010).

By modifying existing ecosystems through dam building, beavers have the capacity to create ponds and wetlands from streams, and are being increasingly reintroduced, partly on the premise that their ecosystem engineering can restore landscape heterogeneity and functional diversity (Burchsted et al., 2010; Halley and Rosell, 2002; Nolet and Rosell, 1998). Beavers construct dams to raise and stabilise water levels thus maintaining a submerged lodge entrance, inundating surrounding land and associated resources, whilst reducing exposure to terrestrial predators (Hartman, 1996). The cost of travel to foraging areas and in transporting bulkier items is also reduced by buoyancy (Law, Bunnefeld and Willby 2014). However, the impoundment of water will also alter the surrounding physical and biological environment. For example, dams retain sediment and organic matter, thereby modifying nutrient cycling and decomposition dynamics which influences water chemistry and materials transported downstream (Naiman et al., 1988). The result is often increased coarse-scale heterogeneity, through the combination of engineered and non-engineered sites in a landscape, as well as from the coexistence of individual engineered sites that represent different successional states from newly formed to long abandoned. This is reported to enhance landscape diversity for many groups of organisms e.g. aquatic plants (McMaster and McMaster, 2001), other herbaceous plants (Wright et al., 2002), invertebrates (Rolauffs et al., 2001), fish (Kemp et al., 2011), amphibians (Dalbeck et al., 2007), bats (Nummi et al., 2011), and waterfowl (Nummi and Holopainen, 2014).

A beaver group (usually 2-6 individuals) typically inhabits a territory for a finite period, generally less than 10 years (Svendsen, 1989; Wright et al., 2002), but this can be considerably longer (Howard and Larson 1985; Zavyalov 2011) depending on topography and food resources (Naiman et al. 1988). However, their imprint on an ecosystem may persist for decades (Bonner et al., 2009; Johnston and Naiman, 1990b) as ponds undergo a cycle of vegetation succession primarily controlled by occupation (McMaster and McMaster, 2001; Ray et al., 2001), but also the initial level of modification. In the short-term (< 1 year) these physical habitat modifications may be destructive, as species assemblages adjust to the rapid change in hydrology. Subsequently however, habitats within beaver ponds may become more dynamic than in other permanent wetlands due to a fluctuating hydrological regime caused by partial collapse, modification and rebuilding of dams that results in intermittent exposure of pond margins (Gurnell, 1998). Hydrological fluctuations are typically coupled with smaller-scale disturbances and linked features, including selective foraging, wind blow of dead trees and accumulation of woody debris that are intrinsic features of these engineered wetlands. Consequently, diversification and increased dynamism of the physical habitat may be reflected in alterations of biodiversity in beaver-created ponds compared to other wetlands (e.g. non-beaver modified, temporary or man-made wetlands), across a range of spatial scales.

Wetland plants (including aquatic taxa) are an ideal group from which to assess differences between beaver ponds and other permanent wetlands as they are susceptible to changes in hydrology, depth, water chemistry and shading (Birk and Willby, 2010), and are selectively foraged by beaver (Law, Jones & Willby 2014; Parker et al., 2007). Any beaver-generated, small-scale disturbances or differences in environmental conditions driven by dam construction should therefore affect the structure and function of wetland vegetation and dependent organisms (Bonner et al., 2009). In addition, beaver-dug canals that aid transportation of felled material, provide elongated vegetated edge habitats dissected by woody debris that creates a series of pools, sheltered from wave action and predators. This combination of conditions is likely to affect macroinvertebrate composition and to enhance their abundance and diversity (Christensen and Crumpton, 2010; Hood and Larson, 2013). A greater dissimilarity of vegetated patches may also provide more opportunities for refuge and successful hunting strategies (Bloechl et al., 2010), which is likely to benefit species particularly associated with wetland margins, such as water beetles (Fairchild et al., 2003). Water beetles are a highly diverse group with 12,600 species described globally and high levels of endemism at the local scale (Jäch and Balke, 2007). As excellent colonists of temporary and semi-permanent wetlands (Fairchild et al., 2003) water beetles are sensitive to environmental variation and easy to sample, their taxonomy and ecology also being well-known (Gioria et al., 2010). Therefore they are an ideal group from which to compare richness and composition between beaver ponds and non-beaver wetlands, and to test for potential secondary effects of wetland plant diversity and composition.

If beavers create hydrologically distinctive ponds within the landscape they have the potential to actively increase species richness and diversity across several organismal groups at a variety of temporal and spatial scales. However, few studies have considered how ecosystem engineering by beavers affects disparate biota in parallel, or in comparison to ‘control’ wetlands formed independently of beaver activity. Indeed most previous studies have focused on successional changes within beaver ponds (McMaster and McMaster, 2001; Ray et al., 2001) or the contribution of abandoned rather than active ponds to landscape diversity (Bartel et al., 2010; Wright et al., 2003). Since both plants and beetles found in wetlands are highly taxonomically diverse, contain species indicative of particular environmental conditions and differ in their mobility and dispersal abilities, they are ideal subjects for a comparative study of biodiversity in beaver-created ponds vs. control wetlands at multiple spatial scales.

Here we test the following hypotheses: (i) beaver ponds contain greater wetland plant and water beetle richness at a range of spatial scales (plot and site) than other wetlands, (ii) differences in environmental conditions between wetland types contribute to compositional differences in plants and beetles, and (iii) the diversity and composition of wetland vegetation affects the beetle assemblage.

5.3 Methods

5.3.1 *Sites*

The study was conducted within a 100 x 100 km area between Örebro and Skinnskatteberg, in southern, central Sweden (59º 30’ N, 15º 10’ W, elevation range: 28-156 m). Within this area, ponds that were created by beaver (i.e. beaver ponds (Fig. 5.1a)) were identified by the presence of well-maintained beaver dams that impounded an area of shallow, standing water upstream. Recently constructed dams and associated wetlands (< 1 year old) were not considered. The minimum age of beaver ponds used in this study was estimated to be 5 years based on the age and extent of standing dead wood and aerial imagery from 2006-2010 (Google Earth 7.1.2.2041). All beaver ponds supported active beaver colonies as indicated by grazing of herbaceous plants, coppiced trees, canal creation, dam maintenance and lodge construction. Non-beaver wetlands (i.e. ‘control’ sites) in this study were defined as areas of permanent, shallow, standing-freshwater (ponds or sheltered lake margins and associated minerotrophic wetlands) where light penetrated the majority of the water column allowing unrestricted aquatic plant growth (Fig 5.1b). Control sites were most likely formed from by geological processes during the last glacial retreat, but crucially, no beaver dams influenced the hydrological regime in these wetlands, although most sites showed evidence (e.g. gnawed trees) of occasional use by beaver. Control sites were located in close proximity (< 5 km) to sampled beaver ponds, but were not paired with specific sites. A total of 10 beaver ponds (1.5 ± 0.5 ha, 0.6 – 2.1 ha; mean ± SD, range) and 10 control wetlands (0.9 ± 0.4 ha, 0.3 – 1.7 ha) were sampled.

Fig. 5.1 An example of; a – beaver-created pond and b – control wetland located within the study area. Note the beaver-generated woody debris, standing dead wood and openings in the canopy in the beaver pond. Whereas, control wetlands display little beaver riparian disturbance or floating woody debris (© Nigel Willby, July 2012).

5.3.2 *Methods*

In order to compare water bodies of varying dimensions and characteristics sampling was undertaken on an area-limited basis with 25 quadrats of 2 x 2 m placed randomly in vegetated areas < 1.5 hectares in size. Quadrats were a minimum of 10 m apart. Wetland vegetation (i.e. all submerged, floating-leaved, emergent and marginal plant species, including tree saplings and bryophytes) were identified to the highest feasible taxonomic level. Nomenclature followed Karlsson & Agestam (2013). Cover was estimated visually and assigned a score on a scale of 1-5 (1 = < 2%; 2 = 3 - 10%; 3 = 11 - 25%; 4 = 26 - 50%; 5 = > 51%). In subsequent analyses all identified species, hybrids, subspecies and indeterminate species were given equal status and no elements of the flora were specifically excluded. In each quadrat maximum plant height and water depth was measured in 6 places. The extent of leaf litter, open water, woody debris, bare ground and visible grazing was also estimated using the 1-5 scoring system. Water conductivity was measured using a conductivity meter (Hanna instruments HI 9033, multi-range conductivity meter) calibrated to 25 ºC. The environmental variables listed were selected on the basis that they could affect wetland plant abundance and composition, and could be measured easily in the field at high spatial resolution.

Within the same sites water beetles were sampled in shallow water (< 0.5 m deep) and associated vegetation using a D-framed net of 1 mm mesh size. The net was swept continuously through the water column, over the pond bed and through any aquatic vegetation within an area of 2 x 2 m for approximately 1 minute, and material sorted on a large white tray in the field. All adult and larval beetles found were preserved in 20 ml vials containing 80% methylated spirit until microscope identification. Five sweep samples were taken per wetland with each sweep being associated with a specific vegetation quadrat. Therefore any effects of plant composition and cover and abiotic environmental factors on beetle composition and density could be tested. Beetles were identified to the highest taxonomic level possible, with individuals that could only be identified to family or genus being assigned to the closest, most commonly identified species for the purposes of subsequent numerical analysis. The definition of whether a beetle species is considered truly aquatic or terrestrial is problematic as the reliance on water varies with developmental stage (Jäch and Balke, 2007). For this study we considered only true water beetles i.e. those “at least partly submerged for most of the time in their adult stage”, as opposed to false water beetles i.e. those “submerged for most of the time of their larval stage, adults always predominantly terrestrial” (Jäch & Balke, 2007). Beetle nomenclature followed Nilsson (2014).

5.3.3 *Exploratory and statistical analyses*

To assess differences between beaver pond and control wetland areas an unpaired *t*-test was used. Linear regression was used to examine effects of wetland area on both aquatic plant and beetle species richness. Richness was assessed in terms of numbers of species at several different spatial scales: plot or sample (both 2 x 2 m), site and landscape. A sample-based species accumulation curve for the wetland vegetation was computed based on a maximum sample size of 250 quadrats (25 quadrats in each of 10 sites) without replacement. An individual-based rarefaction curve (Colwell et al., 2004) was used to observe species accumulation rates for beetles due to pronounced differences in the number of individuals found per sweep (n= 50 sweep samples across 10 sites). The accumulation rate was calculated, firstly for each wetland type individually and secondly for a composite sample of the same size based on data from both wetland types pooled. This provided an indication of landscape scale species accumulation rate based on equal encounter rates of the two wetland types. Data from all plots or samples within a site were then aggregated to examine species accumulation rates at the site scale for both plants (n=10, where the data for each site is based on the aggregation of 25 quadrats) and beetles (n=10, where the data is based on five sweeps per site) and the analyses repeated. Expected species richness was calculated using Chao’s species estimator based on a species abundance matrix (Chao, 1987).

Using generalised linear mixed effect models with a log-link Poisson error distribution (R library lme4 (Bates, Maechler & Bolker, 2012)) the effects of environmental variables on plant richness and beetle abundance were tested. Site was included in all models as a random effect. Prior to running models for aquatic plant richness at the plot and site scale continuous environmental variables i.e. conductivity, mean plant height, mean water depth, leaf litter, area of open water, woody debris and area of bare ground were standardised to zero mean and unit standard deviation (Zuur et al., 2013) and checked for collinearity using the corvif function in the R library AED (Zuur, 2010). No variables were found to be significantly correlated ($P < 0.05$). In addition to these variables, the number of plant species and maximum plant coverage per plot (%) were included in the global beetle model at the plot scale. At the site scale, the mean Bray-Curtis dissimilarity index (BCI) calculated between all pairwise combinations of vegetation plot data from a site was included as a fixed effect. BCI was used a proxy for plant beta diversity between plots within sites. Similarly, all variables were checked for collinearity, with area of bare ground subsequently being removed from both plot and site models for beetles due to its variance being inflated through a negative correlation with the term maximum coverage. No other variables were found to be significantly correlated ($P < 0.05$).

Relationships between both plant and beetle composition and standardised environmental variables were examined using Canonical Correspondence Analysis (CCA). A log (x +1) transformation was applied to aquatic plant and beetle compositional data prior to analysis. An automated, forward stepwise selection of variables was conducted on the initial global model (all measured environmental variables used) with the most parsimonious models being selected based on a significant contribution of each variable ($P < 0.05$). Furthermore, the significance of the most parsimonious model and relationship of each CCA axis to species composition were tested using a Monte Carlo random permutation test (1,000 permutations). Co-correspondence analysis was used to identify any significant effect of vegetation composition on the beetle assemblage (ter Braak & Schaffers, 2004), using the log transformed compositional data. A leave-one-out cross-validation was used to obtain the fit for different number of axes solutions and to select the minimum adequate predictive model (see Gioria *et al.*, 2010). Shannon's Diversity Index (H') was used to describe the diversity of species, with the output analysed using the Mann-Whitney *U* test due to non-parametric data distribution. A Mann-Whitney *U* test was also used to test for differences in mean BCI, and environmental variables between plots from beaver and control sites.

All statistical analyses and graphics were produced using R Studio version 2.15.0 (R Development Core Team, 2013) with the additional packages; vegan (Oksanen *et al*., 2012), fossil (Vavrek, 2011), BiodiversityR (Kindt & Coe, 2005), ecodist (Goslee & Urban, 2007), plyr (Wickham, 2011) and cocorresp (Simpson, 2009).

5.4 Results

5.4.1 *Species richness*

Wetland areas did not significantly differ between beaver ponds and control wetlands ($t_{16} = 2.02$, $P = 0.06$), nor did area have any effect on plant ($F_{1,18} = 0.66$, $P = 0.42$) or beetle ($F_{1,18} = 0.01$, $P = 0.96$) species richness.

A total of 156 species of plants were recorded in the wetlands studied. Sites were particularly rich in marginal species such as sedges (18 species) and rushes (6 species). *Lysimachia thyrsiflora* L. (41% of plots overall) and *Carex rostrata* Stokes (40% of plots overall) were the most frequently recorded species. Both were recorded more commonly in beaver ponds (63.8% and 57.0% respectively) compared to control wetlands (36.2% and 43.0% respectively) (Appendix 5.1).

A total of 60 beetle species, across 9 families (11 subfamilies) were identified from the 590 individuals collected (Table 5.1) (Appendix 5.2). Species from the family Dytiscidae accounted for the majority of individuals (77.9%) followed by Haliplidae (6.5%) and Hydrophilidae (5.0%). The most speciose family was the Dytiscidae (36 species), with *Ilybius ater* (De Geer, 1774) and *Ilybius fuliginosus* (F.) being found most often across all samples (48% and 42% sweeps respectively). *I. ater* was found more often in beaver ponds (n=16) compared to control wetlands (n=8), but the frequency of occurrence in sweeps was similar for *I. fuliginosus* (11 for beaver and 10 for control wetlands). These species together accounted for 12.9% of individuals found; *Hydroporus palustris* L. accounted for the largest proportion of individuals recorded (11.5%), and was dispersed evenly across site types (9 for beaver ponds and 11 for control wetlands).

For both plants and beetles a greater number of species were found in beaver ponds, almost a third of which occurred only in this habitat, whereas a fifth of species were unique to control wetlands (Table 5.1). Beaver ponds were more species-rich at both plot and site scales in comparison to control wetlands, for both plants (15% and 33% greater richness at plot and site scales respectively) and beetles (16% and 19% greater richness at sample and site scales respectively).

Table 5.1 Observed aquatic plant and beetle species richness summaries per wetland type.

Group	Wetland type	Mean species per quadrat or sweep (range)	Mean species per site (range)	Unique to wetland (% of overall total)	Total species observed	Total species expected (Chao1)	Mean no. of individuals per sweep (total sampled)
Plants	Beaver	7.1 (1-18)	40.9 (29-53)	48 (30.8%)	126	128.3	-
	Control	6.2 (2-17)	30.7 (19-60)	30 (19.2%)	108	109.5	-
	Combined	6.7 (1-18)	35.8 (19-60)	-	156	158.6	-
Beetles	Beaver	3.6 (1-11)	12.8 (10-19)	18 (30.0%)	48	67.1	6.7 (327) 1-31
	Control	3.1 (1-7)	10.8 (6-16)	12 (20.0%)	42	61.0	5.3 (263) 1-32
	Combined	3.3 (1-11)	11.8 (6-19)	-	60	68.7	6.0 (590) 1-32

At the plot scale a greater number of plant species were found in beaver ponds in comparison to control wetlands, although plots from control sites did contribute to the total species pool (Fig. 5.2a). A similar sized random subsample from both wetland types combined therefore yielded fractionally (4%) more species than a sample of the same size from beaver ponds only. Rarefaction indicated that for an equivalent level of sampling effort (i.e. the same number of individuals) a marginally greater number of beetle species were found in beaver ponds compared to control wetlands (Fig 5.2c). Compared to a landscape from which beaver ponds were absent a composite sample of both wetland types contained on average 14% more plant species and 24% more beetle species. Accumulation curves did not fully reach an asymptote, the total number of plant species recorded was very close to the expected value generated by the Chao estimator indicating that sampling was adequate. In the case of water beetles it was evident that greater un-sampled richness existed within both wetland types. The tendency for higher plant and beetle richness in beaver ponds was maintained at the site scale (Fig. 5.2b and d). Accumulation curves based on site scale data did not reach an asymptote for both groups indicating that a greater number of species would be found if more sites were sampled, though perhaps not within the overall confines of the study region. The greater gamma diversity found in beaver sites compared to combined sites (beaver + control), indicated a higher absolute turnover of plant species between beaver ponds than other wetlands (Fig, 2b); this pattern did not occur for beetles (Fig. 2d).

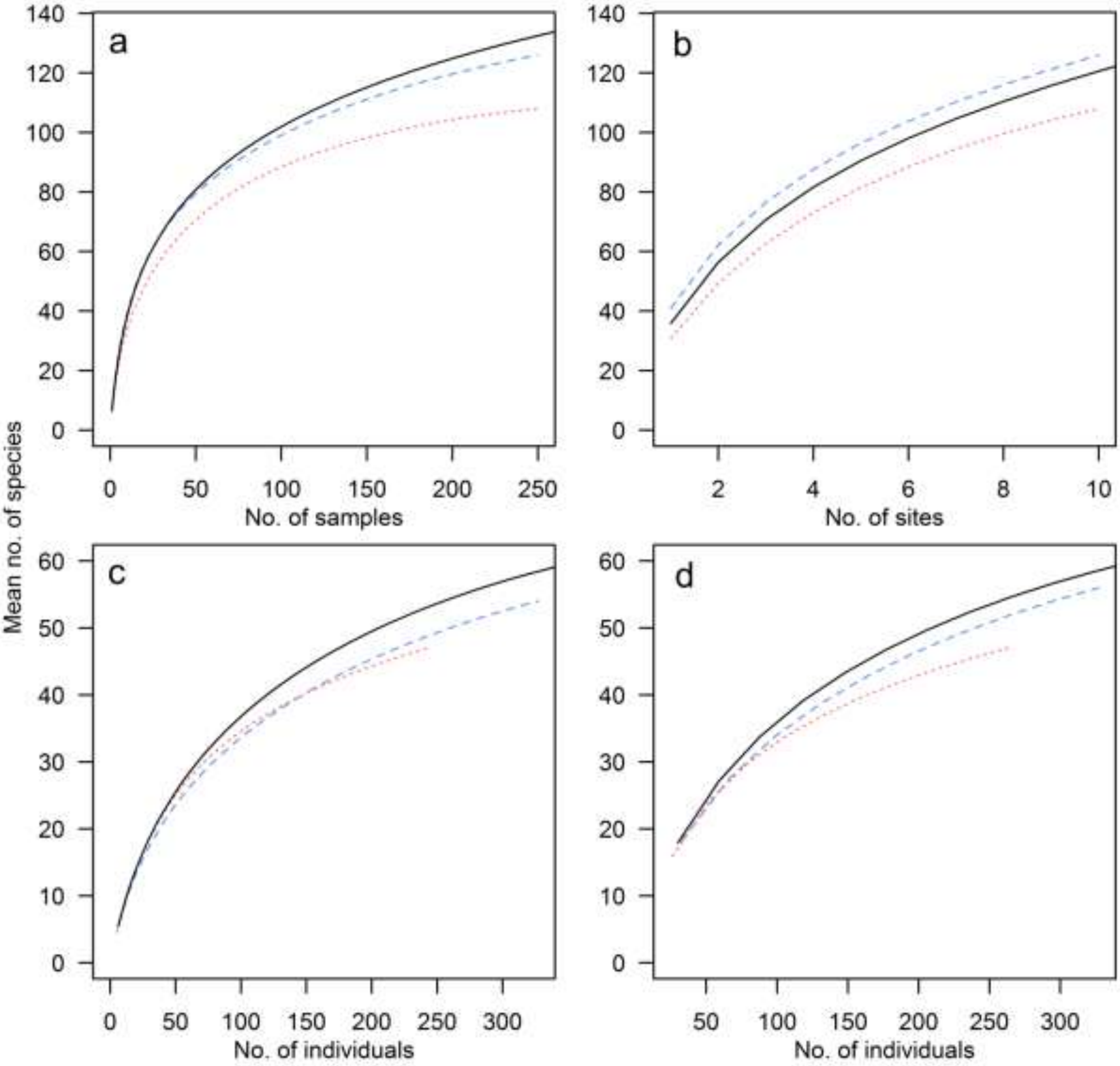

Fig 5.2 Species accumulation curves for beaver ponds (blue, dashed lines), control wetland (red, dotted lines) and both wetland types combined (black, solid lines). a – plants (sample-based accumulation at plot scale; mean SD ± 4.3, ± 4.0 and ± 4.7 species for beaver ponds, control wetlands and composite sample respectively), b – plants (sample-based accumulation at site scale; mean SD ± 5.7, ± 9.6 and ± 8.0 species), c – beetles (individual-based rarefaction at plot scale mean SD ± 2.0, ± 1.8 and ± 2.1 species) and d – beetles (individual-based rarefaction at site scale, mean SD ± 2.0, ± 1.8 and ± 2.2 species).

Environmental variables that could affect plant species richness did so in different ways, e.g. water depth and leaf litter had a negative effect on modelled richness at the plot scale, while richness increased with conductivity (Table 5.2). Some of these variables differed consistently between wetland types (Table 5.3). Plant height, a common indicator of competitiveness, was greater in control wetlands and had a significant negative association with modelled plant richness. Conductivity, despite having a positive relationship with species richness, was higher in control wetlands where observed richness was lower. As plots from beaver ponds were, on average, more species rich in comparison to control wetlands, the differences in richness are not completely accounted for by the measured environmental variables, hence the term wetland type was significant in the model.

Table 5.2 Generalised linear mixed effect model outputs for plant richness at plot and site scales.

Scale		Coefficient estimate	SE	*Z*	P
Plot (N=500)	Intercept	1.9322	0.0332	58.21	< 0.001 ***
	Conductivity (µS cm^{-1})	0.0351	0.0175	2.00	0.045 *
	Plant height (cm)	-0.0708	0.0219	-3.23	0.001 **
	Water depth (cm)	-0.0774	0.0231	-3.35	< 0.001 ***
	Leaf litter (%)	-0.0719	0.0226	-3.18	0.001 **
	Open water (%)	-0.0479	0.0203	-2.36	0.018 *
	Woody debris (%)	-0.0103	0.0187	-0.55	0.581
	Bare ground (%)	-0.1241	0.0205	-6.05	< 0.001 ***
	Wetland type (control)	-0.1306	0.0493	-2.65	0.008 **
Site (N=20)	Intercept	3.6784	0.0660	55.71	< 0.001 ***
	Conductivity (µS cm^{-1})	0.1289	0.0370	3.48	< 0.001 ***
	Plant height (cm)	0.0191	0.0619	0.31	0.757
	Water depth (cm)	-0.1010	0.0590	-1.71	0.087
	Leaf litter (%)	-0.1422	0.0591	-2.41	0.016 ***
	Open water (%)	0.0198	0.0427	0.46	0.642
	Woody debris (%)	-0.0122	0.0566	-0.22	0.829
	Bare ground (%)	-0.0652	0.0624	-1.05	0.296
	Wetland type (control)	-0.2704	0.1146	-2.36	0.018 *

At coarser spatial scales (i.e. sites), fewer environmental variables explained variation in modelled richness, with those factors proving significant at the plot scale not necessarily contributing to explanatory power at site scale (Table 5.2). However, at both spatial scales the term wetland type, regardless of the effect of other environmental variables, still accounted significantly for variation in aquatic plant richness.

Table 5.3 Summary of the means ± standard errors (range) and coefficient of variation (COV) of measured abiotic factors per plot for each wetland type. Asterisks indicate significantly greater differences from Mann-Whitney U tests within groups (< 0.001 ***, < 0.01 **, < 0.05 *).

Wetland type	Beaver (n=250)		Control (n=250)	
	Mean ± SE	COV (%)	Mean ± SE	COV (%)
Conductivity (µS cm^{-1})	58.5 ± 2.7 (24 – 242)	4.7	82.8 ± 6.9 *** (23 – 1050)	8.4
Plant height (cm)	75.9 ± 2.3 (5 – 220)	3.1	83.5 ± 2.0 *** (15 – 200)	2.4
Water depth (cm)	20.7 ± 1.2 (1 – 100)	5.7	22.3 ± 1.0 * (0 – 80)	4.4
Leaf litter (%)	1.8 ± 0.4 (0 – 75)	23.1	4.8 ± 0.5 *** (0 – 38)	10.2
Open water (%)	5.6 ± 0.7 *** (0 – 75)	13.4	3.1 ± 0.5 (0 – 38)	14.4
Woody debris (%)	3.4 ± 0.4 *** (0 – 38)	11.0	0.1 ± 0.1 (0 – 6)	36.5
Bare ground (%)	19.0 ± 1.7 (0 – 77)	6.2	17.5 ± 1.1 (0 – 73)	6.3

Beetle abundance was used as the response variable in models in order to correct for observed differences in abundance between wetland types, since a higher number of individuals indicated a higher number of species (Fig. 5.2c). At the plot scale water depth and woody debris had significant positive and negative effects on beetle abundance respectively, though these did not fully explain differences between wetland types (Table 5.4). In contrast, at the site scale, only woody debris had any effect on beetle abundance. Plant richness, coverage and turnover had no effect on beetle abundance at either plot or site scale.

Table 5.4 Generalised linear mixed effect model outputs for beetle abundance at plot and site scales.

Scale	Fixed effects	Coefficient estimate	SE	*Z*	*P*
Plot (N=50)	Intercept	1.9410	0.1509	12.86	< 0.001 *
	Conductivity (µS cm^{-1})	-0.1095	0.0855	-1.28	0.200
	Plant height (cm)	-0.0481	0.0520	-0.93	0.355
	Water depth (cm)	0.2108	0.0579	3.64	< 0.001 ***
	Leaf litter (%)	0.0693	0.0706	0.98	0.327
	Open water (%)	-0.1081	0.0595	-1.82	0.069
	Woody debris (%)	-0.1081	0.0477	-2.27	0.024 *
	Max. cover (%)	0.1150	0.0596	1.93	0.054
	Wetland type (control)	-0.5045	0.2209	-2.28	0.022 *
	Plant richness	0.0555	0.0612	0.91	0.364
Site (N=20)	Intercept	3.3283	0.1353	24.61	< 0.001 ***
	Conductivity (µS cm^{-1})	0.0491	0.1066	0.46	0.645
	Plant height (cm)	0.0579	0.1478	0.39	0.695
	Water depth (cm)	-0.0153	0.0650	-0.22	0.823
	Leaf litter (%)	-0.2290	0.1579	-1.45	0.147
	Open water (%)	0.0122	0.0663	0.18	0.854
	Woody debris (%)	0.1755	0.0812	2.16	0.031 *
	Max. cover (%)	-0.0242	0.1274	-0.19	0.849
	Wetland type (control)	-0.0583	0.2503	-0.23	0.816
	Plant richness	-0.0085	0.1260	0.07	0.947
	Mean BCI	-0.0756	0.0963	-0.79	0.432

5.4.2 *Species composition and diversity*

The vegetation composition of plots separated between beaver ponds and control wetlands, with limited areas of overlap i.e. shared species (Fig. 5.3). Permutation tests of the overall analysis indicated that plant composition was significantly related to the measured environmental variables ($F = 3.44$, $P < 0.001$), with all terms significant ($P < 0.010$). Overall however, these environmental variables only explained a small amount of the global variation observed in plant composition at the plot scale (adj. $R^2 = 6.0\%$). At the site scale, permutation tests of the analysis of plant composition in relation to environmental variables indicated only weak effects ($F = 1.23$, $P = 0.052$).

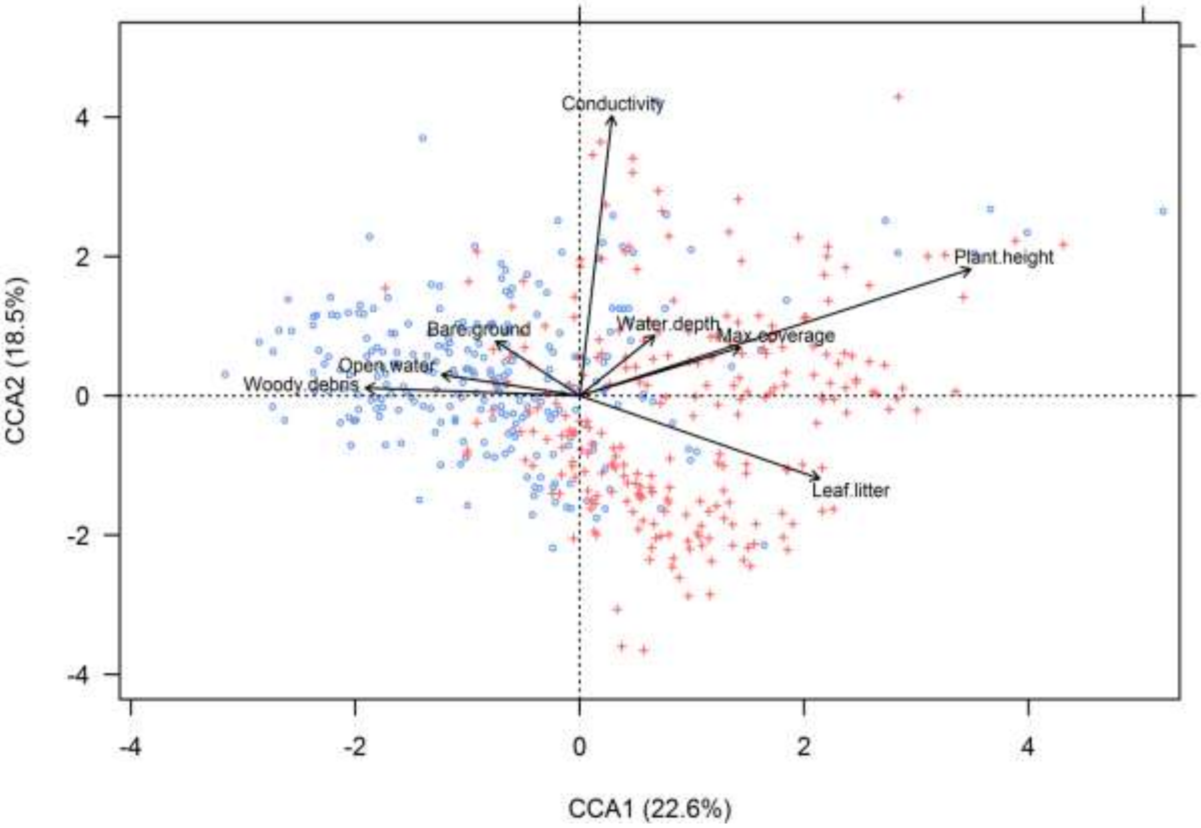

Fig. 5.3 Output from canonical correspondence analysis (CCA) of plant composition displaying the distribution of plots from both beaver ponds (blue, open circles) and control wetlands (red crosses) in relation to measured environmental variables. The direction and length of the arrows indicate importance and correlation to the respective axes. Percentages show the proportion of the constrained inertia that is explained by each axis.

Compositional differences between wetland types were less apparent for beetle composition with plots from beaver ponds and control wetlands frequently overlapping (Fig. 5.4). Though the overall CCA model was significant (*F* = 1.66, *P* = 0.001), only two of the measured environmental variables explained a significant amount of variation in composition, i.e. leaf litter (*F* = 1.38, *P* = 0.024) and conductivity (*F* = 1.75, *P* = 0.038). Similarly to plant composition, CCA only partially explained beetle composition at the plot level (adj. R^2 = 5.0%). At the site scale, permutation tests of the analysis between beetle composition and environmental variables indicated no significant effects (*F* = 1.15, *P* = 0.091).

Co-correspondence analysis estimated that cross-validatory accuracies were less than zero, therefore plant community composition had no predictive effect on beetle communities.

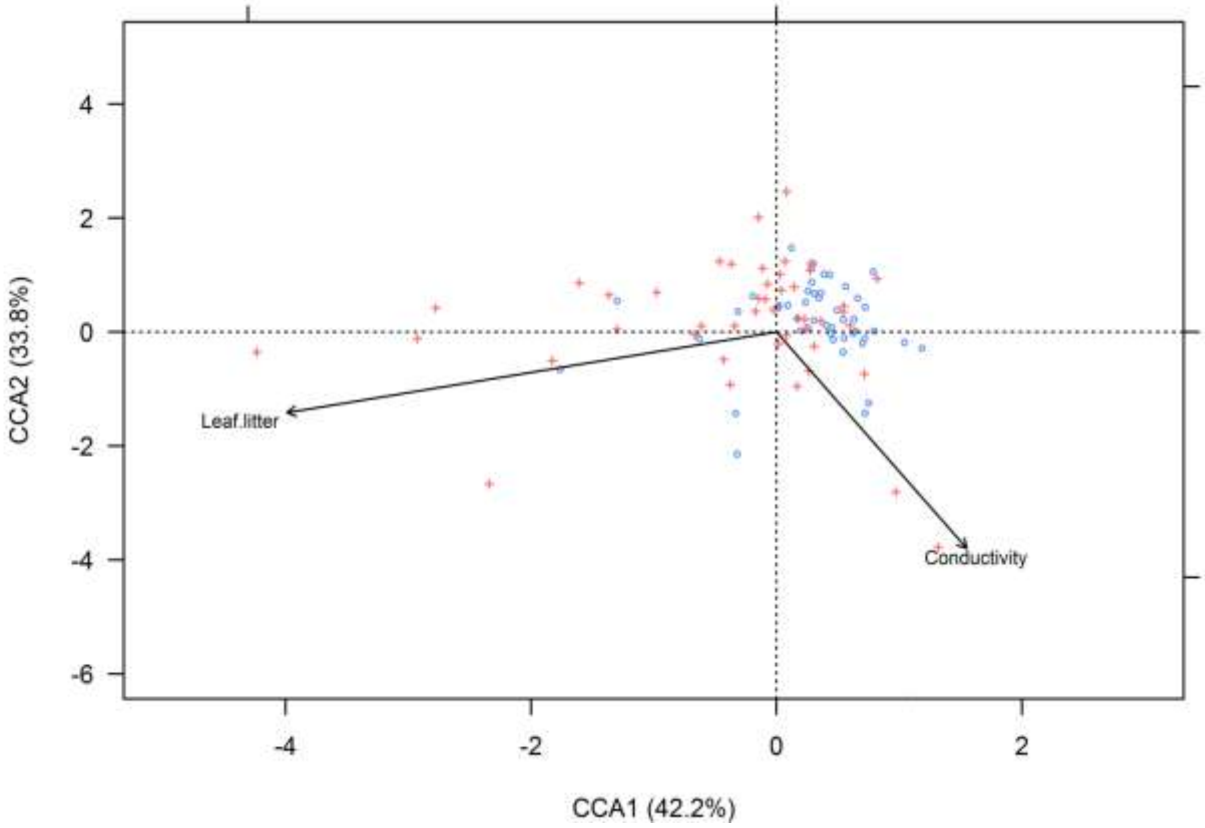

Fig. 5.4 Output from canonical correspondence analysis (CCA) of beetle composition displaying the distribution of plots from both beaver ponds (blue, open circles) and control wetlands (red crosses) in relation to measured environmental variables. The direction and length of the arrows indicate importance and correlation to the respective axes Percentages show the proportion of the constrained inertia that is explained by each axis.

Beaver ponds had significantly greater plant diversity than control wetlands at both the plot level and site level (Table 5.5), indicating a more even distribution of species cover. Within beaver ponds, plots were also relatively more dissimilar to each other, indicating higher within-site beta diversity compared to plots from control wetlands. However, the opposite trend applied at the site scale as plant assemblages within control wetlands displayed significantly greater mean dissimilarity between pairs of sites than did beaver ponds. Thus, although control wetlands gained new plant species at a slower absolute rate than beaver wetlands (Figure 5.3a) in relative terms the gain in species and its effect on dissimilarity was higher in control wetlands than in beaver sites. Similarly for beetles, species diversity was greater in beaver ponds and samples from these compared to control wetlands, but not significantly so (Table 5.5). Turnover in beetle composition between samples was the same in the two wetland types, but at the site scale a significantly greater dissimilarity occurred in control compared to beaver sites.

Table 5.5 Mean (± standard error) Shannon's diversity index (H') and Bray-Curtis dissimilarity index (BCI) for both aquatic plants and beetles from beaver ponds and control wetlands at the plot and site scale. Asterisks indicate significant differences from Mann-Whitney U tests (< 0.001 ***, < 0.01 **, < 0.05 *).

		H'		BCI	
Group	Scale	Control	Beaver	Control	Beaver
Aquatic plants	Plot	3.8 ± 0.1	4.3 ± 0.1**	0.72 ± 0.004	0.84 ± 0.003***
	Site	12.7 ± 1.6	19.3 ± 1.3**	0.76 ± 0.2***	0.66 ± 0.01
Beetles	Plot	2.8 ± 0.2	3.2 ± 0.2	0.86 ± 0.02	0.86 ± 0.02
	Site	7.9 ± 1.0	9.5 ± 1.0	0.84 ± 0.01***	0.73 ± 0.02

5.5 Discussion

The creation of ponds and wetlands by beavers through the damming of streams is unique amongst global fauna and has the potential to create, modify and restore aquatic habitat. Beaver-created habitats differ from wetlands formed due to topographic factors or artificial impoundment. Fluctuations in water levels can be more rapid due to changes in dam height or integrity, and, due to the limited storage capacity of beaver ponds and their typical bank profile, small changes in depth can result in extensive exposure of marginal habitat (Gurnell, 1998; Pollock et al., 1998). In addition, a number of smaller scale disturbances are unique to beaver ponds that serve to enhance habitat complexity, e.g. selective plant foraging and herbivory, canal building and felled or wind-blown trees, plus lodges and cached material contributing to woody debris accumulations.

5.5.1 *Comparison between beaver ponds vs. control wetlands at the plot scale*

Creation of wetlands, whether by natural physical processes, by ecosystem engineers or artificially, can be destructive in the short-term (e.g. the initial 1-3 years), due both to the physicochemical changes that occur and the lag between replacement of terrestrial taxa by water-tolerant ones. For example, Bloechl et al. (2010) found that newly-created, artificial wetlands had lowest species richness and abundance (in terms of coleoptera and heteroptera) of all wetland age classes. However, new water bodies colonise quickly, with accumulation plateaus after 3-4 and 6 years for macroinvertebrates and aquatic plants respectively, as few new species join established communities after periods of stabilisation (Bloechl et al., 2010; Williams et al., 2008). Following the initial colonisation phase, studies on the effect of wetland age on aquatic plant and beetle richness and composition are inconclusive (Bonner et al., 2009; Fairchild et al., 2000; Lundkvist et al., 2001; Wright et al., 2003), but the contemporary biota are most likely related to the changing habitat complexity, landscape connectivity and diversity of abiotic conditions associated with succession (i.e. ecological age) rather than chronological age. None of the beaver ponds we studied were recently formed, i.e. within the last 1-2 years, indeed some may have derived from reworking pre-existing beaver ponds > 50 years old. The fact that active beaver ponds remain more diverse than other wetlands in the surrounding landscape suggests that within-pond dynamic processes associated with beaver presence (e.g. tree fall, herbivory, dam repair, canal building, water level fluctuations) continue to promote or sustain local heterogeneity, even as the pond itself ages. By ensuring continued high abiotic habitat diversity these processes are conducive to coexistence (Huston, 1994).

Of the environmental variables measured, the majority contributed in some way to the explanation of plant species composition. For example, leaf litter negatively affected plant richness, whilst partially explaining plant composition. Leaf litter was expected to be lower in beaver ponds due to physical disturbance and a reduction in standing vegetation by grazing beavers (Parker et al., 2007), although shallow fluctuating water may also promote litter breakdown. Also, conductivity had a significant, positive effect on plant species richness, yet was, on average, higher in control wetlands. Since the effect of some environmental variables was inconsistent with the observed difference in richness and composition between wetland types we cannot fully account for these differences. For water beetles, fewer of the environmental variables explained abundance or composition, and, as with plants, the effects of explanatory variables did not differ consistently between wetland types in the manner expected. For example, water depth was on average higher in control wetlands and had a positive effect on beetle abundance, despite the richness and abundance of beetles being greater in beaver ponds. Interestingly the abundance of woody debris had a negative effect on beetle richness at the plot scale. This may be an artefact of lower efficiency of sampling beetles from areas containing high volumes of woody debris, since, at the site scale, the effect of woody debris was positive in accordance with other studies (Benke and Wallace, 2003; France, 1997; Steel et al., 2003). There will most likely be temporal and other inherent differences between wetland types that influence species richness and composition but which are difficult to capture adequately during spatial studies, e.g. selective grazing (Law, Jones & Willby 2014), biotic interactions (Ray et al., 2001), felling disturbance, water level variation and relics of the previous hydrology and land use e.g. forestry and agricultural ditches.

Differences in plant richness and composition between wetland types were expected to lead to differences in beetle composition. For example, size and density of vegetated edges has previously been related to beetle abundance (Bloechl et al., 2010), whereas specific plant communities may affect the stability of the substratum and the cycling of nutrients (Gioria et al., 2010). Therefore increases in patch heterogeneity could explain the higher diversity of beetles found in beaver ponds (Hood and Larson, 2013), or, since habitat can be more finely partitioned, the chance of density-dependent conspecific encounters will be lower and dispersal away from a patch may therefore decrease (Yee et al., 2009). However, despite plant richness and diversity being greater in beaver ponds, there were no quantifiable effects on beetle abundance and composition at the plot scale. Therefore it seems likely that the interaction between beaver-created temporal and spatial disturbance within wetlands that promotes plant richness will also benefit beetles, but the grain size at which these effects operate differs between plants and beetles.

The species richness and composition of newly-created beaver wetlands will depend on active and passive immigration from the surrounding landscape which will be governed by reproductive strategies (Ray et al., 2001), the quality of the surrounding species pool and proximity of colonists. Wetland plants may colonise via a pre-existing dormant propagule bank that is activated by inundation, which may determine germination success and the sediment nutrient balance (Coops et al., 2003). Alternatively, propagules may be introduced from external sources via passive water-borne transport or animal vectors e.g. through beaver faeces or waterfowl that benefit from these wetlands (Nummi and Holopainen, 2014; Ray et al., 2001). Compared to plants, beetles are most likely to colonise by active mechanisms i.e. dispersal by flight (Fairchild et al., 2003).

5.5.2 *Comparison between beaver ponds vs. control wetlands at the site and landscape scale*

At the site scale beaver ponds also supported greater plant and beetle species richness than other wetlands, although at this scale fewer environmental variables contributed to the explanation of plant species richness. However, most importantly, wetland type remained a significant explanatory variable for plants, indicating sources of variation associated with wetland type but not accounted for by directly measured variables. Similarly for beetles, fewer environmental variables explained abundance and composition, perhaps not surprisingly, as the environmental factors behind habitat selection by beetles are poorly known and likely to be scale-, species-, and life stage-dependent (Lundkvist et al., 2001; Yee et al., 2009). Bloechl et al. (2010) and Lundkvist et al. (2001) found that variance in water beetle composition across the landscape was low in both artificially-created and agricultural ponds. Therefore the lack of strong differences in assemblage between sites in this study is not unexpected and most likely reflects active, direct dispersal between sites and the proximity of source populations. As vegetation composition had no predictable effect on beetle composition in this study, the presence of particular plants in a wetland cannot be used as an indication of beetle richness or abundance.

Greater species diversity in beaver ponds was also found at the site scale. However, species turnover between sites did not follow this trend as control wetlands were more dissimilar to each other compared to beaver ponds. Thus, proportionally more variation in plant and beetle assemblages occurred within than between beaver ponds, indicating local heterogeneity but regional uniformity within this resource (at least within the phase of active pond usage by beavers). By contrast, control wetlands were locally relatively uniform but regionally heterogenous. This finding could be due to the method of wetland formation, as all beaver ponds were created by a common method (beaver dams) and mostly affected forested streams, whereas control wetlands were created via multiple processes (e.g. glacial and geological formation) in different landscape types. In principle, we could have constrained our selection of control wetlands more tightly to cover a narrower set of conditions or methods of formation. This would likely have reduced regional heterogeneity, but would have failed to capture a random sample of other wetlands within the landscape and would therefore have restricted our ability to assess the relative value of beaver ponds at larger scales. High turnover in plant composition between plots within beaver ponds, as indicated by greater BCI, had no significant effect on beetle abundance at the site scale. Therefore in this study, local scale beaver-driven spatial heterogeneity in vegetation is not necessarily the factor underlying increased beetle abundance. This may partly reflect the inefficiency of univariate diversity indices in explaining community patterns (Gioria et al., 2010).

In accordance with Jones et al. (1997), at the scale that encompasses both beaver-created and non-modified wetlands, ecosystem engineering (i.e. dam-building, tree-felling) and subsequent foraging and other disturbances by beaver resulted in an increase in species richness, and in this study, increased species diversity and compositional differences. Beavers can therefore justifiably also be regarded as architects of heterogeneity.

5.5.3 *Implications of beaver-created ponds in the environment*

Beaver ponds are a natural component of the wetland landscape throughout the native ranges of beaver, even though these ponds may be managed in order to maintain drainage and restrict forestry losses and to protect the integrity of highways. Beaver ponds can be individually numerous but their collective effect on a stream network is variable, the proportion of the length affected being reported to range from 10 – 43% (Anderson et al., 2014; Ford and Naiman, 1988; Johnston and Naiman, 1990a; Snodgrass, 1997). The proportion of the total wetland area that is beaver-generated also varies widely, from almost the entire resource (e.g. Wright et al., 2002), through to a very small percentage in naturally wetland-rich regions (e.g. Johnston and Naiman, 1990b). In our study region, active beaver ponds accounted for a small proportion of the total wetland resource, which, combined with the naturally high extent of wetland habitat in Scandinavia might suggest only modest dependency on beavers to maintain aquatic biodiversity, at least at coarse (site to landscape) scales.

However, it is not sufficient to merely compare the biota of beaver-created and non-beaver wetlands to gauge the significance of beavers for aquatic biodiversity (Wright et al., 2002). At finer scales beaver ponds are hotspots of heterogeneity that may be otherwise missing from the wetland landscape, while beaver ponds increase landscape connectivity and thus affect the larger scale distribution and mobility of wetland biota (Milligan and Humphries, 2010). Moreover, beaver ponds are needed to sustain beaver populations at sufficiently high densities for them to influence other ecosystem types, such as lakes and riparian forest, where their dynamic effects are generally likely to prove positive for biodiversity.

How then will the restoration of beavers and their ecosystem engineering contribute to aquatic biodiversity in degraded landscapes, and are the effects of well-established beaver populations a useful guide to their potential effects when reintroduced elsewhere? In human-impacted landscapes greater inter-wetland distances may be enough to limit dispersal of wetland biota, in contrast to the weak effects of isolation on beaver ponds observed under natural conditions (Wright et al., 2004). The absence of a diverse and highly connected regional species pool might also be expected to constrain local heterogeneity. However, at a site scale, recent experiences in Scotland suggests that effects of beavers on local habitat heterogeneity (Law, Jones & Willby 2014) mirror those observed in forested landscapes, such as Sweden, where beavers already occur naturally at high densities (Hartman, 2011).

5.6 Conclusion

The reintroduction or re-establishment of beavers in their native range in itself enriches the freshwater fauna. However, through their ecosystem engineering activities, beavers then create unique habitats within the landscape, and thus indirectly modify and benefit wider biodiversity at multiple spatial scales. This study confirms that wetland creation by beavers will enhance landscape scale diversity of wetland plants and beetles through the formation of a different and uniquely heterogeneous habitat. Such benefits accrue within the phase of active pond use, not simply as a consequence of dam failure, pond abandonment and recolonisation, although these processes will undoubtedly magnify the landscape scale benefits of ecosystem engineering by beavers (e.g. Snodgrass (1997) and Wright et al. (2003)). The capacity of beavers for ecosystem engineering may yet prove most valuable in wetland-poor, degraded or homogenised landscapes where natural dynamic processes have been tamed. It is highly tempting to assume that any natural process or feature can be replicated through human intervention. However, while anyone can make a pond there is only one way to make a beaver pond.

CHAPTER 6 – Creating heterogeneity from uniformity: can beaver dams enhance aquatic macroinvertebrate assemblages in agricultural landscapes?

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6.1 Abstract

Naturally-occurring small-scale discontinuities such as woody debris dams are recognised as a key feature of functionally intact river systems because they aid organic matter retention, increase habitat complexity and provide flow refugia. Re-establishing such features in homogenised channels is therefore a common target of river restoration schemes. Habitat-engineering by beavers has been considered a potential natural mechanism for restoring degraded streams and is often invoked as a reason for the reintroduction of beavers. Here we investigated if hydromorphological changes caused by beavers are still translated into biological changes when the streams affected have a long history of physical degradation and modification of the regional species pool. Beavers modified in-stream habitat by creating a series of dams that impounded water, interspersed by flowing water conditions. Beaver-modified habitats displayed lower macroinvertebrate richness in comparison to un-modified habitats, independent of dams. However, due to significant compositional differences between influenced vs. non-modified habitats, a composite sample from all habitats displayed increased richness and functional feeding diversity. Our findings confirm that physical habitat heterogeneity associated with dam building by beavers has the ability to increase landscape-scale macroinvertebrate species richness, whilst modifying composition. Therefore even within degraded agricultural landscapes beavers can re-establish physical and biological diversity which may have catchment-wide implications.

6.2 Introduction

Small scale discontinuities, e.g. woody debris dams, are recognised as a natural part of functionally intact stream systems, a key concept in the maintenance and regulation of rivers globally and what is often strived for when restoring degraded systems (Burchsted et al., 2014; Poole, 2002). Yet such discontinuities are often removed by humans in the interests of improved drainage and flood conveyance, with channels becoming further homogenised and riparian zones encroached upon for agricultural use, or being engulfed by much larger scale artificial discontinuities, e.g. hydropower dams (Burchsted et al., 2010; Wohl, 2005). Efforts to restore natural discontinuities and associated heterogeneity in degraded stream systems e.g. by re-meandering or removing artificial structures such as weirs, can often be expensive, with monitoring being required for several years after to quantify effects (Jähnig et al., 2010). In addition, solutions to stream restoration e.g. woody debris accumulation or gravel bar development, may require machinery for fabrication, be limited by site accessibility or availability of suitable materials, or be constrained by legislation, and are only an interim solution to the common, long-term problem of loss of riparian habitat and degraded water quality (Palmer et al., 2010; Reich et al., 2003). With the potential to create series of natural discontinuities and unique associated habitats, engineering by beavers has been considered as a possible approach to restoring degraded stream channels (Burchsted et al., 2010; Harthun, 1999; Pollock et al., 2003), arid and semi-arid environments (Gibson and Olden, 2014), wetlands (Elmeros et al., 2003; Sjöberg and Ball, 2011), functional diversity and landscape structure (Byers et al., 2006).

A crucial part of beaver behavioural ecology is to reduce exposure to terrestrial predators whilst maintaining access to resources. Beavers achieve this by building dams, thereby raising and stabilising water levels and maintaining a submerged lodge or burrow entrance, at the same time rendering low-lying wooded riparian zones more accessible due to inundation (Rosell et al., 2005). When dam integrity is maintained over the long-term (> 5 years) areas of open water may become well-vegetated by aquatic plants. Alternatively, partial dam collapse and pond drainage will result in extensive colonisation of formerly inundated sediments thus forming so called ‘beaver meadows’ (Butler and Malanson, 2005; Naiman et al., 1988; Wright et al., 2002). However, more dynamic situations may prevent such classic wetlands from forming, for example if cycles of occupation and re-occupation by beaver groups are short and flood-mediated ‘wash-out’ of old dams and subsequent construction of new dams is common. Formation of step-pond/pool profiles then occurs, possibly more commonly in steeper gradient headwater streams (Burchsted et al., 2010), with dam ponds then connected by sections of running water. Physical and hydraulic diversity is thus increased both temporally and spatially.

Beaver dams directly dissipate stream energy and slow water flow, whilst altering hydraulic connectivity and discharge (Benke and Wallace, 2003; Margolis et al., 2001), thereby transforming sections of channel from erosional to depositional environments (Butler and Malanson, 2005) and acting as a sink for organic matter (Anderson et al., 2014). Upstream of these dams there is increased accumulation of plant propagules, fine-grained, nutrient-rich sediment and coarse organic matter. This storage potential can alter downstream water and sediment chemistry, particularly in areas dominated by agriculture where nutrient losses may be high (Correll et al., 2000; Hill and Duval, 2009). Beaver dams therefore directly or indirectly modify a range of physical and chemical processes in streams thus creating a mosaic of habitats, and food resources which benefits numerous trophic levels (Margolis et al., 2001; Rolauffs et al., 2001; Smith et al., 1991; Steel et al., 2003; Westbrook et al., 2010). Thus the species assemblages of disparate taxa from beaver-created ponds therefore can differ significantly from those of adjacent non-beaver constructed ponds (Willby *et al.* 2014). Changes in species composition have been observed both within the beaver ponds themselves, but also within the local landscape. Thus, modified physical and biological linkages and subsidies between aquatic and terrestrial ecosystems occur through the alteration of food webs (Gratton et al., 2008; Hill and Duval, 2009) and increased dissolved organic carbon export (Cirmo and Driscoll, 1993), whilst downstream nutrients, resources and consumers may also change (Fuller and Peckarsky, 2011). Most of these changes are also affected by pond age as younger beaver ponds may have higher hydrological and physical connectivity compared to older ponds (Malison et al., 2014).

Ponds formed due to beaver dams differ significantly from the habitat heterogeneity created by naturally occurring large woody debris (LWD) accumulations and human interventions, e.g. artificially constructed ponds. This is due to the intermittent disturbance within beaver ponds associated with foraging, caching of woody material, maintenance of dams and fluctuating water levels. The physical structures created by beavers, e.g. dams, lodges, food caches (fine woody debris with higher surface areas than conventional LWD) and canals, are additional sources of habitat complexity that are unique to beaver-created ponds (Clifford et al., 1993; France, 1997; Hood and Larson, 2013; McMaster and McMaster, 2001; Rolauffs et al., 2001).

The habitat transformational effects of beaver dams have long been recognised (e.g. Sprules (1941), Gard (1961)), although a global understanding of effects on associated biota has proved elusive due to the temporal and spatial variation in communities both within and between ecosystems and biogeographically. Studies on the effects of beaver modified systems on aquatic macroinvertebrate richness and diversity are numerous (e.g. Clifford *et al.* (1993), France (1997), Benke & Wallace (2003), Batzer, Palik & Buech (2004) and Anderson & Rosemond (2007)), partly due to ease of sampling and a traditional focus on biomonitoring in lotic environments using macroinvertebrates, but also because invertebrates are highly responsive to changes in sediment and water velocity (Naiman et al., 1988; Nummi, 1989) and display a range of life history and feeding strategies. Despite multiple studies, none have specifically used the ecosystem engineer concept applied to beaver (Jones et al., 1994) to answer a question that is integral to the reintroduction and introduction of beavers globally; can ecosystem engineering by beavers restore macroinvertebrate functional diversity within degraded freshwater systems? The ‘passive’ restoration of degraded systems is one of several motivations behind beaver reintroduction, but this will fall short of expectations if the transformation of physical habitat does not translate into biological changes.

Our study therefore focuses on changes in richness, abundance, composition and feeding function of *in-situ* aquatic macroinvertebrates over multiple seasons in a stream situated within an agricultural landscape in Scotland following the reintroduction of beavers. We tested the following hypotheses: (i) beaver-modified habitats increase species richness and alter associated species accumulation rates, (ii) species turnover between habitats types is greater with beaver-created habitats present in the landscape and (iii) species composition and functional diversity are modified within newly-created habitats as a result of beaver constructed dams.

6.3 Methods

6.3.1 *Site and habitats*

The study took place on a private estate situated near Blairgowrie, Perth in east Scotland (56º64’42.91”N, 3º27’34.99”W). The site receives approximately 1400 mm of rain annually, with a mean maximum temperature of 12°C and mean minimum temperature of 5°C from 1981-2010 (Meteorological Office UK, 2013), and lies at an elevation of 200m. A spring-fed stream (known as the Burnished Burn) of 0.5 – 2 m width and depth of 0.1 – 0.3 m runs for ~2 km through agricultural land dominated by permanent pasture that is grazed by sheep and beef cattle. The stream was straightened and realigned some time prior to 1860, most likely in the late 1700s. A mature conifer plantation (*Picea* spp. and *Larix* spp.) forms the southern edge of the catchment while an area of mixed deciduous trees (mainly *Betula pubescens*, *Salix* spp., *Alnus glutinosa* and *A. incana*) encloses the source resulting from a woodland planting scheme in the early 1990s. A pair of adult Eurasian beavers, *Castor fiber*, were introduced to this stream in 2002. Breeding first occurred in 2005 and 4-6 animals have been present each year thereafter. The beaver family first constructed a dam in the upstream, western part of the stream in 2003 and subsequently built eight more dams (three upstream, and four downstream of this original dam) (Fig 1.3) all of which were sampled in this study. Following the first sampling of invertebrates in spring 2011, a further dam was constructed that summer which was also sampled. The mean distance between dams was 53 ± 28 m (± SD). The observed frequency of 5 dams km^{-1} of stream channel is within the range 0.14 – 22 dams km^{-1} reported from Russia and North America (Zavyalov, 2014).

Dam construction resulted in modification of the surrounding habitat. Immediately upstream of the dam (habitat US) lentic conditions occurred (water velocity 0 - 3 cm s^{-1}), with high volumes of organic matter accumulating. This habitat was moderately disturbed and turbid due to beavers regularly maintaining dams with mud, rocks and tree branches and their movement between foraging areas; therefore aquatic vegetation was sparse. The dam structure itself often supported ruderal terrestrial plants (e.g. *Urtica dioca* and *Rumex obtusifolius*) during summer. For 5 - 10 m upstream from the dams the shallow (0.5 - 0.8 m deep), still to slow moving waters were well vegetated (habitat VG) by aquatic plants e.g. *Potamogeton natans*, *Callitriche stagnalis, Glyceria maxima, G. fluitans*, *Roripa nasturtium-aquaticum*, *Myosotis scorpiodes* and *Elodea canadensis*. Habitats downstream of the dams (habitat DS) were characterised by flowing water and overhanging trees e.g. *B. pubescens*, *Salix* spp. and *Larix* spp. Where beaver dams had no influence on water flow sites were classed as unmodified (habitat UM) and were considered indicative of the stream condition prior to dam construction. At these sites the stream-bed comprised a mixture of sand and coarse gravel which supported a sparse growth of the moss *Fontinalis antipyretica*.

6.3.2 *Methods*

Data on water quality parameters from the beaver-modified stream were obtained from McLean (2011), who used an ISCO 3700 automatic water sampler to obtain 282 x 750 ml samples from upstream and downstream of one beaver dam from 23/6/10 to 13/5/11. Water samples were collected on a 12, 24 or 72 hour sampling frequency dependant on rainfall. The stream sediment was quantified in summer 2013 using a bottomless bucket (10 x 10 cm) which was pushed into the substrate and the contents removed to a depth of 5 cm. Samples were taken upstream and downstream of 10 dams, with 10 samples taken from unmodified habitats and 7 samples taken within available vegetation habitats. Sediment samples were subsequently rinsed through sieves of 21.4 mm, 16 mm, 11.2 mm, 5.6 mm, 2 mm, 1 mm, 500 µm, 250 µm and 125 µm mesh size. Each sieves' contents were dried in an oven at 80°C for 24 h and weighed before being used to calculate diversity and evenness scores. Sieved, dried samples were then combined and mixed to form coarse (1 - 21.4 mm) and fine (125 - 500 µm) fractions with approximately 10 g of each fraction placed in crucibles. Crucibles were oven-dried at 105ºC for one hour and weighed, before being burned at 550ºC for 24 h and re-weighed to assess the percentage of organic matter based on loss on ignition. Aquatic plant biomass per habitat was estimated by removing above-ground vegetation within 20 cm x 20 cm quadrats placed randomly within vegetation habitats (n = 7) and unmodified habitats (n = 7), where vegetation was present. Biomass samples were dried in an oven at 80ºC for 24 h and weighed.

Macroinvertebrates were sampled over three seasons during 2011 i.e. spring (n = 35), summer (n = 37) and autumn (n = 37) and within the four described habitat types; immediately upstream of the beaver dam (US; n = 29), immediately downstream of the dam (DS; n = 29), within aquatic vegetation located 5 - 10 m upstream of the dam (VG; n = 21) and unmodified sites (UM; n = 30). All samples were collected for one minute using a D-framed kick net (mesh size 500 µm), over an area of approximately 1 m^2 by sweeping the net through the water column and any accumulated organic material in order to collect both benthic, water surface and plant-associated organisms. Where there was active flow the stream-bed was disturbed by kicking to loosen material which was then caught in a net placed immediately downstream. The contents of each sample were preserved using 70% denatured methylated spirit, sorted in the lab and identified to the highest practicable taxonomic resolution. Five measurements of water depth were taken at each kick sample site. Species were also assigned to functional feeding groups (FFG) and allocated water current preferences according to Schmidt-Kloiber & Hering (2012). As the ecological preferences and feeding habits of many species span multiple categories of these two traits (e.g. adaptive feeding strategies) the total number of individuals per species per sample were divided across the preference range based on the ten point assignment system (Moog, 1995).

Species rarity was assessed using UK mainland species distribution data obtained from the National Biodiversity Network (NBN, 2014). A species rarity score was formed from the reciprocal of the log number of hectads in which a species was recorded. The sample rarity score was based on abundance weighted mean species rarity score, where abundance corresponded to the log number of the individuals of each species recorded. Therefore, high sample scores represent a greater than average abundance of rare species.

6.3.3 *Exploratory and statistical analyses*

Water quality parameters, sediment organic matter content, Shannon's diversity Index (H'), Shannon's equitability (E_H) and aquatic plant biomass did not meet requirements of linear analysis and therefore differences between habitats were analysed using Kruskal-Wallis tests using post hoc multiple comparisons. Macroinvertebrate species richness was expressed as the number of taxa per sample or as H', with species evenness represented by E_H. Differences in species richness between seasons were analysed using a generalised linear model with a Poisson error distribution and log-link function. General linear models with post-hoc multiple comparisons using Tukey's Honestly Significant Differences (HSD) were used to assess differences in H' and E_H between habitats within seasons, and also within habitats between seasons. H' and E_H were normalised prior to statistical analyses using natural log to the base 10 (x +1) transformations. Estimates of total species richness were calculated using an abundance-based estimator (Chao, 1987). In order to compare the accumulation rates of species per habitat type accumulation curves were created using the rarefaction method based on number of individuals rather than samples (Colwell et al., 2004), as macroinvertebrate abundance varied strongly between some samples and species richness was highly sensitive to the number of individuals sampled. Species abundance data were log-transformed before being converted to a Bray-Curtis dissimilarity Index (BCI). Therefore species composition and turnover per habitat and season could be compared using non-metric multidimensional scaling (NMDS). A permutational multivariate analysis of variance was used to test the effects and interaction of season and habitats based on the BCI community dissimilarity matrix. Species characteristic of particular habitats per season were identified using the Indicator Value method (Dufrêne and Legendre, 1997). Ecological trait data were removed from analyses where a low number of individuals occurred in a group (< 3% of total). This included the FFGs ‘miner’, ‘xylophagus’ and ‘parasite’, and the water flow preferences; limnobiont (obligate standing water species) and rheobiont (obligate fast flowing water species). This trait data did not meet assumptions of linear tests, even after transformation, therefore a Kruskal-Wallis one-way analysis of variance with post hoc multiple comparison tests was used to assess differences in FFG composition and flow preferences between habitats within seasons, and within habitats between seasons.

All statistical analyses and graphics were produced using R Studio version 2.15.0 (R Development Core Team, 2013), with the additional packages; vegan (Oksanen *et al*. 2012), plyr (Wickham, 2011), ecodist (Goslee and Urban, 2007), sciplot (Morales and Murdoch, 2011), reshape (Wickham, 2007), labdsv (Roberts, 2010) and fossil (Vavrek, 2011).

6.4 Results

6.4.1 *Physical habitat characteristics*

Phosphate, conductivity and nitrate were all significantly greater upstream of the beaver dam (Table 6.1). Conversely, total suspended sediment (TSS) was greater downstream. Vegetation and upstream habitats both had a greater mean depth and higher percentage of coarse and fine organic matter in comparison to downstream and unmodified habitats. Downstream and unmodified habitats had the greatest diversity of substrate, with unmodified samples being the most uneven. For aquatic plant biomass, vegetated habitats had a significantly greater biomass than unmodified habitats. Other habitats were un-vegetated.

Table 6.1 Observed water quality parameters obtained from McLean (2011) and sediment structure and diversity per habitat, mean ± SE (min-max). Abbreviations; VG – vegetation, US – upstream, DS – downstream and UM – unmodified. Where numbers share a superscript letter they are not significantly different from each other ($P > 0.05$).

	VG	US	DS	UM
Total suspended solids (mg l^{-1})	-	13.2 ± 2.0^{a}	62.3 ± 8.6^{b}	-
		(0.0 - 188)	(4.0 - 696)	
Extractable P (µg l^{-1})	-	42.3 ± 7.5^{a}	20.0 ± 1.3^{b}	-
		(0 - 792.0)	(0 - 123.5)	
Conductivity (µS cm^{-1})	-	99.9 ± 1.3^{a}	92.4 ± 0.7^{b}	-
		(34 – 136.0)	(75 – 110.5)	
Nitrate (mg l^{-1})	-	5.4 + 0.2^{a}	4.3 ± 0.2^{b}	-
		(0.56 – 14.8)	(1.8 – 13.9)	
Depth (cm)	47.8 ± 3.7^{a}	54.0 ± 3.9^{a}	13.2 ± 2.2^{b}	6.5 ± 0.5^{b}
	(12 - 78)	(15 - 100)	(1 – 49)	(2 - 14)
Coarse (> 1 mm) organic matter (%)	25.4 ± 3.6^{a}	24.0 ± 4.4^{a}	7.5 ± 3.9^{b}	3.0 ± 0.7^{b}
	(11.3 – 45.6)	(8.5 – 51.6)	(1.0 – 41.2)	(1.3 – 6.2)
Fine (< 1 mm) organic matter (%)	18.5 ± 2.5^{a}	18.1 ± 3.0^{a}	8.2 ± 4.9^{b}	3.1 ± 0.6^{b}
	(5.7 – 29.5)	(7.9 – 36.7)	(0.0 – 50.4)	(1.2 – 5.4)
Shannon's diversity (*H'*)	1.24 ± 0.05^{a}	1.35 ± 0.05^{ad}	1.70 ± 0.04^{bc}	1.52 ± 0.03^{cd}
Shannon's equitability (E_H)	0.88 ± 0.02^{a}	0.87 ± 0.03^{a}	0.80 ± 0.03^{ac}	0.65 ± 0.02^{bc}
Biomass (DW g m^{-2})	554.9 ± 60.4^{a}	-	-	27.84 ± 18.5^{b}
	(329.0 – 835.8)			(0 – 117.9)

6.4.2 *Species richness*

In total 109 samples were taken across 3 seasons with 170 taxa recorded from a total of 84,520 individuals (Table 6.2). Vegetation (43.0%) and upstream (21.2%) habitats contributed most individuals, followed by unmodified (18.9%) and downstream habitats (16.9%). In terms of species richness the opposite trend occurred, as unmodified (34.1%) and downstream (24.6%) habitats had the highest mean richness, compared to upstream (21.5%) and vegetation (19.8%) habitats. Of the three seasons sampled, spring contributed the largest number of species unique to a specific habitat (44.2%), followed by summer (30.7%) and autumn (21.2%). Autumn samples had significantly lower richness in comparison to spring ($Z_{106} = 2.52$, $P = 0.012$), but autumn richness was not significantly different from summer ($Z_{106} = 0.76$, $P = 0.446$). Within habitats, unmodified habitats contributed 38.6% of species unique to a single habitat, followed by vegetation (22.8%), upstream (21.0%) and downstream (14.0%) habitats.

The most frequently occurring taxa were; Chironomidae spp. (98% of samples), *Asellus aquaticus* (90%), Oligochaeta spp. (81%) and *Crangonyx pseudogracilis* (71%), with *A. aquaticus* (27.6%), *C. pseudogracilis* (19.3%) and Chironomidae spp. (14.2%) also contributing the highest numbers of individuals. The tendency for higher richness to be coupled with lower abundance generally resulted in the greatest diversity (H') being observed in unmodified and downstream habitats (Table 6.2). Significant differences in diversity between seasons within habitats, occurred only within the upstream habitat, where spring samples had a greater mean diversity compared to summer and autumn ($F_{2,26} = 6.33$, $P = 0.006$). Unmodified and downstream habitats also had higher community evenness (E_H) across seasons in comparison to the upstream and vegetation habitats. Within-habitats, diversity in samples from the vegetation habitat was consistently most unevenly distributed, with summer evenness in this habitat being significantly lower in comparison to autumn ($F_{2,18} = 4.19$, $P = 0.032$).

Table 6.2 Observed macroinvertebrate summaries per habitat and season (mean ± SE). Abbreviations; VG – vegetation, US – upstream, DS – downstream and UM – unmodified. Where numbers share a superscript letter they are not significantly different from each other (P > 0.05).

	Spring					Summer					Autumn					Reach
	VG (no=7)	US (no=9)	DS (no=9)	UM (no=10)		VG (no=7)	US (no=10)	DS (no=10)	UM (no=10)		VG (no=7)	US (no=10)	DS (no=10)	UM (no=10)		no=109
Richness	22 ± 2	16 ± 2	18 ± 3	22 ± 2		20 ± 1	14 ± 1	15 ± 2	20 ± 2		13 ± 3	12 ± 1	16 ± 1	24 ± 2		17 ± 1
Min-Max	14-27	9-24	5-33	11-28		17-25	8-20	8-23	14-28		6-23	9-17	10-22	16-32		5-32
Total richness	65	55	65	62		56	55	50	64		47	43	64	57		170
Abundance-based species estimator	72	65	87	67		65	64	54	72		58	48	74	62		167
Species rarity	0.36 ± 0.005	0.36 ± 0.005	0.36 ± 0.007	0.38 ± 0.005		0.36 ± 0.005	0.35 ± 0.003	0.35 ± 0.004	0.37 ± 0.003		0.35 ± 0.003	0.35 ± 0.003	0.35 ± 0.003	0.35 ± 0.003		
No. of individuals	1053 ± 252	364 ± 85	485 ± 214	605 ± 308		3161 ± 1541	665 ± 199	446 ± 223	387 ± 98		1012 ± 453	640 ± 218	552 ± 231	616 ± 266		761 ± 93
Min-Max	386-1634	153-549	84-1147	182-1840		678-7344	160-1219	47-1192	178-698		274-2234	182-1222	177-1226	109-1683		47-7344
Total individuals	7373	3643	3876	6054		22,124	7314	4460	3870		7082	7040	5523	6161		84,520
Shannon's diversity (H')	5.5 ± 0.8^{a}	5.9 ± 0.6^{a}	5.2 ± 0.5^{a}	7.7 ± 1.0^{a}	$F_{3,31}$ = 2.28, P = 0.098	4.0 ± 0.7^{a}	3.9 ± 0.4^{a}	5.3 ± 0.4^{ab}	7.0 ± 0.7^{b}	$F_{3,33}$ = 9.31, P < 0.001	3.7 ± 0.6^{a}	3.9 ± 0.4^{a}	5.4 ± 0.6^{a}	8.6 ± 1.0^{b}	$F_{3,33}$ = 11.65, P < 0.001	5.6 ± 0.2
Shannon's equitability(E_H)	0.26 ± 0.03^{a}	0.37 ± 0.03^{a}	0.35 ± 0.06^{a}	0.36 ± 0.04^{a}	$F_{3,31}$ = 1.54, P = 0.223	0.19 ± 0.02^{b}	0.31 ± 0.05^{ab}	0.37 ± 0.04^{a}	0.36 ± 0.04^{a}	$F_{3,33}$ = 4.73, P = 0.007	0.31 ± 0.03^{a}	0.33 ± 0.04^{a}	0.33 ± 0.03^{a}	0.39 ± 0.06^{a}	$F_{3,33}$ = 0.74, P = 0.538	0.33 ± 0.01

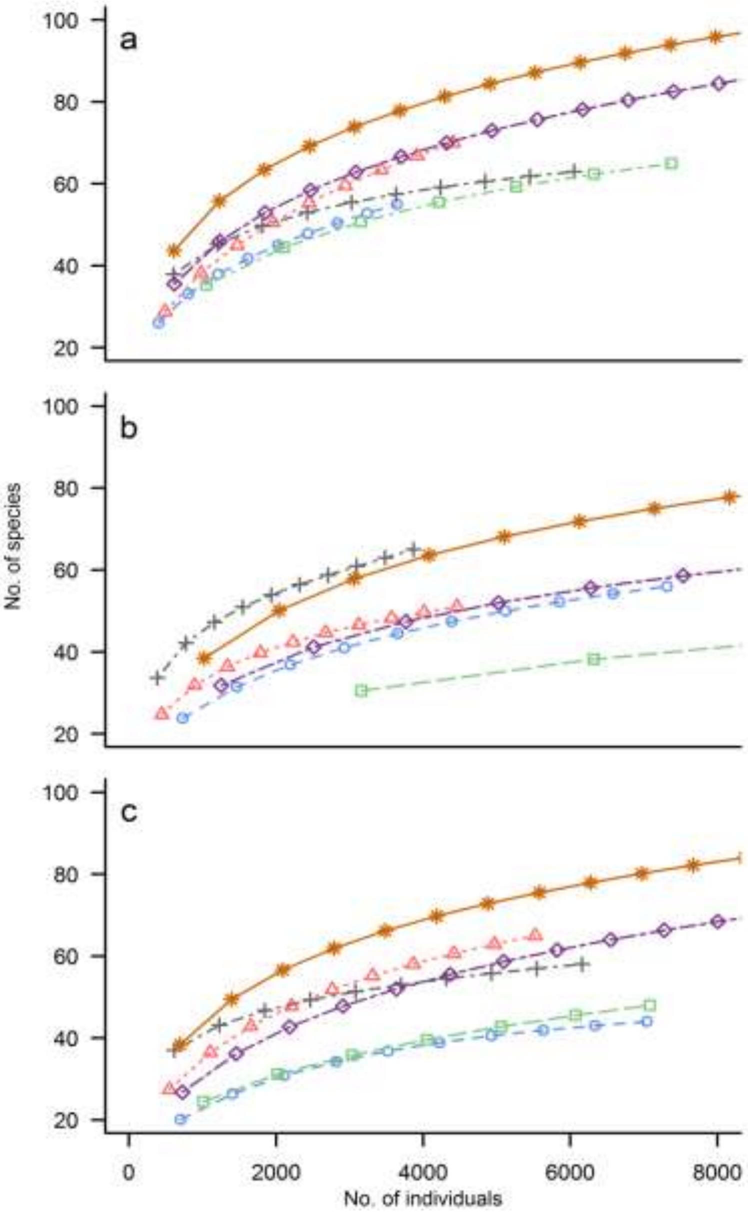

Fig. 6.1 Species accumulation curves based on number of sampled individuals for: a - spring, b - summer and c – autumn, per habitat; vegetation (green open squares, long dashed lines), upstream (blue open circles, short dashed line), downstream (red open triangles, dotted line), unmodified (black crosses, dot-dashed lines), beaver-modified habitats combined (purple diamond, long/short dashed lines) and all habitats combined (orange stars, solid lines). 95% confidence intervals are not shown for clarity but were approximately ± 2.0, ± 2.2, ± 1.8, ± 2.0, ± 2.7 and ± 2.7 species for upstream, downstream, unmodified, vegetation, beaver-modified and all habitats respectively.

At the lowest number of individuals per sample, regardless of season, unmodified sites were more species rich in comparison to any beaver-modified habitats (Fig. 6.1). This was particularly evident in summer where the initial taxon accumulation rate was higher than for all beaver habitats combined (Fig. 6.1b). Beaver-influenced habitats followed similar trends seasonally with upstream and vegetation habitats consistently having the lowest taxon accumulation rates. Downstream habitats displayed most seasonal variation in accumulation rate, as samples in summer were notably less taxa-rich in comparison to spring and autumn, although relative to beaver-modified habitats as a whole, downstream areas still had highest accumulation rates regardless of season. In all habitat types the individual-based taxon accumulation curve rarely reached a plateau, implying that further sampling would yield greater species richness. This is also reflected in the computed species richness estimates, as the number of species found per habitat was consistently lower than the extrapolated richness (Table 6.2). Most importantly, due to a combination of variable accumulation rates, plus large differences in richness and abundance between habitats and the presence of unique taxa in all habitats, a composite sample from all four habitat types together resulted in a greater landscape-scale richness in macroinvertebrate species than for a similar sized sample of beaver-influenced or non-influenced sites independently.

6.4.3 *Species composition*

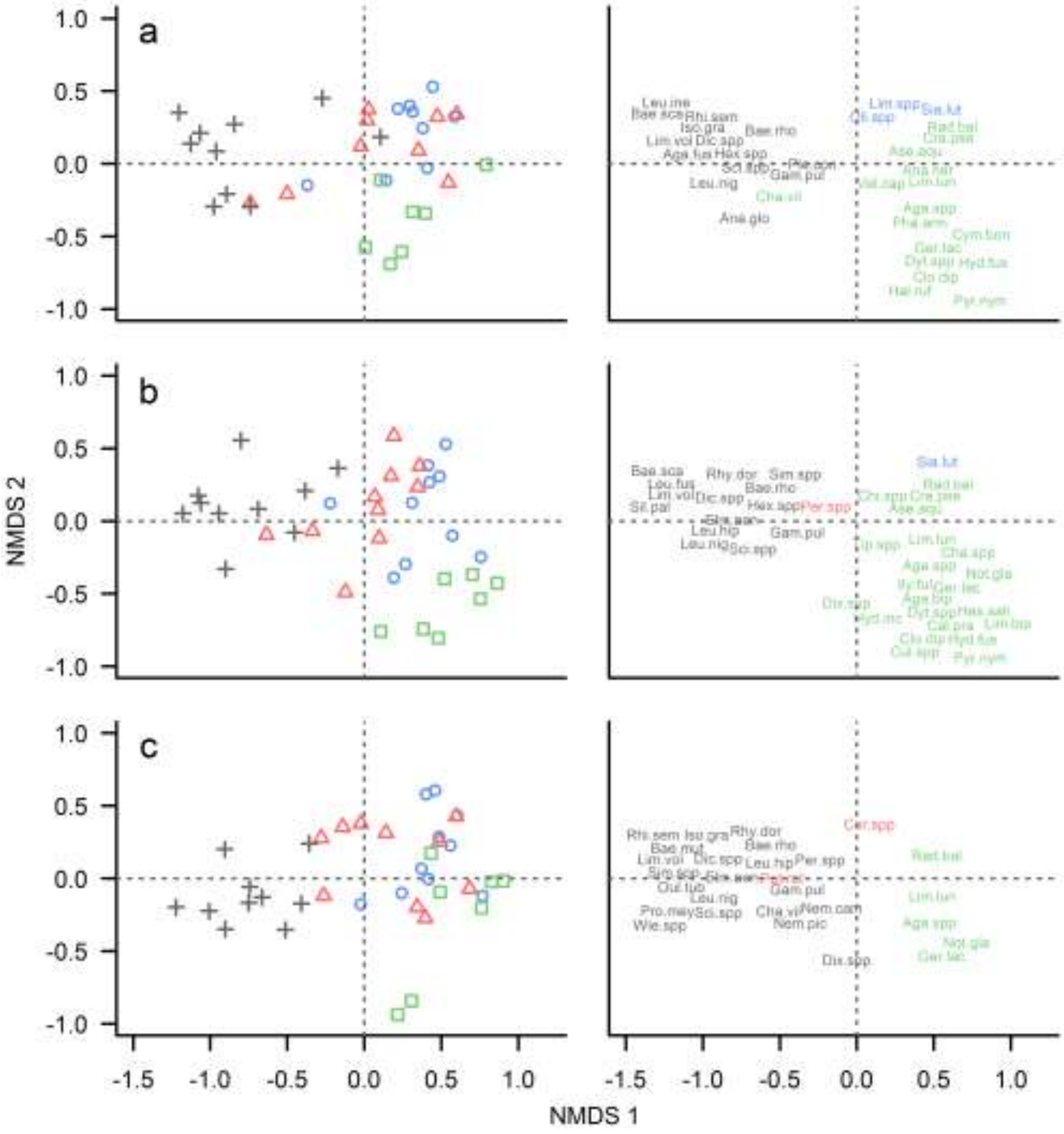

Fig. 6.2 Non-metric multidimensional scaling ordination (NMDS) for macroinvertebrate species composition, based on a Bray-Curtis dissimilarity matrix for; a - spring, b - summer and c - autumn per habitat; vegetation (green, open squares), upstream (blue, open circles), downstream (red, open triangles) and unmodified (black, crosses). All stress values were < 0.12. Indicator species that were significantly related to a habitat per season (*P* < 0.05) are plotted on the right figure of each row, on the same NMDS axes. A key to species abbreviations is given in Appendix 6.1.

Across all seasons, the fauna of unmodified sites were compositionally distinct from beaver-influenced habitats. There was considerable overlap in species composition within beaver habitats with this amount of overlap varying between seasons (Fig. 6.2). For example, macroinvertebrate communities from vegetation samples were more similar to upstream habitats in spring and autumn, but less so in summer when vegetation cover was at a peak. Also, upstream and downstream habitats displayed a large degree of compositional overlap regardless of season, with downstream habitats also sharing part of their composition with unmodified sites. A mean BCI across all habitats of 0.61 ± 0.002 (± SE) (range: 0.15-1.00) indicated that, on average, ~39% of the overall taxon assemblage was shared between samples. Samples from downstream and vegetation habitats frequently differed visually across seasons, an indication of greater seasonal turnover in composition within these habitats. Differences in species composition between seasons were significant (F = 4.08, R^2 = 0.05, P = 0.001), although the R^2 value was low in comparison to the strength of the habitat effect (F = 15.78, R^2 = 0.30, P = 0.001). There was no interaction between season and habitat (F = 1.21, R^2 = 0.05, P = 0.145), indicating that community differences between habitats were consistent between seasons.

Unmodified and vegetation habitats had the highest incidences of indicator taxa of all the habitats per season (Table 6.3) reflecting the contrast between lotic and lentic habitat. Species within the Dytiscidae family, Heteroptera order and gastropods (e.g. *Radix balthica*) were strongly associated with vegetation habitats, whereas those accustomed to flowing water were associated with unmodified habitats e.g. species of Leuctridae and Baetidae., free-living caddis (e.g. *Rhyacophila dorsalis*) and Elmidae spp. Of the amphipods *Crangonyx pseudogracilis* was found more often in beaver-modified habitats (75.4% US and VG), whereas *Gammarus pulex* was more common in unmodified sites (77.8%).

Table 6.3 Distribution of the number of taxa significantly associated ($P < 0.05$) with each habitat type based on IndVal analysis.

Season	VG	US	DS	UM	Total
Spring	16	3	-	14	33
Summer	22	1	1	14	38
Autumn	6	-	-	22	28

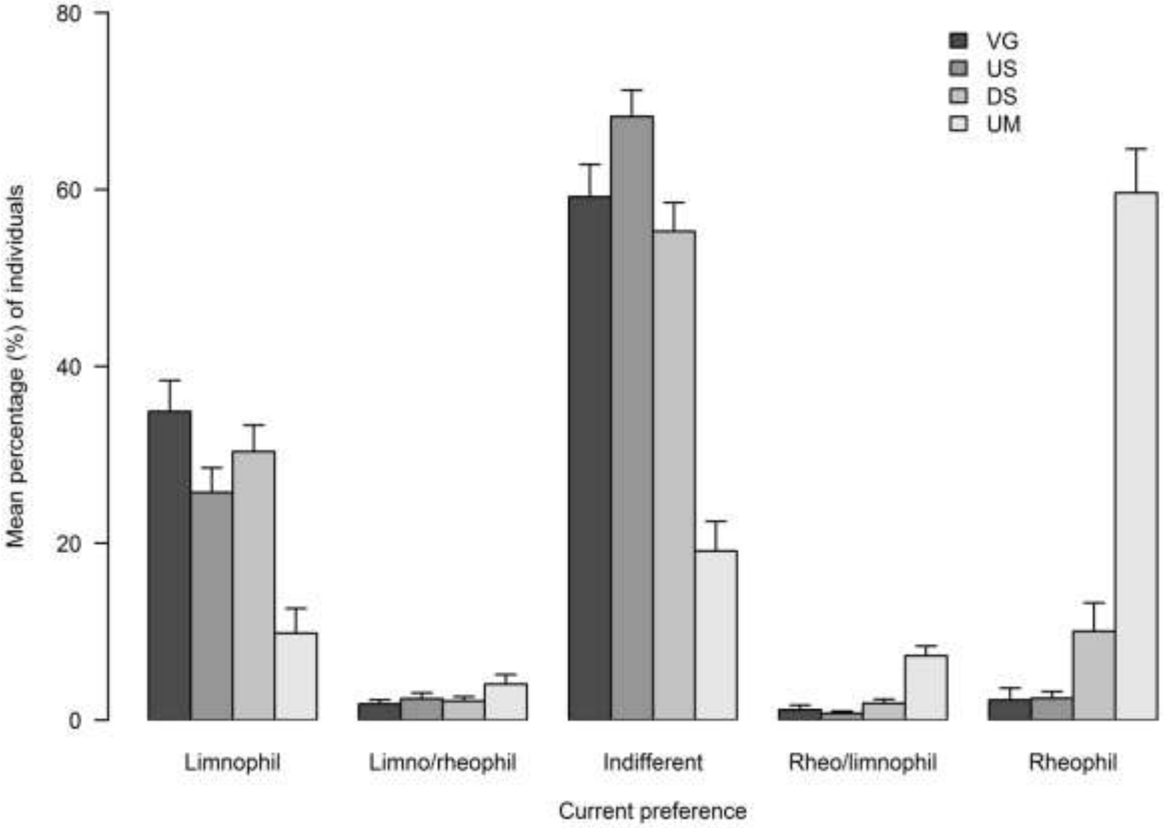

Fig. 6.3 The mean percentage of individuals present in each water current preference by habitat. Error bars indicate standard error. Legend abbreviations; VG – vegetation, US – upstream, DS – downstream and UM – unmodified.

There were significant differences in the mean percentage of individuals for each current preference ($X^2_4 = 238.1$, $P < 0.001$) (Fig. 6.3). Within current preference groups unmodified habitats had a significantly lower number of individuals than US, DS and VG habitats for limnophil ($X^2_3 = 33.3$, $P < 0.001$) and indifferent categories ($X^2_3 = 53.4$, $P < 0.001$). Yet, unmodified habitats had a greater number of individual for both rheo/limnophil ($X^2_3 = 43.0$, $P < 0.001$) and rheophil current preferences ($X^2_3 = 62.6$, $P < 0.001$). No differences occurred in the abundance of individuals in the limno/rheophil category ($X^2_3 = 3.0$, $P = 0.394$).

The majority of individuals belonged to taxa that were indifferent with respect to flow, with the exception of invertebrates from the unmodified habitats, which were mostly rheophilic. The abundance of individuals found in each habitat type corresponded to the expected velocity of patches. Thus, species indicative of lentic conditions, e.g. *Nemurella pictetti* and *Cloeon dipterum* (high tolerance of anoxic conditions), were concentrated in upstream and vegetated patches, whereas unmodified sites were dominated by taxa of moderate to fast currents e.g. Simulidae spp., *Rhithrogena semicolorata* and *Baetis rhodani*.

6.4.4 *Functional feeding groups*

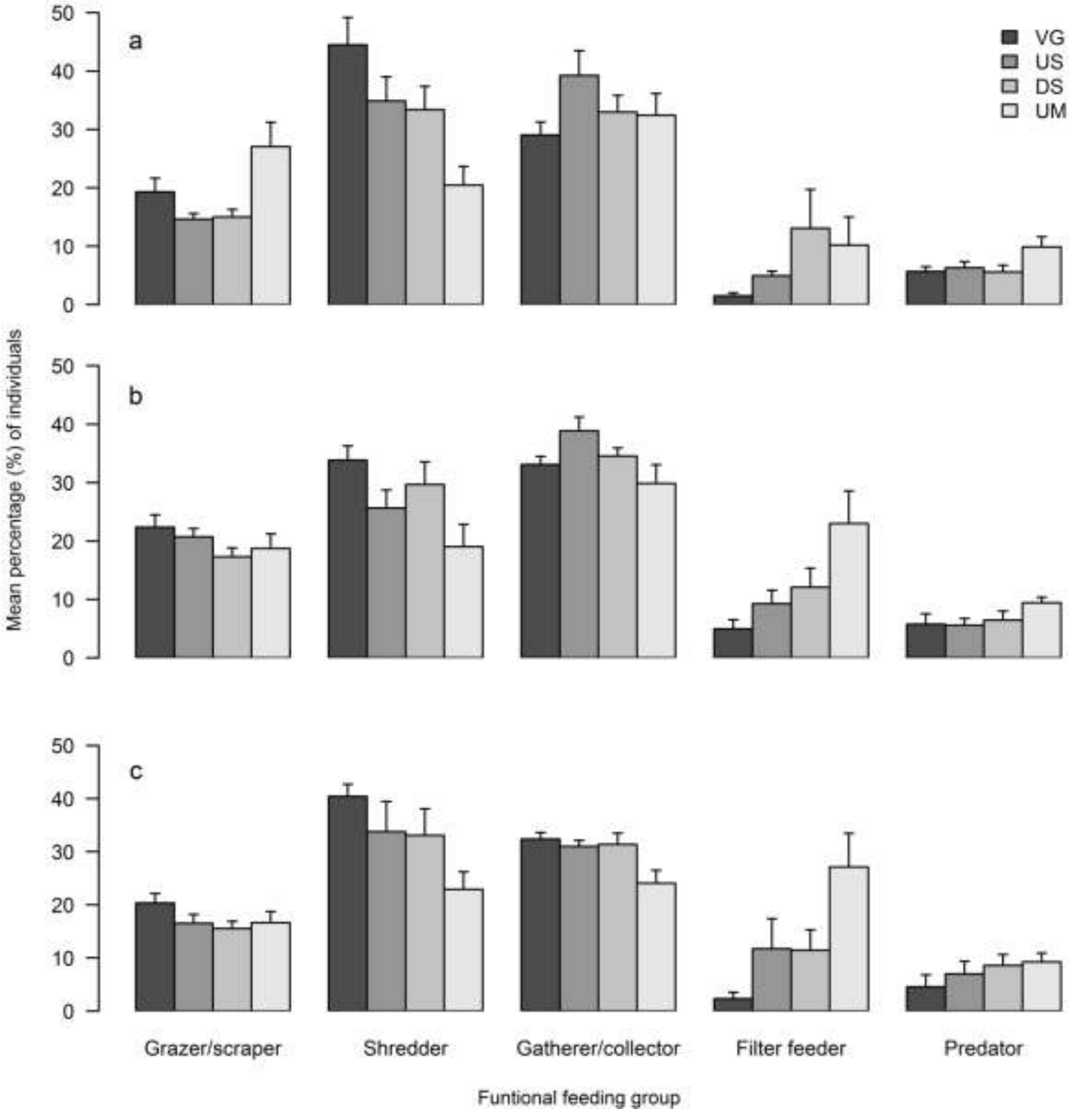

Fig. 6.4 The mean percentage of individuals allocated to each functional feeding group per season, a - spring, b - summer and c - autumn per habitat. Error bars indicate standard error. Legend abbreviations; VG – vegetation, US – upstream, DS – downstream and UM – unmodified.

The distribution of macroinvertebrates between FFG was significantly uneven within all seasons; spring ($X^2_4 = 112.7$, $P < 0.001$), summer ($X^2_4 = 104.2$, $P < 0.001$) and autumn ($X^2_4 = 90.0$, $P < 0.001$) (Fig. 6.4). Across seasons, the major differences in relative abundance applied to gatherer/collectors, with summer having a greater mean abundance than autumn ($X^2_2 = 8.18$,

$P < 0.017$), and filterers, with summer having a greater abundance than spring ($X^2_2 = 6.35$, $P < 0.042$). No other differences in the relative abundances of FFGs occurred across seasons (all tests: $P > 0.14$). Vegetation habitats were particularly rich in shredders, more so in spring compared to summer ($X^2_2 = 6.08$, $P = 0.048$). By contrast, the abundance of gatherer/collectors was greatest in upstream and downstream habitats, with seasonal differences occurring only within upstream habitats, where the abundance of grazer/scrapers was significantly higher in summer compared to spring ($X^2_2 = 7.41$, $P = 0.025$), and gatherer/collectors were higher in summer compared to autumn ($X^2_2 = 8.48$, $P = 0.014$). Excluding spring, unmodified habitats were rich in filter feeders, with autumn having a greater abundance than spring ($X^2_2 = 7.28$, $P = 0.026$). Variations in predator abundance were low between all habitats and seasons.

6.5 Discussion

Small, straightened uniform streams draining agricultural land are ubiquitous habitats in human-modified landscapes. These streams lack the significant variation in depth, substrate, velocity or hydrological connectivity of their natural counterparts. This lack of physical diversity has catchment-wide implications, including reduced biodiversity, low nutrient retention and poor flood attenuation, and does not reflect the historical condition of such streams. At our study site, the introduction of beavers resulted in several years of habitat engineering that served to re-establish physical heterogeneity by creating series of pools, ponds, woody debris caches and aquatic plant-rich habitats, commonly interspersed with running water. Evidently, and despite a long history of alteration of the drainage network in this and adjoining catchments, habitat engineering by beavers had profound effects on macroinvertebrate abundance, composition and taxonomic and functional feeding diversity.

6.5.1 *The effect of beaver-modifications on species richness*

Richness varied between- and within-habitats across the seasons sampled, but in general, unmodified habitats had higher species richness in comparison to upstream and vegetation habitats. Published comparisons of the effects of beaver dams on invertebrate richness provide a varied picture. In South America, where *Castor canadensis* is an invasive species, beaver ponds had lower richness compared to unmodified sites (Anderson and Rosemond, 2007), while in North America and Northern Europe either no richness differences were noted (McDowell and Naiman, 1986; Naiman et al., 1988; Redin and Sjöberg, 2013), or richness was reduced below the dam in comparison to reference conditions (Smith et al., 1991). The effects of beaver dams on richness will be species-, reach- and season-specific. For example, sites downstream of dams may be periodically exposed to invertebrate and organic matter drift (Redin and Sjöberg, 2013). Equally, the dams themselves or abundant pond vegetation could become sinks of drifting matter, sediment, or pollutants from agricultural run-off, thus possibly reducing downstream sedimentation. Since TSS was greater downstream of one dam in this study the movement of sediment by beavers to maintain dams may alternatively contribute to release of suspended solids downstream. Effects of dams are also likely to be species specific, e.g. no effect of season on Chironomidae abundance was observed in beaver dams, yet abundance differed for Simulidae with individuals appearing in later sampling dates (Clifford et al., 1993).

One of the main reasons for inconsistencies between studies in effects of habitat engineering by beavers on invertebrate richness may relate to varying methods of analysis. As the number of individuals sampled is commonly extremely variable between samples and richness is strongly affected by this difference in sampling effort, richness should strictly be estimated using rarefaction techniques based on individuals. Therefore, as well as under- or over-estimating richness for a given sampling effort, the opportunity is missed to quantify and compare accumulation rates from different habitats. In the present study, habitat-specific accumulation curves confirmed that vegetation and upstream habitats accumulated species at a lower rate in comparison to downstream and unmodified sites. Since higher richness occurred when a composite sample from different habitats was obtained, this alludes to compositional differences between habitats thus leading to greater richness in landscapes where beaver-engineered habitat occurs.

Regardless of the species richness in beaver-modified habitats, the lentic conditions, specifically in the vegetation habitat, supported consistently greater macroinvertebrate abundance, often dominated by few taxa e.g. Chironomidae spp. and *A. aquaticus*, as indicated by the lower evenness of these samples. It is possible that the habitat upstream of beaver dams, e.g. US and VG, becomes more homogenous due to the larger volumes of trapped organic-rich sediment, whilst disturbance by beavers moving between foraging areas or during dam maintenance may further suit dominance by habitat generalists. The number of individual macroinvertebrates was generally highest in summer in beaver-modified habitats in this and other studies (McDowell and Naiman, 1986; Smith et al., 1991), and is likely to reflect basic seasonal trends in temperate climates. Discharge and rainfall is also generally lower in summer which reduces the likelihood of wash-out and favours concentration of animals in smaller areas (McDowell and Naiman, 1986), with high volumes of living plant tissue. The difference in macroinvertebrate abundances between habitats is likely to be an attribute of beaver ponds that benefits other trophic levels by staggering the delivery of prey. For example, emerging aquatic insects act as conduits of material, energy and nutrients to terrestrial ecosystems with the potential to alter the dynamics of terrestrial trophic interactions (Gratton et al., 2008; Knight et al., 2005). This occurs not only for micro- and macro-invertebrate detritivores, but higher organisms will also benefit e.g. bats consuming aerial invertebrates (Nummi et al., 2011) or salmonids, as beaver-impounded streams contain a greater number and size range of fish (Malison et al., 2014; Schlosser and Kallemeyn, 2000).

Overall, when habitats are combined and viewed at the scale of the whole stream, a greater taxon richness occurs since multiple habitats promote coexistence at this spatial scale (Anderson and Rosemond, 2007; Harthun, 1999). In landscapes where lentic habitats are already common, the effects of unique beaver-created habitat on richness may be less significant, while if beaver-created habitats fully dominate the landscape there may be a negative effect on richness due to a scarcity of lotic habitat patches (Rosell et al., 2005; Wright et al., 2002).

6.5.2 *The effect of beaver-modifications on species composition*

Documenting patterns in species richness in beaver-modified habitats is of secondary importance compared to the changes in species assemblages, as modifications in compositions allow for a greater confidence from which to gauge ecosystem changes. As a result of beaver-created dams differences in physical habitat structure translated to significant changes in macroinvertebrate composition. Thus, species suited to well-aerated flowing water and low rates of sediment deposition, e.g. trichopterans such as *Drusus annulatus* and *Sericostoma personatum*, are replaced by species such as the ephemeropteran, *Cloeon dipterum*, which can persist in still waters due to adaptations such as facultative anaerobic metabolism. Colonisation of these newly available lentic niches from the surrounding landscape is by active (e.g. flight) and inactive (e.g. drift) dispersal mechanisms. As newly-created artificial ponds reach colonisation saturation within 3-4 years (Williams et al., 2008) it is likely the ponds upstream of beaver dams contained a mature macroinvertebrate assemblage as they were a minimum of 8 years old (excluding the one dam constructed during 2011).

The abundance of different species within any macroinvertebrate community will be influenced by immigration and reproductive rates (Hood and Larson, 2013), but greater habitat diversity further facilitates coexistence. For example, *G. pulex* is known to utilize multiple freshwater environments and was found in all habitat types while *C. pseudogracilis* prefers littoral habitats with soft sediments and rich submersed and emergent vegetation (MacNeil et al., 2001; Mayer et al., 2012), and was found more often in beaver-influenced sites. The habitat requirements of both species were met, but as species distribution was not even, competitive displacement further modifies composition. Species replacement in beaver-impounded areas is commonly reported in other studies, but the identities of the major colonists vary, including, for example, Oligochaeta (Margolis et al., 2001; McDowell and Naiman, 1986), Chironomidae, *A.*

aquaticus or Simuliidae (Sprules 1941; Nummi 1989; Clifford *et al.* 1993; this study), at the expense of Ephemeroptera, Trichoptera and Plecoptera (Nummi, 1989; Sprules, 1941). Patterns of colonisation appear to be highly species-specific and more than likely dependent on geographic area, and to a lesser extent season. Caution should therefore be exercised in making predictions based on identification to a coarse taxonomic resolution, particularly for the Ephemeroptera and Plecoptera, as general assumptions about orders or families will not apply to all member species.

All habitats contained unique taxa that were not necessarily a subset of generalists from unmodified habitats. But consistent overlaps in composition were common, principally between upstream and downstream habitats. This could reflect continued high hydrological connectivity (water flow over, around and through the dam) maintaining downstream drift. Flow below dams created some similar physical conditions to unmodified sites, and therefore downstream sites appeared to be biologically and physically intermediate between the more extreme unmodified and vegetation habitats. Under low flow conditions, dams may become physical barriers to drift, by retaining water, and intercepting organisms and organic material (Clifford et al., 1993) and, as older dam structures become highly vegetated in summer, their porosity may be further reduced (A. Law, pers. obs.). Thus, downstream and upstream assemblages differed most in summer compared to spring and autumn, whilst downstream sites were most dissimilar from vegetated habitats in summer (Fig. 6.2). In spite of the apparent seasonal influence on macroinvertebrate composition, the effects were low in comparison to variance between habitats.

As a result of altered community composition by beaver modifications, the community functioning also changed. Unmodified sections of stream were most often characterised, in this and other studies, by a greater abundance of filter feeders, grazer/scrapers (particularly in spring) and low numbers of shredders (Margolis et al., 2001; McDowell and Naiman, 1986). In contrast, the most abundant functional groups associated with downstream, upstream and vegetation habitats were shredders and gatherer/collectors. These most likely profit from entrapment of fine and coarse particulate organic matter, plant tissue and detritus (McDowell and Naiman, 1986; Naiman et al., 1988; Simanonok et al., 2011). This may create small-scale homogenisation of the benthic habitat behind the dam, thereby reducing species richness (Anderson and Rosemond, 2007), but not necessarily abundance. Accumulation and processing of organic matter and its potential downstream drift, coupled with the possibility of increased phytoplankton growth in fertile standing waters may benefit filterer feeders both upstream (Nummi, 1989; Rolauffs et al., 2001), and downstream (Fuller and Peckarsky, 2011; Margolis et al., 2001; Redin and Sjöberg, 2013).

Community functioning will change seasonally with changes in the physical characteristics of each habitat, e.g. leaf fall autumn, and the cover of aquatic plants in summer. But beaver activity, such as herbivory or preparation of food caches in late summer and autumn (Milligan and Humphries, 2010), will be superimposed on general seasonal changes. Significantly more grazer/scrapers and gatherer/collectors were found in summer compared to spring and autumn in upstream habitats respectively. However, as with compositional dissimilarity and turnover, any seasonal affect on FFG per habitat were minor in comparison to differences between habitat types.

6.6 Conclusion

The potential for restoration of degraded freshwater habitat has been a driving force behind the reintroduction of the beaver to many parts of Europe and North America, despite this potential being largely untested. With hundreds of thousands of kilometres of human-engineered streams existing globally and overlapping the native range of either Eurasian or North American beaver habitat engineering by beavers offers the potential to reinstate small scale discontinuities and thus restore the natural structure and function of aquatic macroinvertebrates over short sections of stream. In this study, macro-invertebrate compositional changes were associated with beaver-induced changes in physical habitat that increased organic matter retention and stimulated growth of aquatic vegetation, but a combination of multiple and interacting factors prevents the observed biological changes from being attributed to a single cause (Palmer et al., 2010; Townsend et al., 2008).

The scale at which beaver habitat modifications are viewed is critical is assessing their overall impact. If habitat units are considered in isolation and relative to un-engineered units, loss of richness and diversity may be inferred. By considering the cumulative effect of beaver-influenced vs. unmodified habitats at the landscape scale, it is evident that richness, abundance, diversity and composition of macroinvertebrates are modified in a positive way. As beaver-modifications were localised in this study (e.g. habitat to reach scale) habitat heterogeneity was restored at a similar or coarser scale (e.g. reach to landscape); whether such benefits would be realised at the catchment scale is unclear. Nevertheless, our findings support claims that ecosystem engineering by beavers can restore macroinvertebrate functional diversity within degraded freshwater systems by creating unique habitats and conditions that are difficult to replicate by conventional methods of habitat creation.

CHAPTER 7 – General summary, implications and recommendations

7.1 The context of research on beavers

The growing number and variable success of many species reintroduction programmes led to the creation of a completely new research field in the late nineties; reintroduction biology (Armstrong and Seddon, 2008). This field continues to grow, with hundreds of peer-reviewed studies published over the past two decades that document biotic, abiotic, social and economic aspects of species reintroductions (Armstrong and Seddon, 2008; Seddon et al., 2007). Much of the research conducted on beavers could be classed within the field of reintroduction biology, due to their numerous worldwide introductions, reintroductions and translocations, with an estimated 200 discrete releases in Europe alone (Halley and Rosell, 2002). Subsequently, studies have documented multiple aspects of the biology of (re-)introduced beavers, including ecosystems impacts, survival, dispersion, predation and foraging (e.g. Dewas et al., 2012; Elmeros et al., 2003; John et al., 2010; Nolet and Baveco, 1996; Winter, 1997).

Yet, many beaver studies often rely on retrospective analyses of routinely collected data as part of monitoring programmes. Questions posed within this thesis were derived from field observations and literature reviews, with research being carried out in areas where these questions could be tested and potentially answered. Therefore this thesis differs, especially from the beaver (re-)introduction-related literature, in that it is driven by *a priori* questions rather than inferring impacts and behaviours from general monitoring data. Specifically, questions posed were based on the reported effects of beaver on aquatic systems elsewhere, both directly and indirectly, at different spatial and temporal scales, documenting novel behaviours and the impact of ecosystem modifications on aquatic plants and macroinvertebrates.

7.2 Thesis summary

The first experimental chapter of the thesis (Chapter 3) documents the effect and selectivity of beaver foraging on aquatic plants, which are an understudied and underestimated food resource in comparison to terrestrial resources. Specifically, as beavers were observed removing the pads of white water lilies (*Nymphaea alba*) (Fig. 7.1), and returning to a central place they provided a model system to test foraging selectivity and behaviour in comparison to conventional terrestrial foraging. Using biometric relationships, the sizes of pads consumed were reconstructed indicating that beavers selected pads of greater than average size. Though the impact of this selectivity was low, the implications were that beavers feed optimally, *in situ* in aquatic systems (Fig. 7.2), as opposed to terrestrial systems where they forage according to central place foraging theory. Therefore, beavers display adaptive foraging strategies depending on the habitat occupied or the resource that is being utilised. Although this novel behaviour was documented for a single plant species, it seems likely, based on personal observations and discussions with other scientists, that this foraging behaviour is the norm when feeding on aquatic vegetation. Therefore, in light of the importance of plants as a food resource and coupled with knowledge of adaptive foraging strategies, scientists and practitioners may be able to predict the impact of beavers with greater confidence in the event of further reintroductions or range expansion.

Fig. 7.1 A water-level view of *Nymphaea alba* petioles projecting above the water as a result of beavers removing the pads (© Nigel Willby, Knapdale August 2011).

Fig. 7.2 A beaver transporting lily pads (*Nymphaea alba*) for consumption (© Philip Price, Knapdale, July 2012).

If the direct impacts from beaver foraging on aquatic plants in Chapter 3 were low in terms of biomass removed and changes in plant assemblages, then the results from Chapter 4 document the capacity of beavers to significantly modify their ecosystems through herbivory alone (Fig. 7.3). Selective grazing by beavers over the 9-year study period significantly reduced specific aquatic plant height and abundance, whilst also modifying species composition at plot and site scale. This resulted in increased diversity and turnover between dominant habitats, although, in the short term (1 year), effects were not as pronounced. This study is unique within the literature as other studies typically document changes in aquatic plant richness and assemblage as a result of indirect beaver effects, i.e. dam building. The one study that did report significant alterations in aquatic plant biomass and composition as a result of beaver foraging was conducted over a two year period in North America (Parker et al., 2007). Since we documented changes in vegetation due to foraging alone, over longer periods of occupation, it seems likely that the direct effects of foraging are potentially underestimated when predicting the impacts of reintroduced beaver populations upon aquatic vegetation.

Fig. 7.3 The effect of foraging on *Menyanthes trifoliata* in; a – May (© Nigel Willby, Bamff, 2011) and b – July (© Alan Law, Bamff, 2011). Exclosed areas on the right hand side of each picture and areas open to beaver foraging on the left.

Despite this finding, results from the literature meta-analysis (Chapter 2) indicated that the scale of impact of beavers on aquatic vegetation is generally greater, both spatially and temporally, when beavers modify ecosystems through the creation of dams. As multiple beaver-created wetlands are not present in Scotland, data was collected for Chapter 5 in central Sweden, where there is an abundance of both beaver-created and non-beaver ponds and wetlands in the landscape. Specifically, Chapter 5 documented the spatial effects of beaver-created wetlands versus independently formed 'control' wetlands (Fig.7.4) by comparing the richness and assemblages of aquatic plants and beetles. Our study confirmed that by having both beaver and non-beaver wetlands in a landscape there is a greater beta and gamma diversity. This was the first study in Europe to document differences between active beaver ponds and other wetlands at large spatial scales. In comparison, North American studies have been fixated on beaver-modified riparian vegetation (e.g. Bartel, Haddad & Wright (2010)) or 'beaver meadows', i.e. the habitat formed after beavers have deserted an area when areas of open water are often replaced by emergent vegetation (e.g. Wright, Jones & Flecker (2002)). Also, due to the creation of wetland habitat by beavers, studies documenting increased heterogeneity for one group of organisms often infer that benefits are observed across multiple trophic levels (e.g. Schlosser (1995) and Nummi & Holopainen (2014)), yet no studies have directly shown this. We found no statistically significant direct linkage between plants and beetles in Swedish wetlands, although greater sampling of beetles, or sampling of alternative taxa with less active dispersal mechanisms, may reveal inter-related compositional trends, whilst also documenting greater richness.

Fig. 7.4 An example of a; a – beaver-created pond and b – control wetland in Sweden. Note the stands of dead trees in the beaver pond due to inundation resulting in increased light reaching the water (© Nigel Willby, July 2012).

The first three data chapters of this thesis documented beaver effects at plot, site and landscape scale, demonstrating various scales and types of impact on aquatic vegetation. Chapter 6, like other chapters focuses on the effects of beavers on aquatic biodiversity, but in this case deals specifically with diversity and composition of macroinvertebrates. Macroinvertebrates are commonly used in freshwater studies as they are excellent indicators of environmental change (Naiman et al., 1988) and the functional properties of ecosystems. Numerous studies document the effect of beaver-created dams on richness and abundance of invertebrates in both aquatic and emergence/flight phases (e.g. McDowell & Naiman (1986), Rolauffs, Hering & Lohse (2001) and Hood & Larson (2013)). However, there is considerable variability in the temporal and spatial structure of macroinvertebrates globally, and no clear trends in beaver-induced changes in functional diversity. By creating a series of dams along a historically straightened and realigned stream in an agricultural setting (Fig. 7.5), beavers modified the physical habitat and hydrological regime resulting in a significantly altered species composition and functional feeding diversity, at the same time increasing gamma richness and beta diversity. Therefore, in terms of enhancing biodiversity and restoring natural discontinuities, the beaver modifications documented at this site could be perceived as a passive solution (from a human perspective) for restoring degraded habitats. The potential for habitat restoration was one of the original reasons behind the trial reintroduction of beavers to Scotland (Gaywood et al., 2008) and this rationale is supported by the findings presented in Chapter 6.

Fig. 7.5 Sampling macroinvertebrates upstream of a beaver-constructed dam at the Bamff estate, Scotland (© Alan Law, March 2011).

7.3 Wider implications, management and future research

7.3.1 *Implications and predictions of beaver impacts*

Excluding populations of the Asian beaver subspecies (*Castor fiber birulai*), which remain small and under serious threat (Batbold et al., 2010), there is no doubt that the global reintroductions of both *C. fiber* and *C. canadensis* have been successful if measured in terms of population growth, survival without human intervention, general acceptance from the public and acknowledgement of ecosystem services provided. Indeed, beaver populations of *C. fiber* in Scotland could be unofficially considered as “naturalised”, i.e. established in the wild in self-maintaining and self-perpetuating populations unsupported by man (Lever, 1977), if not for a crucial government decision on their future.

One of the most fundamental aspects of the Scottish governments’ decision as to whether beavers should be formally, fully reintroduced to Scotland concerns the question of whether significant or unsustainable damage will be incurred by the receptor ecosystems. Results from Chapters 4, 5 and 6 provide evidence that beavers, either directly or indirectly, have the potential to increase biodiversity through increasing biological or physical habitat heterogeneity. However, most importantly, any beaver-created effects or modifications are habitat- and scale-dependent and this should always be taken into consideration when evaluating effects. Consider a hypothetical environment where high quality habitats for beavers are defined as streams, rivers, ponds or lakes with a riparian buffer of 10 m consisting of mixed deciduous and coniferous trees, meso- to eutrophic conditions, high morphological diversity and connectivity with a variety of lotic or lentic aquatic plants present (Fig. 7.6a and b). Low quality habitats (from a beaver perspective) are similar habitat types but with sparse terrestrial or aquatic vegetation, low connectivity, low morphological diversity and oligotrophic (Fig. 7.6c and d). In the following example beaver impacts are linked to commonly exhibited behaviours such as tree coppicing, aquatic plant foraging and woody debris constructions (dams and lodges).

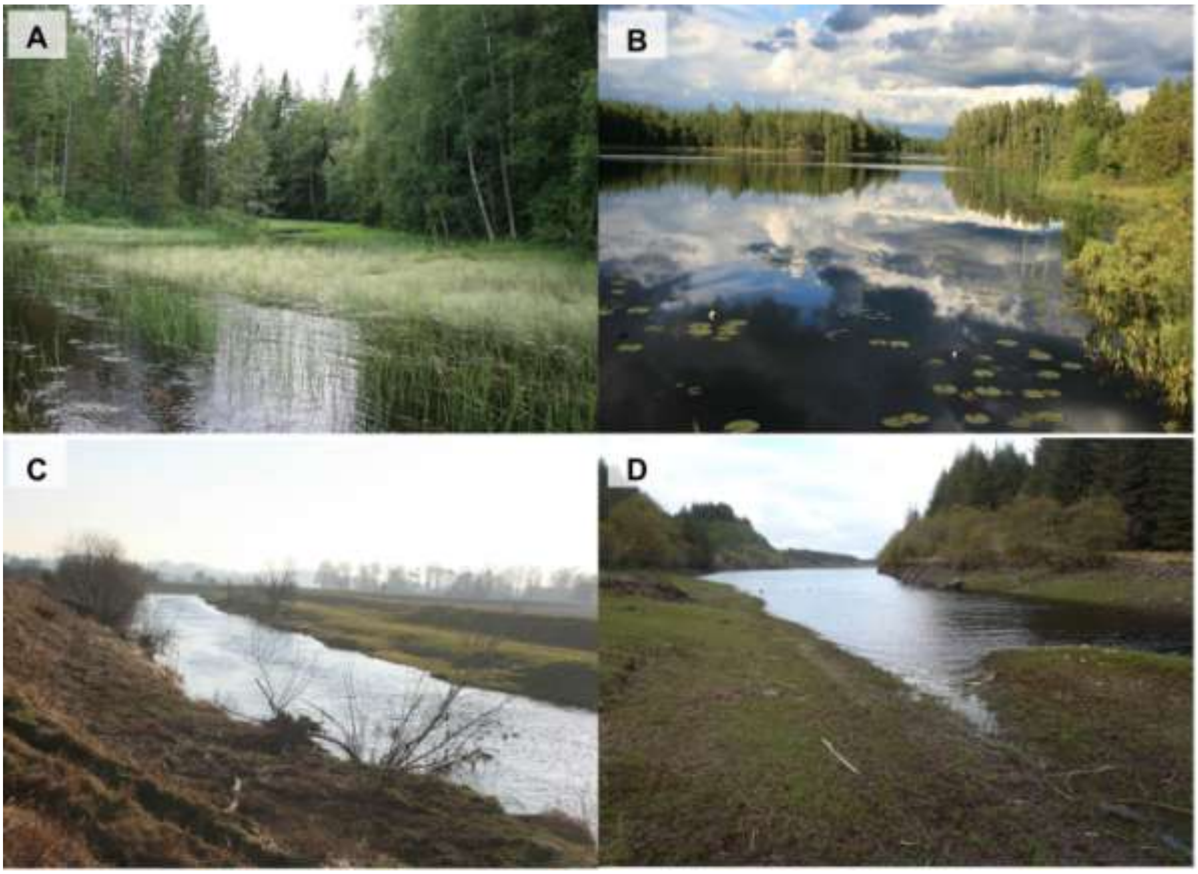

Fig. 7.6 An example of a; a – high quality river (Sweden, 2012), b – high quality lake (Sweden, 2012), c – low quality river (River Isla, Scotland 2011) and d – low quality regulated lake (Loch an Add, Knapdale, Scotland 2013) from a beaver's point of view (all pictures © Nigel Willby).

If beavers were (re-)introduced to any of these areas their impacts will be mediated by habitat quality and the resolution at which impacts are viewed. At the plot scale, regardless of habitat quality, the likelihood of observing any impacts by beavers is high (Fig. 7.7). As the scale increases (plot to reach/site scale) beaver impacts become less apparent, particularly in high quality habitats as foraging rates are proportional to the resource availability, which is greater in this scenario. Recovery from beaver impacts will also be more rapid in high quality habitats as they will be more resilient due to their higher productivity

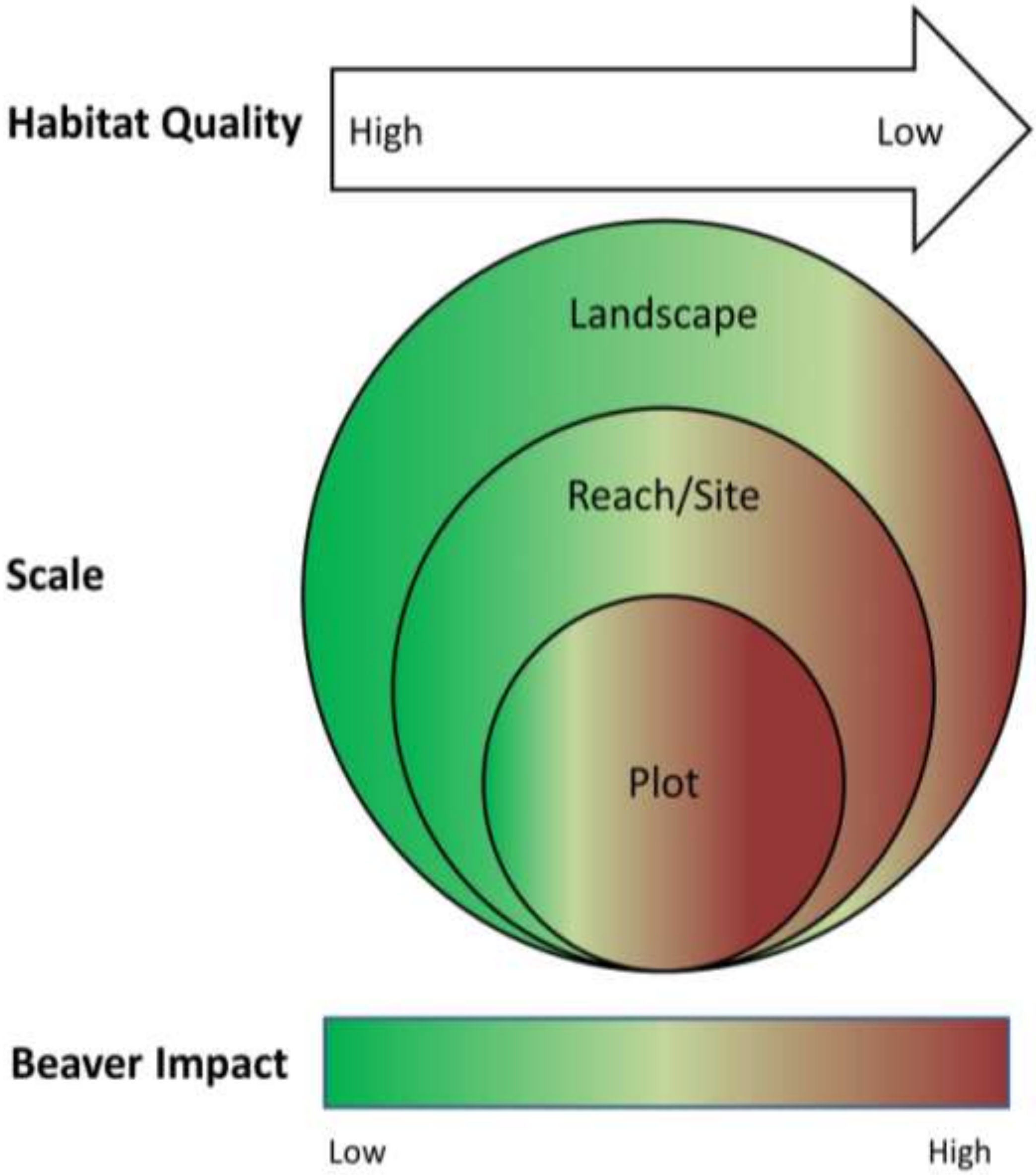

Fig 7.7 A prediction of the likelihood of beaver impact on physical and biological habitats at multiple spatial scales based on the evidence collected in this thesis. Impacts may be positive or negative.

Determining whether these beaver impacts are positive or negative, in terms of benefits to the ecosystem, is firstly dependent on the type of landscape occupied. For example, the creation of beaver ponds are likely to be more biologically valuable, in terms of spatial refugia and in promoting connectivity, in landscapes lacking abundant standing waters, e.g. arid and semi-arid environments (Gibson and Olden, 2014). Effects of foraging are more likely to be positive where other top-down foraging pressures are weak and where the targeted species are naturally-abundant, e.g. willow and birch dominated woodlands or riparian zones (Jones et al., 2009). Fig. 7.7 is an example of beavers as spatial units of biological disturbance within an ecosystem, but adding a temporal aspect to the hypothetical environments adds a further level of complexity (Fig. 7.8).

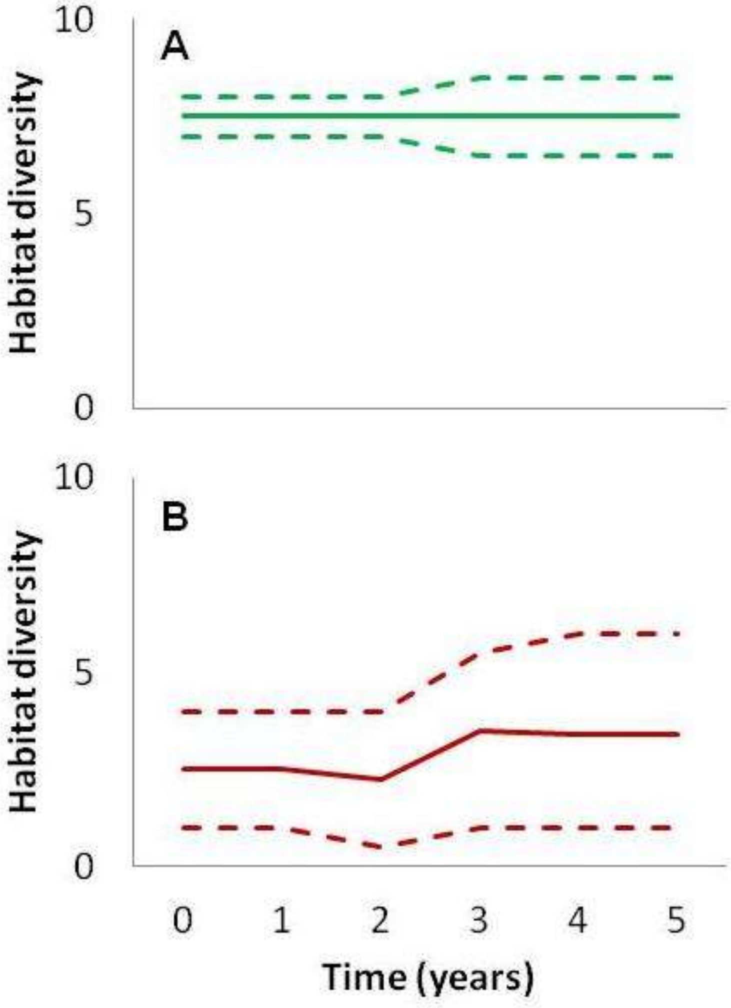

Fig. 7.8 An example of change in habitat diversity over time as a result of beavers being introduced at time 0 for; a – high quality and b – low quality habitats. Solid lines represent averaged diversity trends for positive (upper, dashed line) or negative (lower, dashed line) impact scenarios. High diversity scores are associated with a greater number of habitat types, distributed evenly within a site.

In the author’s experience, high quality beaver habitats generally have higher physical and biological habitat heterogeneity than low quality habitats. As a unit of feeding disturbance, or physical habitat modification, a beaver may create unique patches within a high quality site that can have small positive (e.g. localised tree felling reduces shading that may be beneficial for terrestrial or aquatic plants) or small negative (e.g. loss of species sensitive to disturbance) repercussions over time. Therefore temporal change in high quality systems may be negligible as a result of beaver (re-)introduction at the site and landscape scale.

But at low quality sites, beaver impacts will be much more pronounced and prolonged with initial foraging and water level increases causing significant changes in biodiversity. For example, in a pond or lake system where the changes in water level are likely to affect the whole site, significant reductions in aquatic plant abundance will occur (e.g. Dubh Loch, Knapdale (Willby, Perfect & Law, 2014)). Whereas, in low quality stream systems dams may create areas of lentic water amongst lotic sections that may increase the abundance of plants and alter composition (e.g. Chapter 6). High physical habitat diversity is presumed to already exist in high quality habitats, so beaver impacts may not be as apparent. Regardless of the site type, when areas influenced by beaver become the majority habitat type physical and biotic diversity may be reduced due to habitat homogenisation (Anderson et al., 2014; Wright et al., 2003). The effects of reduced habitat diversity from over-engineering by beaver may be compounded if dispersal is limited by hydrological connectivity or when regions affected have reached their carrying capacity. In these situations adaption and recovery of local biota will be slower due to continued disturbance. However, it is likely that low quality habitats will reach equilibrium with beaver impacts as continual, major hydrological changes through dam building are not always necessary once water levels are stabilised. Moreover, if sparse resources become exhausted due to foraging it is unlikely the area would remain inhabited. Therefore, regardless of habitat quality, all beaver-affected sites have the potential to recover given time, albeit at different rates depending on their productivity and connectivity with the regional species pool.

Preferentially a beaver should choose a high over a low quality habitat, as resources are greater and less energy will be spent engineering the habitat to their specifications. But in landscapes with saturated beaver populations or where optimal, high quality habitats are limited beavers may have no choice but to utilise suboptimal, low quality habitats. Such habitats will most likely be commonplace in areas that are heavily influenced by humans, e.g. regulated lakes/rivers, flood defences or agriculturally-dominated lowland catchments. As beavers are robust animals with varied diets they can survive in small areas of inferior habitat and may engineer the habitat to improve access to resources. But it is in these situations where humans and beavers co-exist that conflicts will most likely arise.

7.3.2 *Perception of beaver impacts*

Determining whether beaver impacts are positive or negative is also influenced by human perspective. Specifically, beaver impacts can be deemed positive or negative depending on the context in which they are described, or whom they are described by. For example, Figure 7.9 shows a collapsed beaver burrow on the River Isla, eastern Scotland. Seasonal, heavy rainfalls within the catchment increased water levels with the resulting flood engulfing the burrow and causing it to collapse. Subsequent floods fill the collapsed burrow, removing the exposed, unconsolidated soil and thereby further erode the river bank which could result in areas of the riparian zone being lost. Since the Isla flows through an area of intensive cultivation there is a possibility that individual landowners may lose parts of their land to beaver-induced erosion, or have to repair the river bank at significant cost to avoid the loss of land.

Fig 7.9 A collapsed beaver burrow on the banks of the River Isla, Scotland (March, 2011 © Alan Law).

Taken in isolation, this burrow collapse and subsequent bank erosion will generate negative publicity for beaver reintroductions across Britain as it is a new problem facing landowners that can be easily attributed to beavers (although cumulatively rabbits probably have similar effects). But further downstream, considering a larger stretch of the river, it is clear that this river has been heavily human-modified (Fig. 7.10). Riparian vegetation, which will help reduce top-soil erosion, stabilise banks and increase flood attenuation, is scarce or has been removed, while livestock grazing right to the water’s edge prevents regeneration. The river banks have been artificially heightened and straightened thereby further channelizing the water and reducing energy dissipated locally. The presence of beaver in this highly modified environment creates a potential problem, but it should be taken in context and shouldn’t distract from the greater problem of continued riparian encroachment for agriculture.

Fig. 7.10 The removal of riparian vegetation combined with seasonal floods, top-soil erosion and strong currents creates significant bank erosion, regardless of the presence of beavers (River Isla, March 2011 © Nigel Willby).

Further controversy will continue to surround beaver reintroductions in temperate regions regarding the impact of beaver dams on movement of fish (mostly salmonid spp.) and the siltation of their spawning grounds. Taking Fig. 7.11a as an example, this beaver dam is likely to become a further obstacle to fish movement in addition to the effects of the thousands of already-existing weirs, hydro-schemes and human-made dams. However, as the beaver reintroduction is in such an early phase there is not yet a general appreciation that beaver dams, unlike artificial structures, have gaps around and through them, and are rarely permanent features (Figs. 7.11b and c show the same dam washed out after a heavy rainfall). Also, it is unlikely that the majority of Scotland’s migrating fish depend on the furthest upstream kilometre of a spring-fed agricultural ditch at the Bamff estate.

Fig. 7.11 An example of the temporal nature of a beaver dam in the Bamff estate; a – 2011, b – 2012 and c – 2014 (all © Nigel Willby). Within 3 years of the dam collapsing due to heavy rainfall the river banks have fully re-vegetated.

Perception is something that can change given time and balanced reporting. For example, beavers in Norway and now Sweden are considered a part of the everyday environment with felled trees commonplace and beaver dams considered part of the natural discontinuity of rivers. Beaver impacts that are perceived as negative in the short-term and which are sources of conflict between opposing parties may be resolved in the long-term due to human habituation to beavers and their impacts.

7.3.3 *Management and future research on beavers*

If beavers remain in Scotland, there will undoubtedly and understandably be issues regarding management of the population and their ecosystem effects. Consequently, continued monitoring of felling rates, dam building and distribution will be needed over the next 5-10 years in areas where human activities encroach on riparian habitats to identify, record, resolve and predict future sources of conflict. Therefore, establishing beaver management protocols and supporting principles for balancing conservation and human needs is a current key priority. These should be developed by governmental organisations in consultation with national experts, whilst utilising the experience of other European countries. For example, after being reintroduced in 1927, Latvia now has one of the highest and densest populations of beavers in Europe (Halley and Rosell, 2003) due to a lack of natural predators, an abundance of suitable habitat and no desire for hunting. Subsequently, conflicts with landowners, farmers, fisherman and public has increased (Pillai et al., 2012). In terms of population management, non-lethal methods are used to control or deter beavers, e.g. destruction of breeding/resting sites or relocation, but lethal control may also be necessary e.g. a seasonal, fixed period hunting is permitted in Sweden (Hartman 2011). Though the biggest obstacle to beaver management will be the legal implications of culling an animal that is protected under EU law (Pillai et al., 2012). It is also likely that the British public will be highly averse to lethal control. However, without giving individual landowners special permission to remove beavers or their dams, as is the case in Sweden (Hartman, 2011), landowners are likely to feel powerless and thus opposed to beaver reintroduction.

By identifying conflict and management protocols, whilst providing continued monitoring, fundamental questions concerning beaver ecology could be documented in Scotland that may have global implications, e.g. effects of dams on salmonid fish or survival and colonisation rates of beavers in various habitat types and qualities. Unfortunately, regardless of any beaver research conducted this is unlikely to appease all interested parties such are the strong feelings for and against their reintroduction. Therefore the biology of beavers and their ecosystem-influencing activities should be used for educational purposes to demonstrate the pros and cons of nature-created disturbances that were, and hopefully will continue to be, an integral component of functional ecosystems in Britain.

At a larger scale, population growth and further colonisation by beavers may present opportunities to study the chemical and physical behavioural interactions between individuals and families, which are understudied relative to habitat modifications and will be an important determinant of future distribution patterns. Also, if beaver-created ponds become a more common part of the Scottish, and possibly British landscape, their potential benefits for flood mitigation and in regulating climate and water quality (storage of carbon, nutrient retention) would merit further investigation.

Early in this chapter the term ‘reintroduction biology’ was used to describe the majority of research on beavers i.e. behaviours and patterns derived from monitoring data. But the term reintroduction biology has connotations of being single-species focussed and with many reintroduction projects this appears to be the case, e.g. bison reintroduced to Romania, wolves reintroduced to Yellowstone and bears reintroduced to Italy. At first sight and from a perspective outwith these projects or field of expertise, these are examples of one species being translocated to an area they previously occupied. But on closer examination these are examples of animals that have disproportionally large effects on their ecosystem and are therefore reinstated to restore a missing ecological function. Thus the term ‘rewilding’ should be used more commonly when referring to reintroductions of this sort. Rewilding encompasses an ecosystem approach to restoration and has been used steadily throughout the last 20 years in conjunction with re-establishment of natural processes. Specifically, the reintroduction of beavers should be applied to the rewilding context (and has been occasionally in national newspapers, but not as yet in the scientific literature) due to the ecosystem services they can provide by attenuating floods and agricultural run-off, whilst creating a mosaic of habitats for other species. Moreover, if beavers remain in Scotland it may set the foundations for further, necessary rewilding across the UK; although it's important to have realistic rewilding objectives. For example, beavers could be reintroduced into areas that have experienced catastrophic floods in recent years (e.g. South-west England) on the premise that floods will be alleviated due to the presence of their dams promoting the headwater retention that is currently lacking. But years of poor land management and flood-plain encroachment will have a far greater influence on ecological processes at the landscape scale than beavers. Therefore, even though beavers have the potential to restore and rewild degraded ecosystems at smaller spatial and temporal scales, they are only one piece of the ecological jigsaw, but still a step in the right direction.

It is essential to better understand how freshwater systems function as they are directly or indirectly related to all the major biomes and are declining at a much faster rate than terrestrial ecosystems. Also, as pressures on the majority of freshwater systems are likely to increase with human population expansion and changing climate, the understanding, conservation, creation and reclamation of wetlands is a major scientific and practical issue. Therefore in being able to quantify effects on ecosystems we may be able to predict current and future impacts whilst integrating sufficient protection and awareness of freshwater systems to maintain the ecosystem services they provide. Furthermore, the ability of organisms, whether native, reintroduced or non-native, to modify their habitat adds additional layers of complexity and intrigue that should not be overlooked. This thesis represents a small but significant step in understanding these processes.

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Appendices

Appendix 2.1

Impact	Strength	Area	Author	Year
Direct	0	N. America	Aleksiuk	1970
Indirect	2	N. America	Bason	2004
Direct	0	N. America	Belovsky	1984
Indirect	2	N. America	Bonner	2009
Direct	0	N. America	Brenner	1962
Direct	0	N. America	Chabrek	1958
Indirect	2	N. America	Cunningham et al	2006
Direct	0	Europe	Curry-lindahl	1967
Direct	0	N. America	Doucet and Frxyell	1993
Direct	0	N. America	Dyck and MacArthur	1993
Direct	0	Europe	Elmeros	2003
Indirect	2	N. America	Feldmann	1995
Direct	0	N. America	Fryxell	2001
Direct	0	Europe	Ganzhorn	2000
Direct	0	Europe	Histol	1989
Indirect	0	Europe	Johansson and Nilsson	1993
Indirect	2	N. America	Johnston and Naiman	1990
Direct	0	Europe	Krojerová-Prokešová	2010
Direct	0	Europe	Lahti	1974
Direct	1	Europe	Law, Jones & Willby	2014
Direct	1	Europe	Law, Bunnefeld & Willby	2014

Indirect	2	N. America	Little	2012
Indirect	2	N. America	McMaster	2000
Indirect	2	N. America	McMaster	2001
Direct	0	N. America	Milligan and Humphries	2010
Direct	0	Europe	Nolet	1994
Direct	0	N. America	Northcott	1971
Direct	0	N. America	Northcott	1972
Indirect	1	Europe	Nummi	1989
Direct	0	N. America	O'Brien	1938
Direct	1	N. America	Parker	2007
Indirect	2	N. America	Ray et al.	2001
Indirect	1	N. America	Reddoch and Reddoch	2005
Indirect	2	N. America	Remillard et al	1987
Direct	0	N. America	Roberts and Arner	1984
Direct	0	N. America	Severud et al	2013
Direct	0	N. America	Shelton	1966
Indirect	1	N. America	Snodgrass	1997
Direct	0	N. America	Svendson	1980
Indirect	2	N. America	Syphard and Garcia	2001
Indirect	2	N. America	Westbrook	2010
Indirect	2	Europe	Willby, *et al.*	2014
Direct	1	Europe	Willby, Perfect and Law	2014
Direct	0	Europe	Willson	1971
Indirect	2	N. America	Wright	2002

Indirect	2	N. America	Wright	2003

Appendix 3.1

Estimates and standard errors (SE) from generalised mixed, linear mixed and generalised linear models used in the study.

Model	Response	Explanatory variable(s)	Estimate	SE	d.f.	z value	t value	P-value
M1	Mid-line distance	Intercept Petiole diameter (log transformed)	7.378449 1.113829	0.024900 0.001719	4 4	296.30 647.80	- -	< 0.001 < 0.001
M2	Dry weight	Intercept Petiole diameter (log transformed)	1.30256 2.43489	0.06541 0.01941	3 3	19.91 125.42	- -	< 0.001 < 0.001
M3	Dry weight	Intercept Mid-line distance (log transformed)	-15.52507 2.25163	0.17251 0.01793	3 3	-90.00 125.60	- -	< 0.001 < 0.001
M4	Selected (Y/N)	Intercept Mid-line distance	-2.546521 0.028799	0.413381 0.004047	480 480	-6.16 7.12	- -	< 0.001 < 0.001
M5	Selected (Y/N)	Intercept Size (medium) Size (small)	0.03922 -1.79882 -4.27333	0.15444 0.24481 1.57828	57 57 57	- - -	0.25 -7.35 -2.71	0.800 < 0.001 0.008
M6	Weighted average (log transformed)	Intercept Depth (cm) Feeding in quadrat Depth x feeding	4.5209119 0.0010602 -0.1614120 0.0004597	0.0774364 0.0004619 0.0708713 0.0007350	7 7 7 7	- - - -	58.38 2.30 -2.28 0.63	< 0.001 0.025 0.028 0.534

M7	Grazed (Y/N)	Intercept	0.8092643	1.1502575	72	0.70	-	0.482
		Depth (cm)	-0.0147126	0.0048542	72	-3.03	-	0.002
		Weighted average (mm)	0.0003711	0.0116011	72	0.03	-	0.974
M8	Consumed (%)	Intercept	59.34879	6.04334	36	-	9.82	< 0.001
		Depth (cm)	-0.01847	0.07196	36	-	-0.26	0.799
		Size (medium)	-49.64359	8.54658	36	-	-5.81	< 0.001
		Depth x size (medium)	0.06579	0.10176	36	-	0.65	0.522
M9	Total pad count	Intercept	7.0193	0.1600	5	43.87	-	< 0.001
		Beaver present, no *N. alba* feeding	0.1223	0.1696	5	0.72	-	0.471
		No beaver present	0.2251	0.1555	5	1.45	-	0.149
M10	Species count	Intercept	0.32541	0.06086	3	5.35	-	< 0.001
		Feeding in site (Y)	-0.17703	0.14473	3	-1.22	-	0.221
M11	Species count	Intercept	0.13005	0.15617	3	0.83	-	0.405
		Feeding in quadrat (Y)	0.06408	0.28847	3	0.22	-	0.824
M12	*N. alba* flower count	Intercept	-0.5321	0.6094	4	-0.87	-	0.383
		Feeding in quadrat (Y)	-0.5137	0.3870	4	-1.33	-	0.184
M13	*N. alba* flower count	Intercept	3.4821	0.4204	4	8.28	-	< 0.001
		Feeding in site (Y)	0.3804	0.3503	4	1.09	-	0.278

Appendix 3.2

The graphical relationships between *N. alba* organs and dry weight.

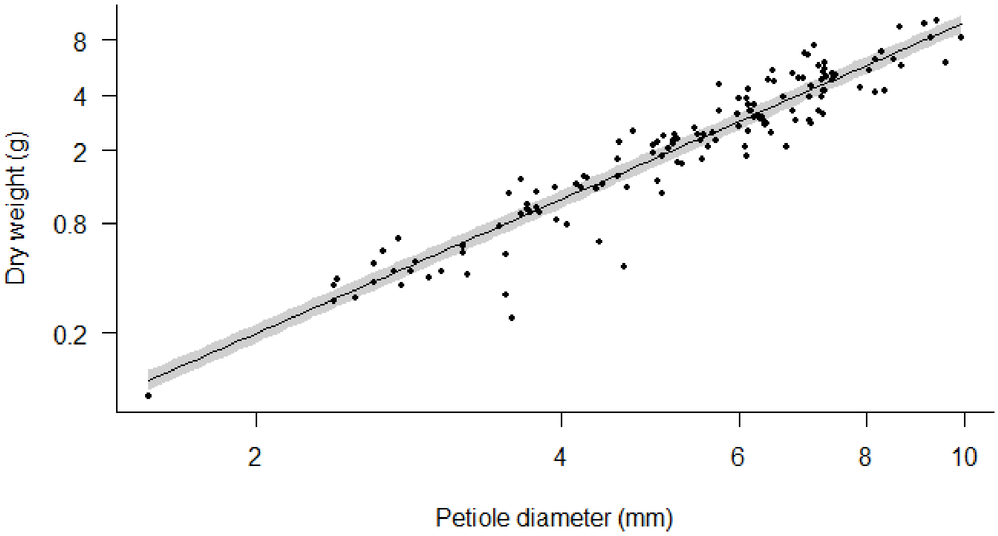

Fig. 3.2.1 The relationship between *N. alba* petiole diameter and dry weight (solid line with 95% confidence intervals, on a log scale) based on pads collected from lakes where beavers are absent or where there is no evidence of grazing.

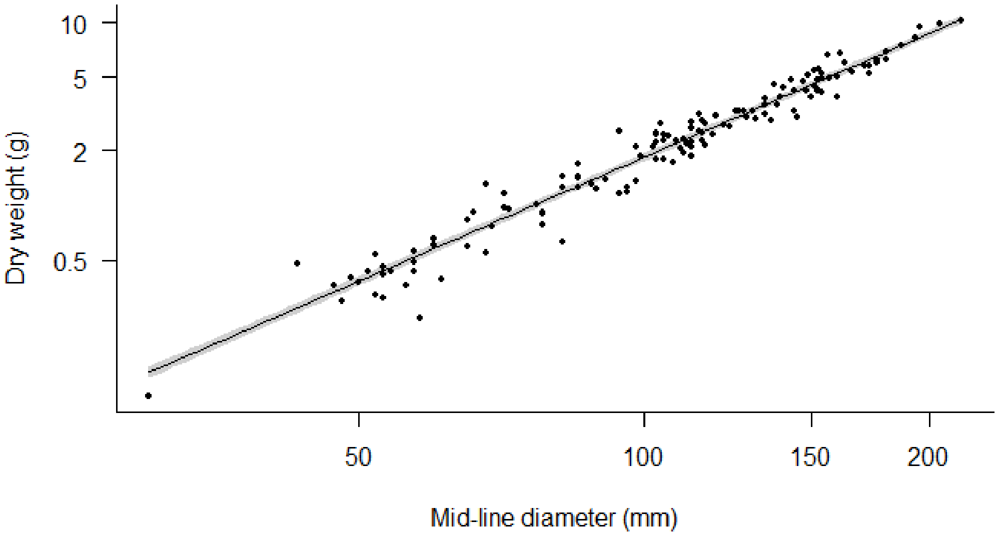

Fig. 3.2.2 The relationship between *N. alba* mid-line distance and dry weight (solid line with 95% confidence intervals, on a log scale) based on pads collected from lakes where beavers are absent or where there is no evidence of grazing.

Appendix 4.1

Outputs from Kruskal-Wallis (KW) one way analyses of variances with post hoc multiple comparisons for coverage (%), Shannon's diversity (H') and Bray-Curtis dissimilarity indices per habitat.

Habitat	Index	KW Chi-squared	d.f.	P-value	Post-test multiple comparisons			
					Year	Obs. difference	Critical difference	Significant difference
Emergent	Coverage	0.19	2	0.9112	2003-2004	1.27	14.66	False
					2003-2012	1.34	14.52	False
					2004-2012	2.61	14.52	False
Emergent	H'	26.97	2	< 0.001	2003-2004	10.83	14.66	False
					2003-2012	30.97	14.51	True
					2004-2012	20.13	14.51	True
Emergent	Bray-Curtis	65.57	2	< 0.001	2003-2004	5.18	50.81	False
					2003-2012	146.15	50.81	True
					2004-2012	151.33	50.81	True
Mat	Coverage	3.51	2	0.1727	2003-2004	2.75	6.1	False
					2003-2012	2.0	6.1	False
					2004-2012	7.75	6.1	False
Mat	H'	4.27	2	0.118	2003-2004	3.00	6.10	False
					2003-2012	2.25	6.10	False
					2004-2012	5.25	6.10	False
Mat	Bray-Curtis	14.39	2	< 0.001	2003-2004	6.33	7.38	False
					2003-2012	11.67	7.38	True
					2004-2012	5.33	7.38	False

Open	Coverage	9.82	2	0.007	2003-2004	5.44	11.85	False
					2003-2012	9.84	11.85	False
					2004-2012	15.28	11.85	True
Open	H’	6.97	2	0.031	2003-2004	4.72	11.85	False
					2003-2012	2.94	11.85	False
					2004-2012	7.66	11.85	False
Open	Bray-Curtis	3.77	2	0.152	2003-2004	10.31	32.16	False
					2003-2012	25.90	32.16	False
					2004-2012	15.60	32.16	False

Appendix 4.2

Estimates and standard errors from generalised mixed linear models used in the study.

Model	Response	Explanatory variable(s)	Estimate	SE	d.f.	Z value	P-value
M1	Species count (emergent)	Intercept	1.1865	0.1263	72	9.393	< 0.001
		Year 2004	0.2053	0.1516	72	1.354	0.176
		Year 2012	0.9262	0.1323	72	7.0	< 0.001
M2	Species count (open habitat)	Intercept	0.44629	0.2	47	2.231	0.0257
		Year 2004	0.07696	0.27756	47	0.277	0.7816
		Year 2012	0.11332	0.27516	47	0.412	0.6805
M3	Species count (mat)	Intercept	1.0116	0.3015	11	3.355	< 0.001
		Year 2004	0.1671	0.4097	11	0.408	0.6834
		Year 2012	0.5978	0.3754	11	1.593	0.1112
M4	Species count	Intercept	0.4990	0.2305	9	2.165	0.0304
		Area (grazed)	0.1178	0.1406	9	0.840	0.4011

		Month (Aug)	0.2513	0.2910	9	0.864	0.3877
		Month (Jul)	0.3567	0.2845	9	1.254	0.2100
		Month (Jun)	0.3895	0.2826	9	1.378	0.1682
		Month (May)	0.3567	0.2845	9	1.254	0.2100
		Month (Oct)	0.5390	0.2746	9	1.963	0.0497
		Month (Sep)	0.3228	0.2865	9	1.126	0.2600

Appendix 4.3

The observed within season inventory of macrophyte species per month and area during 2011 (+ present, - absent).

	April		**May**		**June**		**July**		**August**		**September**		**October**	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Menyanthes trifoliata	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Carex rostrata	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Equisetum fluviatile	-	-	+	+	+	+	+	+	-	+	+	+	+	+
Cardamine flexuosa	-	-	-	+	-	+	-	-	-	-	-	-	-	+
Potentilla palustris	-	-	-	+	-	-	+	-	-	-	+	+	-	-
Epilobium palustre	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Epilobium ciliatum	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Salix spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Hippuris vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Cratoneuron spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Myosotis laxa	-	-	-	-	-	-	-	-	-	-	-	-	+	-

Appendix 5.1

List of plant species found and their distribution between beaver ponds and control wetlands.

Species	Control	Beaver
Acorus.calamus	0.0	100.0
Agrostis.canina	81.8	18.2
Agrostis.capillaris	100.0	0.0
Agrostis.stolonifera	71.4	28.6
Alisma.lanceolatum	50.0	50.0
Alisma.plantago.aquatica	81.9	18.1
Alnus.spp. (sapling)	100.0	0.0
Alopecurus.geniculatus	100.0	0.0
Andromeda.polifolia	100.0	0.0
Anemone.nemorosa	100.0	0.0
Angelica.sylvestris	100.0	0.0
Arctostaphylos.uva.ursi	0.0	100.0
Betula.pubescens (sapling)	100.0	0.0
Bidens.cernua	0.0	100.0
Bidens.tripartita	50.0	50.0
Brachythecium.rutabulum	100.0	0.0
Calamagrostis.canescens	47.9	52.1
Calamagrostis.purpurea	72.2	27.8
Calla.palustris	83.9	16.1
Calliergon.cuspidatun	100.0	0.0
Callitriche.cophocarpa	100.0	0.0
Callitriche.hamulata	100.0	0.0
Callitriche.platycarpa	69.2	30.8
Caltha.palustris	60.0	40.0
Campylopus.introflexus	100.0	0.0
Cardamine.pratensis	66.7	33.3
Carex.acuta	2.4	97.6
Carex.appropinquata	100.0	0.0
Carex.aquatilis	0.0	100.0
Carex.chordorrhiza	50.0	50.0
Carex.curta	83.1	16.9
Carex.distica	0.0	100.0
Carex.echinata	66.7	33.3
Carex.elata	100.0	0.0
Carex.elongata	33.3	66.7
Carex.lasiocarpa	20.8	79.2
Carex.lepidocarpa	0.0	100.0
Carex.limosa	0.0	100.0
Carex.nigra	72.9	27.1
Carex.ovalis	33.3	66.7
Carex.panicea	100.0	0.0
Carex.pseudocyperus	100.0	0.0
Carex.rostrata	57.0	43.0
Carex.vesicaria	37.2	62.8
Chara.vulgaris	0.0	100.0
Cicuta.virosa	66.7	33.3
Circaea.nemoralis	100.0	0.0
Cirsium.palustre	0.0	100.0
Cratoneuron.commutatum	60.0	40.0
Deschampsia.cespitosa	88.9	11.1
Drosera.rotundifolia	0.0	100.0
Eleocharis.multicaulis	100.0	0.0
Eleocharis.palustris	36.4	63.6
Eleocharis.quinqueflora	100.0	0.0
Epilobium.montanum	100.0	0.0
Epilobium.palustre	63.6	36.4
Equisetum.arvense	100.0	0.0
Equisetum.fluviatile	41.0	59.0
Equisetum.sylvaticum	100.0	0.0
Eriophorum.angustifolium	42.1	57.9
Eriophorum.vaginatum	100.0	0.0
Filamentous.algae	100.0	0.0
Filipendula.ulmaria	42.1	57.9
Galeopsis.tetrahit	0.0	100.0
Galium.palustris	43.6	56.4
Glyceria.fluitans	90.0	10.0
Glyceria.maxima	0.0	100.0
Gnaphalium.uliginosum	100.0	0.0
Hippuris.vulgaris	100.0	0.0
Hottonia.palustris	36.4	63.6
Hydrocharis.morsus.ranae	74.4	25.6
Hylocomium.splendens	100.0	0.0
Impatiens.noli.tangere	33.3	66.7

Iris.pseudacorus	50.0	50.0
Isoetes.echinospora	0.0	100.0
Juncus.articulatus	100.0	0.0
Juncus.bufonius	100.0	0.0
Juncus.bulbosus	62.5	37.5
Juncus.conglomeratus	0.0	100.0
Juncus.effusus	81.3	18.8
Juncus.filiformis	83.3	16.7
Lathyrus.pratensis	100.0	0.0
Lemna.minor	53.4	46.6
Lobelia.dortmanna	0.0	100.0
Lycopus.europaeus	37.5	62.5
Lysimachia.thyrisflora	63.8	36.2
Lysimachia.vulgaris	39.3	60.7
Lythrum.salicaria	25.6	74.4
Mentha.aquatica	62.5	37.5
Menyanthes.trifoliata	26.5	73.5
Mimulus.guttatus	0.0	100.0
Molinia.caerulea	61.9	38.1
Myosotis.laxa.scorpiodes	36.4	63.6
Myrica.gale	36.9	63.1
Myriophyllum.alterniflorum	66.7	33.3
Myriophyllum.spicatum	0.0	100.0
Myriophyllum.verticillatum	0.0	100.0
Nitella.flexilis	100.0	0.0
Nuphar.lutea	25.0	75.0
Nuphar.pumilla	33.3	66.7
Nuphar.x.spenneriana	0.0	100.0
Nymphaea.alba	10.5	89.5
Nymphaea.tetragona	100.0	0.0
Persicaria.amphibia	0.0	100.0
Persicaria.lapathifolia	100.0	0.0
Peucedanum.palustre	50.0	50.0
Phalaris.arundinacea	35.3	64.7
Phragmites.australis	40.5	59.5
Poa.trivialis	0.0	100.0
Polytrichum.commune	80.0	20.0

Potamogeton.alpinus	81.0	19.0
Potamogeton.berchtoldii	100.0	0.0
Potamogeton.natans	44.4	55.6
Potamogeton.obtusifolius	0.0	100.0
Potentilla.erecta	100.0	0.0
Potentilla.palustris	47.4	52.6
Pseudoscleropodium.purum	100.0	0.0
Ranunculus.flammula	90.0	10.0
Ranunculus.repens	100.0	0.0
Rhynchospora.alba	0.0	100.0
Rhytidiadelphus.spp.	100.0	0.0
Rorippa.palustris	100.0	0.0
Salix.cinerea (sapling)	0.0	100.0
Salix.spp. a. (sapling)	100.0	0.0
Salix.spp. b. (sapling)	60.0	40.0
Sambucus.nigra	100.0	0.0
Scheuchzeria.palustris	0.0	100.0
Schoenoplectus.lacustris	0.0	100.0
Scirpus.sylvaticus	69.4	30.6
Scutelliaria.gallericulata	45.5	54.5
Solanum.dulcamara	30.0	70.0
Sorbus.aucuparia (sapling)	100.0	0.0
Sparganium.angustifolium	100.0	0.0
Sparganium.emersum	100.0	0.0
Sparganium.erectum	55.8	44.2
Sparganium.hyperboreum	0.0	100.0
Sparganium.natans	70.0	30.0
Sphagnum.spp.	34.3	65.7
Spirodela.polyrhiza	100.0	0.0
Stachys.palustris	0.0	100.0
Stellaria.alsine	100.0	0.0
Stellaria.palustris	13.6	86.4
Thalictrum.flavum	14.3	85.7
Typha.angustifolia	36.4	63.6
Urtica.dioica	33.3	66.7
Utricularia.australis	0.0	100.0
Utricularia.intermedia	56.4	43.6

Utricularia.minor	50.0	50.0
Utricularia.vulgaris	81.8	18.2
Vaccinium.oxycoccos	20.0	80.0
Valeriana.officinalis	40.0	60.0
Veronica.beccabunga	0.0	100.0
Veronica.chamaedrys	100.0	0.0
Veronica.scutellata	40.0	60.0
Vicia.cracca	100.0	0.0
Viola.palustris	50.0	50.0

Appendix 5.2

List of beetle species found and their distribution between beaver ponds and control wetlands.

Species	Beaver	Control
Acilius canaliculatus	71.4	28.6
Agabus affinis	100.0	0.0
Agabus bipustulatus	100.0	0.0
Agabus congener	0.0	100.0
Agabus striolatus	100.0	0.0
Agabus sturmii	0.0	100.0
Anacaena lutescens	80.0	20.0
Anisosticta novemdecimpunctata	22.2	77.8
Coelostoma orbiculare	50.0	50.0
Colymbetes spp.	100.0	0.0
Cyphon coarctatus	33.3	66.7
Cyphon palustris	100.0	0.0
Donacia aquatica	50.0	50.0
Donacia simplex	50.0	50.0
Dytiscus marginalis	100.0	0.0
Enochrus coaerctatus	58.3	41.7
Enochrus ochropus	0.0	100.0
Galerucella nymphaeae	0.0	100.0
Graphoderus spp.	0.0	100.0
Graptodytes pictus	0.0	100.0
Gyrinulus minutus	25.0	75.0
Gyrinus substriatus	14.3	85.7
Haliplus fulvus	100.0	0.0
Haliplus heydeni	100.0	0.0
Haliplus ruficollis	55.0	45.0
Haliplus ruficollis group	71.4	28.6
Helophorus brevipalpis	50.0	50.0
Hydaticus seminiger	75.0	25.0
Hydaticus transversalis	100.0	0.0
Hydrobius fuscipes	100.0	0.0
Hydroporus angustatus	100.0	0.0
Hydroporus erythrocephalus	33.3	66.7
Hydroporus figuratus/dorsalis s.s.	0.0	100.0
Hydroporus incognitus	100.0	0.0
Hydroporus melanarius	100.0	0.0
Hydroporus neglectus	100.0	0.0
Hydroporus palustris	24.2	75.8
Hydroporus striola	50.0	50.0
Hydroporus tristis	100.0	0.0
Hydroporus umbrosus	18.2	81.8
Hygrotus decoratus	0.0	100.0
Hygrotus inaequalis	0.0	100.0
Hygrotus versicolor	0.0	100.0
Hyphydrus ovatus	65.0	35.0
Ilybius aenescens	66.7	33.3
Ilybius ater	77.1	22.9
Ilybius fenetratus	66.7	33.3
Ilybius fuliginosus	61.0	39.0
Ilybius guttiger	71.4	28.6
Ilybius quadriguttatus	61.5	38.5
Noterus crassicornis	30.8	69.2
Orectochilus villosus	0.0	100.0
Phaedon armoraciae	100.0	0.0

Plateumaris discolor	100.0	0.0
Plateumaris sericea	100.0	0.0
Porhydrus lineatus	33.3	66.7
Rhantus exsoletus	37.5	62.5
Rhantus grapii	47.1	52.9
Rhantus suturalis	100.0	0.0
Scirtes hemisphaericus	0.0	100.0

Appendix 6.1

Species inventory and abbreviations used in NMDS

Species name	Species abbreviation	Species name	Species abbreviation
Acilius.canaliculatis	Aci.can	Hygrobia.hermanni	Hyg.her
Acilius.sulcatus	Aci.sal	Hygrotus.inaequalis	Hyg.ina
Agabini.spp.	Aga.spp	Ilybius.fuliginosus	Ily.ful
Agabus.bipustulatus	Aga.bip	Isoperla.grammatica	Iso.gra
Agabus.guttatus	Aga.gut	Lestes.sponsa	Les.spo
Agabus.paludosus	Aga.pal	Leuctra.fusca	Leu.fus
Agabus.sturmii	Aga.stu	Leuctra.hippopus.moselyi	Leu.hip
Agapetus.fuscipes	Aga.fus	Leuctra.inermis	Leu.ine
Amphinemura.sulcicollis	Amp.sul	Leuctra.nigra	Leu.nig
Anabolia.nervosa	Ana.ner	Limnebius.truncatellus	Lim.tru
Anacaena.globulus	Ana.glo	Limnephilus.affinis.incisus	Lim.aff
Ancylus.fluviatilis	Anc.flu	Limnephilus.auricula	Lim.aur
Antocha.spp.	Ant.spp	Limnephilus.bipunctatus	Lim.bip
Asellus.aquaticus	Ase.aqu	Limnephilus.centralis	Lim.cen
Alainites.muticus	Bae.mut	Limnephilus.extricatus	Lim.ext
Baetis.rhodani	Bae.rho	Limnephilus.fuscicornis	Lim.fus
Baetis.scambus.fuscatus	Bae.sca	Limnephilus.ignavus	Lim.ign
Beraea.maurus	Ber.mau	Limnephilus.lunatus	Lim.lun
Beraea.pullata	Ber.pul	Limnephilus.marmoratus.flavicornis	Lim.mar
Brachyptera.risi	Bra.ris	Limnephilus.rhombicus	Lim.rho
Callicorixa.praeusta	Cal.pra	Limnephilus.sparsus	Lim.spa
Centroptilum.luteolum	Cen.lut	Limnephilus.vittatus	Lim.vit
Ceratopogonidae.spp.	Cer.spp	Limnius.volckmari	Lim.vol
Chaetopteryx.villosa	Cha.vil	Limoniinae.spp.	Lim.spp
Chaoboridae.spp.	Cha.spp	Lymnaea.stagnalis	Lym.sta
Chironomidae.spp.	Chi.spp	Megasternum.concinnum s. lat.	Meg.con
Cloeon.dipterum	Clo.dip	Melampophylax.mucoreus	Mel.muc
Corixa.panzeri.punctata	Cor.pan	Metalype.fragilis	Met.fra
Crangonyx.pseudogracilis	Cra.pse	Micropterna.lateralis	Mic.lat
Crunoecia.irrorata	Cru.irr	Micropterna.sequax	Mic.seq

Culicidae.spp.	Cul.spp	Nebrioporus.elegans	Neb.ele
Cymatia.bonsdorffii	Cym.bon	Nemoura.avicularis	Nem.avi
Dicranota.spp.	Dic.spp	Nemoura.cambrica.erratica	Nem.cam
Diplectrona.felix	Dip.fel	Nemoura.cinerea	Nem.cin
Diptera.spp.	Dip.spp	Nemurella.pictetii	Nem.pic
Dixidae.spp.	Dix.spp	Notonecta.glauca	Not.gla
Dolichopodidae.spp.	Dol.spp	Odontocerum.albicorne	Odo.alb
Drusus.annulatus	Dru.ann	Oligochaeta.sp.	Oli.spp
Dytiscidae.spp.	Dyt.spp	Oulimnius.tuberculatus	Oul.tub
Ecdyonurus.dispar.torrentis	Ecd.dis	Pedicia.spp.	Ped.spp
Electrogena.lateralis	Ele.lat	Pericoma.spp.	Per.spp
Elmis.aenea	Elm.aen	Phaedon.armoraciae	Pha.arm
Eloeophila.spp.	Elo.spp	Philopotamus.montanus	Phi.mon
Empididae.spp.	Emp.spp	Phryganea.bipunctata	Phr.bip
Erioptera.spp.	Eri.spp	Planorbarius.corneus	Pla.cor
Erpobdella.octoculata	Erp.oct	Planorbis.carinatus	Pla.car
Galba.truncatula	Gal.tru	Planorbis.planorbis	Pla.pla
Gammarus.pulex	Gam.pul	Platambus.maculatus	Pla.mac
Gerris.lacustris	Ger.lac	Plectrocnemia.conspersa	Ple.con
Gerris.odontogaster	Ger.odo	Potamophylax.rotundipennis	Pot.rot
Glaenocorisa.propinqua	Gla.pro	Protonemura.meyeri	Pro.mey
Glossiphonia.complanata	Glo.com	Psychomyia.pusilla	Psy.pus
Glossosoma.conforme.boltoni	Glo.con	Ptychopteridae.spp.	Pty.spp
Glyphotaelius.pellucidus	Gly.pel	Pyrrhosoma.nymphula	Pyr.nym
Gyraulus.albus	Gyr.alb	Radix.balthica	Rad.bal
Gyrinus.substriatus	Gyr.sub	Rhantus.exsoletus	Rhan.exs
Halesus.digitatus.radiatus	Hal.dig	Rhantus.spp.	Rha.spp
Haliplus.fulvus	Hal.ful	Rhithrogena.semicolorata	Rhi.sem
Haliplus.lineatocollis	Hal.lin	Rhyacophila.dorsalis	Rhy.dor
Haliplus.ruficollis	Hal.ruf	Rhyacophila.obliterata	Rhy.obl
Haliplus.sibiricus	Hel.sib	Scirtidae.spp.	Sci.spp
Helobdella.stagnalis	Hel.sta	Sericostoma.personatum	Ser.per
Helophorus.aequalis	Hel.aeq	Serratella.ignita	Ser.ign
Helophorus.brevipalpis	Hel.bre	Sialis.lutaria	Sia.lut
Helophorus.flavipes	Hel.fla	Sigara.distincta	Sig.dis
Helophorus.grandis	Hel.gra	Sigara.dorsalis	Sig.dor
Hemerodromia.spp.	Hem.spp	Sigara.falleni	Sig.fal
Hesperocorixa.linnaei	Hes.lin	Sigara.limitata	Sig.lim
Hesperocorixa.sahlbergi	Hes.sah	Silo.pallipes	Sil.pal
Hexatoma.spp.	Hex.spp	Simuliidae.spp.	Sim.spp
Hippeutis.complanatus	Hip.com	Siphonoperla.torrentium	Sip.tor
Holocentropus.stagnalis	Hol.sta	Sphaeriidae.spp.	Sph.spp

Hydracarina.spp.	Hyd.spp	Stagnicola.palustris	Sta.pal
Hydraena.gracilis	Hyd.gra	Theromyzon.tessulatum	The.tes
Hydrobius.fuscipes	Hyd.fus	Tipula.spp.	Tip.spp
Hydroporini.spp.	Hyp.spp	Velia.caprai	Vel.cap
Hydroporus.incognitus	Hyd.inc	Wiedemannia.spp.	Wie.spp
Hydroporus.palustris	Hyd.pal	Wormaldia.occipitalis	Wor.occ
Hydropsyche.siltalai	Hyd.sil	Wormaldia.subnigra	Wor.sub