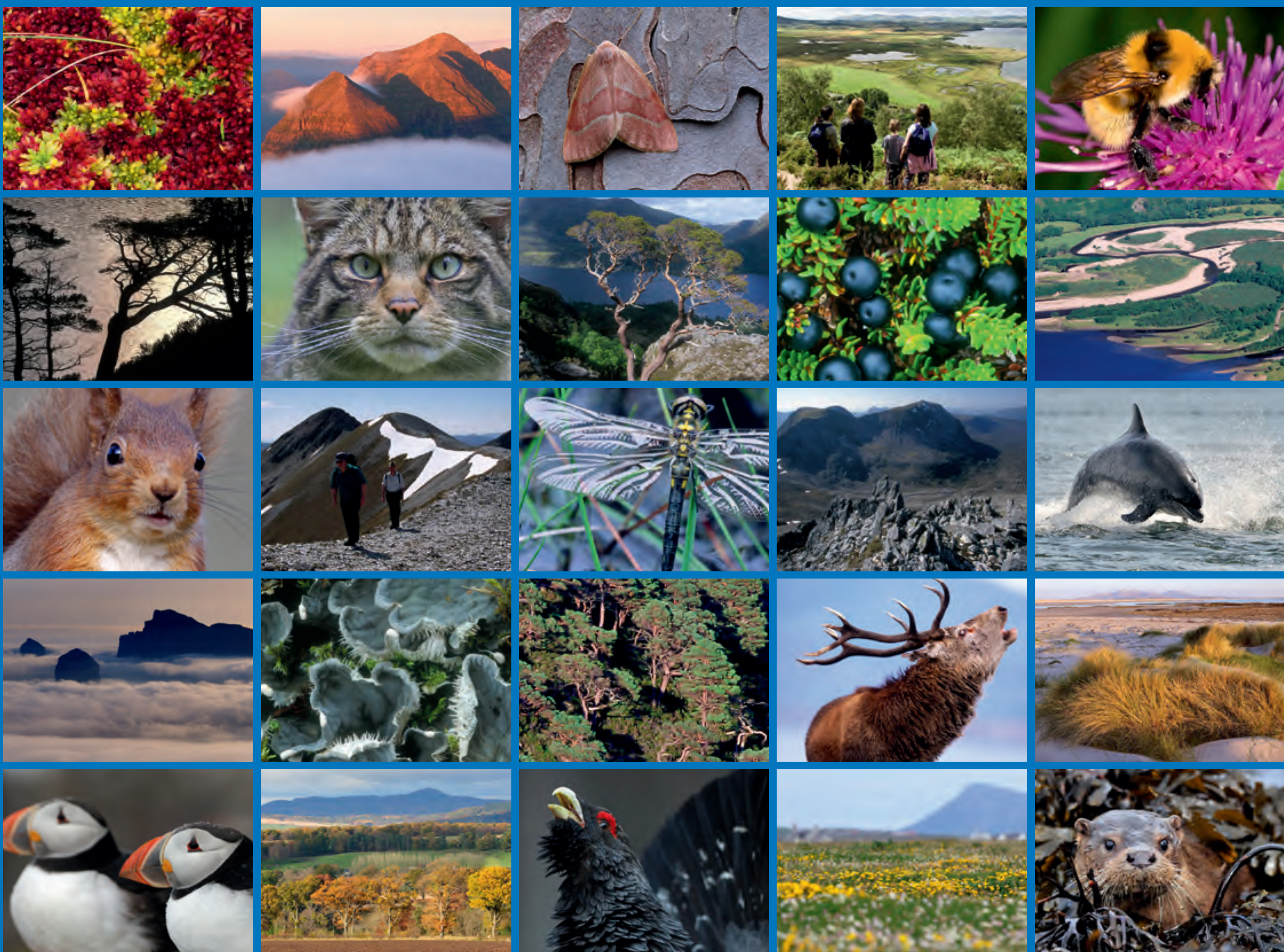
Scottish Natural Heritage
Commissioned Report No. 815

A review of beaver (*Castor* spp.) impacts on biodiversity, and potential impacts following a reintroduction to Scotland



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COMMISSIONED REPORT

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A review of beaver (*Castor* spp.) impacts on biodiversity, and potential impacts following a reintroduction to Scotland

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COMMISSIONED REPORT
Summary

A review of beaver (*Castor* spp.) impacts on biodiversity, and potential impacts following a reintroduction to Scotland

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Keywords

Castor spp; biodiversity; meta-analysis; Scotland; ecosystem engineer; species; habitats.

Background

This report has been published to help inform the Scottish Government on its decision on the future of beavers within Scotland (see Gaywood, 2015). Beavers are widely considered to be 'ecosystem engineers'. This term is reserved for those species that have a large impact on an environment, fundamentally changing ecosystems, and creating highly unusual habitats, often considered unique. This review investigates the evidence that beavers act as ecosystem engineers, and includes a meta-analysis of published studies. The impact on a wider range of species groups were considered, including plants, invertebrates, fish, amphibians, birds and mammals. We then explored how beavers will impact the biodiversity of Scotland. In particular, the effect of a beaver reintroduction on protected or vulnerable species and habitats is examined. Distribution maps of species of conservation interest were overlaid with potential beaver habitat to identify the extent and likelihood of any interaction, and ensuing influences.

Main findings

- A meta-analysis of the literature showed that, overall, beavers have an overwhelmingly positive influence on biodiversity. Their ability to modify the environment through felling trees and impounding watercourses means that beavers not only create unique habitat but fundamentally increase habitat heterogeneity, fully justifying their description as ecosystem engineers. However, in Scotland there are some specific species and habitats which have the potential to be adversely affected, and in the event of any formal beaver reintroduction these would need to be closely monitored, and appropriate management put in place if necessary.
- Beaver herbivory, impoundment, and associated behaviours influence ecosystems through the creation of a variety of features: construction of unique structures such as dams and lodges, important habitat features such as standing dead wood (after inundation), an increase in woody debris, and a graded edge between terrestrial and aquatic habitats rich in structural complexity. Beaver ponds also have unique successional stages such as beaver meadows. These features give rise to riparian ecosystems supporting a diversity not often found in undisturbed areas.
- The impact of beavers is expected to be particularly beneficial for some plants, aquatic invertebrates, fish, amphibians and birds on a landscape scale.

- Some species of conservation importance will benefit. For instance, beaver ponds should benefit otter (*Lutra lutra*) and great crested newt (*Triturus cristatus*) populations. Water vole (*Arvicola amphibious*) habitat will be improved due to an increased abundance of slow moving water bordered by structurally complex vegetation with an open canopy.
- The greatest impact on overall woodland quality is likely to arise from the interaction of beaver and deer browsing – at relatively high densities deer may prevent the regeneration of woodland. Hence, careful management of deer in areas colonised by beavers will improve the availability of diverse woodland ecosystems.
- Beavers cause disturbance, and while this is an important influence on ecological landscapes it is likely to reduce the extent of older growth riparian woodland communities. This can have a negative impact if the affected habitat type is rare, and a large proportion is impacted. However, a lack of woodland regeneration caused by high deer abundance can lead to habitat degradation/loss. Hence, vulnerable habitats and species, such as Atlantic hazelwood and aspen (*Populus tremula*), need to be closely monitored where they are isolated and in close proximity to riparian areas. This is of particular importance due to the variety of associated dependent species of conservation interest, such as lichen communities on Atlantic hazelwood.

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1. AIMS AND OBJECTIVES

1.1 Introduction

Beavers are ecosystem engineers – they fundamentally change the ecosystem and landscape that they live in. This is due, in part, to their extraordinary ability to dam watercourses, and fell trees (Wright *et al*., 2002, Müller-Schwarze, 2011).

Beavers may dam watercourses for a variety of reasons, for example to increase water depth, and decrease the distance between the water's edge and food resources (Hartman & Tornlov, 2006). Damming a river impounds water, which creates standing water (lentic) habitat where previously there was running water (lotic) habitat. The creation of lentic habitat may be important, particularly where landscapes are dominated by lotic habitat such as on upland streams (Dalbeck *et al*., 2007). By interspersing patches of lentic habitat within lotic, the heterogeneity of habitats is also increased, and this is expected to have subsequent positive impacts on biodiversity (Martell *et al*., 2006).

Beaver activity may increase habitat heterogeneity in other ways. Impounding water behind dams creates long-term ecological disturbance with a variety of successional stages. For instance, wetland vegetation composition changes with the age of a pond (Bonner *et al*., 2009). Due to either siltation or dam failure, beaver ponds are often temporary. After a beaver pond has retreated to a terrestrial state, a beaver meadow may be created. Plant succession within beaver meadows is slower than with other disturbances, such as fire, due to the extirpation of soil mycorrhiza during flooding (Terwilliger & Pastor, 1999). There is also succession within the watercourse, as lentic habitat reverts back to lotic habitat. The time scale of these changes is variable, but may be long-term. For instance, beaver meadows may persist for many decades, while ponds may develop into emergent wetland, bogs, or forested wetland which may remain stable for centuries (Naiman *et al*., 1988, Terwilliger & Pastor, 1999). This process of pond creation and subsequent rescindment creates an abundance of temporal habitat diversity, providing a large variety of successional stages. Hence, a mosaic of beaver impoundments at different stages across a landscape is expected to provide a level of abundance of habitat heterogeneity, and hence biodiversity, not associated with any other ecosystem (Wright *et al*., 2002).

Beyond increasing habitat heterogeneity, beaver influenced habitat is also thought to harbour high levels of biodiversity**.** For instance, beaver ponds are thought to contain higher levels of biodiversity than other lentic habitats (Pollock *et al*., 1995, Hood & Larson, 2014). This report reviews evidence of beaver impacts on a variety of species groups, found in the literature. Both the positive and negative impacts of beaver on biodiversity or the abundance of species are identified. Where possible the literature is reviewed using a more formal meta-analysis. It is important to remember that impacts may reverberate through trophic levels. For instance, positive impacts on the abundance or diversity of invertebrates may have a variety of impacts on species that prey on them, such as amphibians, fish, mammals, and birds.

We also attempt to identify Scottish species and habitats that may be vulnerable to beaver impacts following reintroduction. The distributions of some species and habitats are now much more restricted than when beavers were last widespread, often as a result of human pressures. Also, riparian areas have often become a more important habitat for woodland species, and the abundance of large ungulates is now arguably much higher than previously recorded.

1.2 Differences between *Castor fiber* and *Castor canadensis*

It is frequently reported that North American beaver have either a greater propensity or a greater ability to build dams in comparison to the Eurasian beaver. The only evidence for this was found in the Russian north-west where invasive North American beaver and Eurasian beaver could be directly compared. Early data suggested that there were differences in dam building behaviour. However, beaver have now expanded into more comparable, adjacent areas, and no difference in dam building behaviour has been observed (Danilov *et al*., 2011, Danilov & Fyodorov, 2012). The authors suggest that previous results were based on comparing beaver living in different habitats. A much larger population of beaver was present in North America than in Europe throughout the 20^{th} century. This means that more exceptional constructions, such as very large dams, would be more likely in North America. It seems likely that once a narrative had developed suggesting that *C. canadensis* had a higher propensity for dam building was suggested, there tended to be a confirmation bias reinforcing the view.

Data to support any differences in beavers' propensity for dam building exist are limited. For example, Skinner *et al*. (1984) reported that, in North America along 43 km of river within montane rangeland, mean dam density was 9.6 dams/km. However, more exceptional reports of Eurasian beaver dam building include densities ranging between 12.3 and 27.8 dams/km. In reality, dam density seems more likely to be determined by topographic features and beaver density, rather than species differences (Hartman, 1996, Suzuki & McComb, 1998). Indeed, an expensive behaviour like dam-building will presumably be subject to strong selection pressures for parsimony. Unless evolutionary pressure from predators means beaver with deeper ponds are more successful in North America, there seems little reason for species differences.

In this report the extensive North American literature is utilised heavily. However, there is a focus on literature relating to Eurasian examples where it is available.

1.3 Glossary of terms

Lentic	Relating to still and very slow moving water
Lotic	Relating to rapidly flowing water
Impoundment	The creation of both a dam and pond
Beaver pond	The lentic habitat directly upstream from a beaver dam.
SACs	Special Areas of Conservation - protected sites designated under the Habitats Directive

2. METHODS

2.1 Meta-analysis

In July 2014, literature relating to the two beaver species was searched for in the online databases 'Scopus' and 'Zoological Record'. All literature identified as a result of the search terms "*Castor fiber*", "*Castor canadensis*", and "*Castor* spp" was archived within a beaver literature library. Furthermore, all references from the detailed literature review by Rosell *et al.* (2005) were also included in the library. The library was then searched for references that investigated the impacts of beaver on particular species groups (e.g. amphibians).

First, papers were divided into whether they explicitly showed a positive, neutral, or negative effect of beaver on species diversity, abundance or both. This effect was then evaluated and only papers that provided either a statistical test of the effect or a suitable control were retained for further analysis.

At this stage a total number of species, positively or negatively affected by beaver activity could have been presented. However it was noted that certain papers dealing with a high diversity of species (such as those from the southern USA) would dominate the analysis, and hence potentially unfairly bias any final result. Conversely, if papers were simply counted as reporting an overall positive, neutral, or negative effect, then the result would be biased towards species which have received high levels of research. The latter approach was ultimately used, but in an attempt to mitigate bias, papers which repeated the same result with the same species in a paper already included in the analysis were excluded. This means that some reported effects will be much better supported by the literature than others. The papers included in the meta-analysis are identified in Annex 1.

Extensive reviews had already been performed for two of the species groups (aquatic invertebrates and fish). A repetition of this extensive work was judged unnecessary and instead the results of those reviews are presented here. The plant meta-analysis revealed a difference of opinion on the impact of beaver on specific tree species, but a consensus when investigating the effects on biodiversity. Both are reported in the text, but only the effects on biodiversity are reported in the final table (Table 4).

2.2 Predicting beaver interactions in the Scottish context

This review examines what may happen if beavers are reintroduced widely across Scotland. The potential interaction between beaver and relevant, terrestrial/freshwater habitats and species listed in Annexes II and IV of the Habitats Directive which occur in Scotland, and for all non-marine birds listed on Schedule 1 of the Wildlife & Countryside Act 1981, was estimated. These represent habitats and species of greatest European and Scottish importance. Scottish Natural Heritage specialists also identified a small number of other habitats and species of conservation interest, which are particularly likely to be influenced by beaver activity, and these were also assessed. Together these also provide a broad flavour of the types of ways in which beavers may interact with habitats and species. However, there are hundreds of other species and habitats of conservation concern, for example the UKBAP and SBS species, which we were not able to assess, some of which may need further consideration in the event of any future, wider beaver reintroduction.

For these habitats and species, the likelihood of beavers having an impact was estimated. This was based on the amount of overlap between the current distribution and areas of potential beaver habitat (see 2.3). Then the strength of any predicted interaction was estimated, from examples in the literature and by proposing potential mechanisms of interaction.

Some interactions with invasive non-native species, or with similar species, that occur in Scotland have been reported in the literature. However, interactions with invasive non-natives in certain groups (e.g. invertebrates, fish,) were not found. This report therefore provides a few examples of the potential interactions between beavers and invasive non-native species where appropriate. The effect of beaver interaction with some other invasive non-native species may need further consideration in the event of any future, wider beaver reintroduction.

2.3 GIS analysis

Three datasets were created for mainland Scotland and islands <6 km from the mainland. The first included all woodland suitable for beaver within 50 m of watercourses or wetland habitat that were no steeper than 15%, and was referred to as the 'potential beaver woodland' dataset. The second took the first dataset and excluded small fragments of woodland that could not support a beaver territory over the long term. This was done by excluding all fragments that could not be part of >1.9 km of woodland within 4 km of bank (Campbell *et al*., 2005). This was referred to as the 'potential core beaver woodland' dataset. The final dataset attempted to predict where beaver damming was predicted to be less likely to occur. Hence, all watercourses that were >6 m in width, or not adjacent to suitable core beaver woodland identified where beaver were less likely to build dams. Stringer *et al.* (2015) provides a full description of the methodology for the development of all three datasets, including a description of the difficulties faced when mapping potential beaver distribution, and the broad limitations of the data.

These datasets were overlaid with a variety of distributional datasets for species (data from NBN gateway, referenced in text) and habitats (data for SACs) of conservation importance, to identify the extent and likelihood of any interaction. This was done either visually using mapping software, or with a geospatial analysis. The type of analysis is described in the text. The type of dataset used for the overlay depended on any predicted interaction. For instance, some species may be affected by beaver impoundments, but not beaver herbivory.

SACs for the following habitat types were assessed for the amount of potential core beaver woodland that they contain. These were used because suitable national maps of the habitats do not currently exist:

- Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (as an interaction with beavers was considered highly likely, a GIS analysis considering the same overlap was also completed)
- Bog woodland
- Caledonian forest
- Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles
- Tilio-Acerion forests of slopes, screes and ravines
- Active raised bogs

SACs for the following habitat types were visually assessed for the amount of potential core beaver woodland that surrounded their standing water habitats. SACs were used because suitable national maps of the habitats do not currently exist:

- Hard oligo-mesotrophic waters with benthic vegetation of *Chara* species
- Natural dystrophic lakes and ponds
- Natural eutrophic lakes with Magnopotamion or Hydrocharition-type vegetation
- Oligotrophic to mesotrophic standing waters with *Littorelletea uniflorae* and/or of the Isoteo-Nanojuncetea

- Oligotrophic waters containing very few minerals of sandy plains (*Littorelletalia uniflorae*)
- Water courses of plain to montane levels with the *Ranuculion fluitantis* and Callitricho-Batrachion vegetation

Species distributions (as reported on the National Biodiversity Network Gateway (NBN Gateway 2015)) were assessed for their overlap with potential core beaver woodland for the following species:

- Green shield-moss (*Buxbaumia viridis*)
- Slender green feather-moss (*Hamatocaulis* (*Drepanocladus*) *vernicosus*)
- Petalwort (*Petalophyllum ralfsii*)
- Marsh saxifrage (*Saxifraga hirculus*)
- Marsh fritillary butterfly (*Euphydryas aurinia*)
- Natterjack toad (*Epidalea calamita*)
- Otter (*Lutra lutra*)
- European water vole (*Arvicola amphibious*)

Species distributions (as reported on the National Biodiversity Network Gateway (NBN Gateway 2015)) were visually assessed for the amount of potential core beaver woodland that surround their aquatic habitats:

- Slender naiad (*Najas flexilis*)
- Floating water-plantain (*Luronium natans*)
- Great crested newt (*Triturus cristatus*)
- Allis shad (*Alosa alosa*)
- Twaite shad (*Alosa fallax*)

Species distributions (as reported by expert opinion) were assessed for their overlap with potential core beaver woodland:

- Killarney fern (*Vandenboschia speciosa*)

Species distributions (as reported in the Native Woodland Survey of Scotland) were overlapped with both potential beaver woodland and potential core beaver woodland using GIS analysis:

- Atlantic hazelwood
- Aspen (*Populus tremula*)

Species distributions (as reported on the National Biodiversity Network Gateway (NBN Gateway 2015)) were visually assessed for the amount of overlap with areas less likely to be dammed, as it is thought that beaver impoundment specifically will be the main interaction between beaver and these species:

- Round-mouthed whorl snail (*Vertigo genesii*)
- Geyer`s whorl snail (*Vertigo geyeri*)
- Narrow-mouthed whorl snail (*Vertigo angustior*)

A GIS analysis of overlap of the watercourse length within SACs and areas less likely to be dammed by beavers was conducted. However it should be noted that impacts of any unpassable dams could extend upstream from areas of overlap:

- River lamprey (*Lampetra fluviatilis*)
- Brook lamprey (*Lampetra planeri*)
- Sea lamprey (*Petromyzon marinus*)
- Atlantic salmon (*Salmo salar*)
- Freshwater pearl mussel (*Margaritifera margaritifera*)

A GIS analysis overlapping surveyed populations within SACs and areas less likely to be dammed by beavers was conducted. However it should be noted that impacts of any unpassable dams could extend upstream from areas of overlap, and this may affect host fish:

- Freshwater pearl mussel (*Margaritifera margaritifera*)

3. REVIEW OF THE IMPACTS OF BEAVERS ON BIODIVERSITY

3.1 Habitats and associated plants

Beavers have a clear preference for some tree species over others. Flooding and herbivory creates a gradual vegetation change at the boundary between aquatic and terrestrial habitats, which is rich in structural complexity and plant species. Beaver-influenced areas contain habitats and species not commonly associated with other riparian areas. Ultimately, habitat heterogeneity and biodiversity are increased on a landscape scale by beaver activity. A key concern is that the high density of deer in some parts of Scotland may impede the normal regeneration of trees felled by beavers.

3.1.1 Mechanisms of beaver influence

The ability of beavers to fell very large trees is extraordinary, and perhaps only equalled by elephant species (Elephantidae). Indeed, due to their propensity for consuming only a small proportion of the biomass they fell, and also to construct structures such as dams and lodges (Rosell *et al*., 2005), their activity has a larger impact on local ecosystems than many other herbivores.

Beavers have a clear preference for certain woody tree species over others. In particular, Aspen (*Populus* spp.) and willow (*Salix* spp.) are often cited as highly preferred food choices (Johnston & Naiman, 1990, Nolet *et al*., 1994, Gorshkov *et al*., 2002, Urban *et al*., 2008, Jones *et al*., 2009). However, beaver can utilise a large variety of deciduous woodland species including the genera maple (*Acer*), alder (*Alnus*), birch (*Betula*), hazel (*Corylus*), ash (*Fraxinus*), cherry (*Prunus*), oak (*Quercus*), and *Sorbus* (Rosell *et al*., 2005). Species may be utilised proportionally to their abundance (Elmeros *et al*., 2003), or may be preferentially selected to fulfil diverse dietary requirements (Nolet *et al*., 1994, Müller-Schwarze, 2011). Coniferous trees are often cited as the least preferred food choice, but may still be used occasionally (Wimmer, 2006). Smaller stems, <10 cm in diameter, are often preferred (Erome & Broyer, 1984, Barnes & Mallik, 1996, Taylor, 1999, Baccus *et al*., 2007, Moore *et al*., 2013). However, larger stems up to 20 cm may still be commonly utilised (Urban *et al*., 2008), and the use of trees >100 cm in diameter has been recorded (Rosell *et al*., 2005). When choosing building material for the construction of dams, beaver may select based on the size of a stem rather than the species (Barnes & Mallik, 1996).

It is thought that beaver herbivory of preferred species promotes the abundance of non-preferred species, altering the species composition of the plant community**.** Indeed, there seem to be a number of mechanisms that ensure preferred species are rarely extirpated. For example, after beaver browsing aspen and willow can show rapid regrowth (Jones *et al*., 2009), and aspen regrowth may be in a juvenile form avoided by beavers (Basey *et al*., 1988, Basey *et al*., 1990). This suggests that preferred species may have evolved responses to beaver herbivory. Also, the felling of large trees opens the canopy, allowing higher light levels at ground level, aiding the recruitment of a range of species. Furthermore, flooding and the raised water table caused by beaver dams promote the growth of willow and alder due to their preference for wet, marshy soils (Johnston & Naiman, 1987, Donkor & Fryxell, 2000, Marshall *et al*., 2013).

On temporal and landscape scales, beaver herbivory is highly variable. Beaver settlement may not be permanent – after colony abandonment there may be many years before recolonisation, allowing species time to recover (Fryxell, 2001, Hyvönen & Nummi, 2008). On a landscape scale, beaver browse predominantly in close proximity to water (<10 m), and are also central place foragers, which results in gradients of herbivory pressure along watercourses (Hood and Bayley, 2009, Pinto *et al*., 2009, Iason *et al*., 2014). These mechanisms help to ensure that a dynamic equilibrium is usually created, preventing preferred species extirpation (Donkor, 2007).

The results of the meta-analysis support this conclusion. Nine studies investigated the impacts of beaver on willow (*Salix* spp.) abundance, with four studies reporting a negative effect, three a neutral effect, and two a positive effect. The reported positive effects included the impact of elevated water tables on willow recruitment and growth, and the vigorous regrowth of willow after herbivory - although this did not occur in areas with high deer density (Bilyeu *et al*., 2008, Marshall *et al*., 2013). No study reported the local loss of willow from an area.

The impact of beaver on *Populus* spp. may be conspicuous. Seven of nine studies reported a negative impact of beaver on *Populus* spp. abundance, in comparison to two positive impacts. The local loss of *Populus* was reported by Martell *et al*. (2006) within 30 m of some beaver impoundments, while Beier & Barrett (1987) reported a local loss of *Populus* on 4-5% of stream reaches. However, Runyon *et al*. (2014) reported that beaver reduced overstory density, which increased *Populus* sprouting. Furthermore, Rood *et al.* (2003) reported that beaver browsing increased *Populus* dispersal by releasing branches into watercourses that subsequently propagated downstream.

Beaver herbivory of trees will change the nature of riparian woodland. While species may be unlikely to be locally extirpated, the composition of individuals will change. For instance, there will be a shift in the age composition of preferred species towards younger growth.

It has been estimated that 60-80% of beaver diet is made up of aquatic vegetation. However, due to the variation in abundance of aquatic vegetation that will occur in different habitats, it may be a more important component of pond dwelling rather than stream and river dwelling beaver diets (Milligan & Humphries, 2010). Beaver ponds are often rich in macrophyte diversity (Ray *et al*., 2001). Indeed, by reducing dominant species cover and increasing habitat heterogeneity, beaver have been shown to triple macrophyte diversity within ponds (Parker *et al*., 2007, Law *et al*., 2014)**.** However, these positive effects may be restricted to degraded habitats, with beavers having a neutral effect in high quality habitats (Willby *et al*., 2014).

Flooding also has large effects on riparian vegetation as terrestrial habitat is converted to aquatic, lentic habitat. Initially, flooding will kill many tree species that become submerged. However the shallow edges, characteristic of beaver ponds, encourage emergent vegetation (Ray *et al*., 2001, Rosell *et al*., 2005). Also, the hydrological gradient associated with the edge of beaver ponds increases vascular plant diversity, and provides rare habitat in the form of saturated soils with an open canopy (McMaster & McMaster, 2001).

Plant biodiversity within beaver meadows (see section 1.1) is no greater than adjacent riparian communities. However, the community composition of these meadows is fundamentally different from other riparian ecosystems. Hence, the presence of beaver meadows increases habitat heterogeneity, which ultimately increases herbaceous plant species richness by 33% on a landscape scale (Wright *et al*., 2002).

The increase in dead wood supplied by beaver may be of importance for a range of bryophyte species (Ohlson *et al*., 1997), as well as many species of fungi (Nordén *et al*., 2004). Indeed, scars on trees caused by beaver have been known to harbour rare species of fungi (Rikkinen, 2003).

Eleven studies reported the effects of beaver activity on plant biodiversity, and included effects on macrophytes, herbaceous (vascular) terrestrial plants and trees. Eight studies reported a positive effect and three a neutral effect on biodiversity. A combination of beaver flooding and herbivory may produce riparian habitat characterised by flooded emergent vegetation (Grover & Baldassarre, 1995, Brown *et al*., 1996), a grass-forb-shrub layer next to ponds (Edwards & Otis, 1999, Martell *et al*., 2006), and then coppiced and open woodland, where forest gaps have been created by beaver herbivory (Bulluck & Rowe, 2006). This gradual edge provides a rich structural complexity and a wide variety of habitats, ultimately resulting in high levels of plant diversity. Since dams are irregularly established along a watercourse, and because beavers are central place foragers, beaver impacts will also not be consistent along a watercourse. Hence, landscapes which contain beaver will have a patchwork mosaic of different levels of beaver influence. This creates a landscape that is structurally diverse at many scales. Finally there is the further influence of temporal heterogeneity caused by the multiple successional pathways that may develop from beaver ponds (section 1.1).

These mechanisms ultimately result in a landscape richer in habitat heterogeneity and biodiversity than many other landscapes, and hence why beaver are known as ecosystem engineers (Wright *et al*., 2002).

3.1.2 Comparison of Castor fiber *and* Castor canadensis

Preferred tree species between the North American and Eurasian beaver will differ due to the different tree species compositions found where they reside. However, when they are compared when living in the same habitat, diet preference and quantity of ingested material does not seem to differ (Danilov *et al*., 2011).

3.1.3 Scottish context

The lack of any significant predators likely to affect beavers in Scotland may, without management, lead to a higher density population with subsequently greater ecosystem impacts. In particular, while intermediate disturbance is seen as an important mechanism promoting biodiversity, very high levels of disturbance by beaver may be detrimental to ecosystems.

Numerous tree species will coppice or sucker. Indeed, it has been argued that the reintroduction of beaver into Scotland would increase the diversity of aspen age classes across the landscape, with subsequent positive impacts on biodiversity (Jones *et al*., 2009). However, deer browsing may prevent regrowth depending on the amount of browsing, and the species that is browsed (Kuijper *et al*., 2010, Runyon *et al*., 2014). For instance, willow can regrow vigorously when deer density is medium to low, particularly as the raised water tables created by beaver impoundments can greatly improve willow recruitment (Jones *et al*., 2009, Marshall *et al*., 2013). However, when ungulate browsing is high, willow regrowth may be held at hedge height (Baker *et al*., 2005, Baker *et al*., 2012).

Older trees show poorer coppice regrowth than younger trees (Joys *et al*., 2004). Hence, there may be low initial coppice regrowth after beaver reintroduction on older woodland stands. However, beavers should also promote tree recruitment due to enhanced light levels. These young shoots will then coppice more vigorously. This means there may be a lag phase before the establishment of coppiced woodland after beaver reintroduction.

By the end of the five-year post-release monitoring phase of the Scottish Beaver Trial at Knapdale, 26% of beaver browsed stumps were showing regrowth. Regrowth was not equal between species. For instance, very poor re-sprouting was observed on alder (*Alnus glutinosa*) – although overall impacts on this species were low. However, ash (*Fraxinus excelsior*) and willow (*Salix* spp.) showed vigorous re-sprouting, suggesting species will differ in their ability to respond to beaver browsing. Numerous re-sprouting shoots had died over the course of the study. Interestingly, winter frost damage was a key cause of shoot mortality in the early years of the study. However, by the end of the study >68% of re-sprouting stumps or tree stems from four preferred species had been browsed by deer (Iason *et al*., 2014). Therefore high deer density in parts of Scotland may reduce the regrowth of woodland in beaver affected areas.

3.1.3.1 Ecological continuity

Beavers may break the temporal continuity (sometimes called ecological continuity) of a habitat for some species due to tree felling. The impact of this would vary between species but is likely to be greatest on species associated with old woodland. Although the large trees associated with old woodland are not in the preferred size range, they will still be felled. Whether beaver will significantly impact the density of old woodland, or cause its local loss, is unknown, and could not be tested during the timescale of the Scottish Beaver Trial (Genney, 2015).

If woodland with old trees is lost and recovers, the ability of species to recolonise will depend on a number of factors such as their ability to disperse and the distance to the nearest populations in undisturbed habitat. This is illustrated in Figure 1, showing how the continuity of woodland habitat along the north-west river bank may be broken. In this case there is no nearby woodland from which species can re-colonise. However, recovery from a break in continuity on the south-east bank of the river is likely to be quicker, as woodland exists adjacent to the area potentially impacted by beaver. Temporal habitat continuity is particularly important for slow recolonisers of old woodland habitats such as lichens. This is also one of the reasons why ancient woodland harbours a greater diversity of species than more recently planted woodland (Selva, 1994, Manning *et al*., 2006).

This is of particular importance in the modern Scottish landscape, as riparian woodland may be the only woodland area within some landscapes. An established riparian buffer zone that stretches outside the normal impact of beaver would be very useful in mitigating negative effects over the long term.

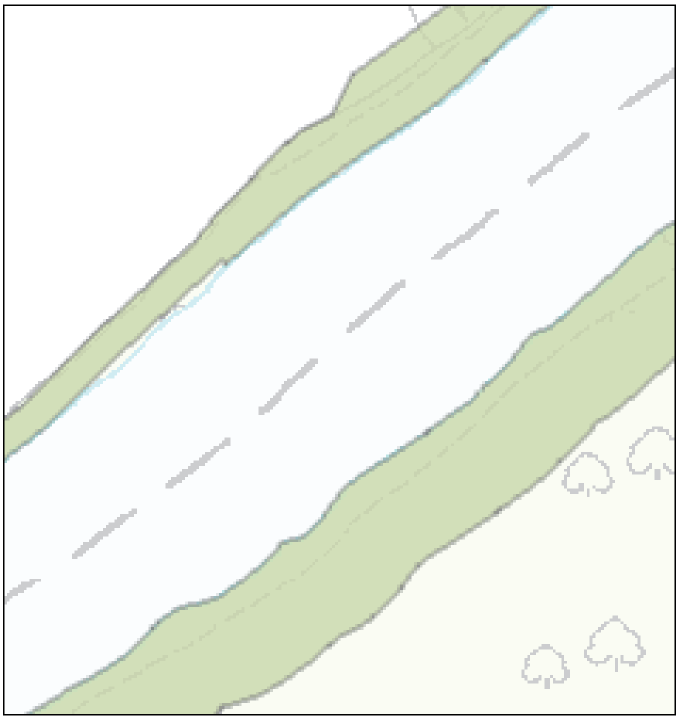


Figure 1. Risks to ecological continuity. The dashed line is the centreline of a river shown in white. On both banks of the river, potential beaver woodland is displayed in dark green, with woodland unlikely to be affected by beavers in pale green. The white area in the north-west corner is open, non-woodland habitat. The ecological continuity of the woodland on the north-west bank of the river is at high risk in comparison to the south-east bank. This is because the south-east bank has adjacent woodland, which contrasts with the narrow strip of woodland on the north-west bank which does not and may all be affected by beaver foraging.

3.1.3.2 Annex I habitats in Scotland

This assessment is restricted to the SACs on which these habitats are qualifying features. It does not cover those areas where these habitats occur in the wider countryside, and may also be affected by beavers in the future. There may also be indirect effects of beaver presence outwith SACs not picked up in these analyses, for example where beavers occur upstream, and could therefore have an effect on downstream standing water habitats.

Woodland habitats:

Alluvial forests with Alnus glutinosa *and* Fraxinus excelsior – *There is a high likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large impact.* There was extensive overlap between potential beaver woodland and alluvial forest SACs. Within non-coastal alluvial forest SACs (Conon Islands, Mound Alderwoods, Shingle Islands, Urquhart Bay Wood) a GIS analysis revealed 69% of the total woodland area may form part of potential core beaver woodland. Hence, a large proportion may be heavily affected by beaver herbivory and would need to be monitored.

Beaver will have an impact on this habitat due to their herbivory of *Salix* spp and *A. glutinosa.* Although *A. glutinosa* is not a preferred species, it is common at the Scottish Beaver Trial at Knapdale where 15% of *A. glutinosa* trees within monitored plots were gnawed (Iason *et al*., 2014). Beaver herbivory is unlikely to cause the loss of the species from these areas, but is likely to shift their relative abundance. However, beaver dams also promote *Salix* and *A. glutinosa* recruitment as they are water-loving species (Donkor & Fryxell, 2000), hence beaver may create alluvial forest habitat in other areas.

Bog woodland – There is a medium likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a low level of impact. A visual assessment showed that there was some overlap between bog woodland SACs and potential beaver woodland. Bog woodland is usually dominated by pine, which is unlikely to be significantly impacted by beaver herbivory. Alternatively, bog woodland may be restored, or more habitat created due to beaver impoundment (Ray *et al*., 2004).

Caledonian forest – There is a low likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have some impact. *Betula* abundance in riparian Caledonian forest may be reduced. This may shift species composition towards pine. Although this would be viewed as a negative impact, the impact will be localised to riparian areas of Caledonian forest, and will not affect the broad distribution of the habitat.

Old sessile oak woods with Ilex *and* Blechnum *in the British Isles – There is a low likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large impact.* A visual assessment showed that there was some overlap between oak woodland SACs and potential beaver woodland. The habitat is dominated by *Quercus* and *Betula*, both preferred species which will be impacted by beaver herbivory. However, the habitat area is extensive, and hence the affected area will likely be small.

Tilio-Acerion forests of slopes, screes and ravines – There is a low likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large impact. A visual assessment showed that in some areas there was extensive overlap between potential beaver woodland and SACs. However, the woodland exists on steep, unstable slopes, and hence the affected area is likely to be confined to the lower fringes of such woods. Of the species common in this habitat, *Fraxinus* and *Acer* are preferred genera, however lime (*Tilia*) and elm (*Ulmus*) are non-preferred genera (Barnes & Dibble, 1988).

Standing water habitats:

Hard oligo-mesotrophic waters with benthic vegetation of Chara *species – There is a high likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large/unknown impact.* Two out of three SACs have very low levels of associated core beaver woodland.

Natural dystrophic lakes and ponds – There is a high likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large/unknown impact. All six SACs have very low levels of core beaver woodland.

Natural eutrophic lakes with Magnopotamion or Hydrocharition-type vegetation – There is a medium likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large/unknown impact. Loch Achnacloich is the only one of five SACs with core beaver woodland. Suitable woodland is abundant around Loch Achnacloich.

Oligotrophic to mesotrophic standing waters with Littorelletea uniflorae *and/or of the* Isoteo-Nanojuncetea *– There is a medium likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large/unknown* *impact.* Four out of 13 SACs have associated core beaver woodland, with suitable woodland in abundance around Loch Ruthven, Loch Ussie and, in particular, Muir of Dinnet.

Oligotrophic waters containing very few minerals of sandy plains: Littorelletalia uniflorae – *There is no likelihood that beaver will interact with this habitat based on levels of potential overlap.* The only SAC is on the Western Isles, which are not predicted to be colonised by beaver.

Other habitat types:

Water courses of plain to montane levels with the Ranuculion fluitantis *and* Callitricho-Batrachion *vegetation – There is a high likelihood that beavers will interact with this habitat based on levels of predicted potential overlap. Any interaction with beavers is likely to have a small to medium impact.* The River Tweed is the sole Scottish SAC.

Active raised bogs – There is a medium likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a low level of impact. A visual assessment showed that there was some overlap between active raised bog SACs and potential beaver woodland. Beaver may impact on raised bogs due to changes in hydrology caused by impoundment.

There is minor or no overlap with all other Annex I habitats on SACs, including a range of wetland/bog habitats.

3.1.3.3 Other woodland habitats of conservation importance

Atlantic hazelwood –There is a high likelihood that beaver will interact with this habitat based on levels of potential overlap. Any interaction with beaver is likely to have a large impact. A GIS analysis showed that the overlap between Atlantic woodland dominated by hazel (>80%) and potential beaver woodland was 27% (Table 1). Since hazel is a preferred species, beaver may have a large impact within the zone of overlap. In particular, the ecological continuity of lichen communities may be impacted where small Atlantic hazelwood riparian patches exist (see section 3.1.3.1). Genney (2015) provides an in-depth assessment of the potential influence of beavers on lichen communities.

Table 1. Overlap of all and core potential beaver woodland with Atlantic hazelwood. Values are provided for three thresholds of hazel as % of the woodland canopy within an NWSS woodland polygon. From Genney (2015).

Atlantic hazel percentage	**Total area (ha)**	**Overlap with potential beaver woodland [ha (%)]**	**Overlap with potential core beaver woodland [ha (%)]**
≥ 25%	7207	2215 (31%)	1796 (25%)
≥ 50%	2660	753 (28%)	544 (20%)
≥ 80%	934	252 (27%)	176 (19%)

European aspen (*Populus tremula*) woodland – There is a high likelihood that beaver will interact with this species based on a GIS analysis of levels of potential overlap. Any interaction with beaver is likely to have a large impact.

Beaver may cause the localised loss of *P. tremula* in specific zones close to watercourses in areas of core beaver woodland (i.e. where beaver presence is near permanent, therefore preventing substantial regrowth) (Beier & Barrett, 1987, Martell *et al*., 2006). The interaction may be especially damaging in areas of high deer density, since browsing by deer on aspen regrowth is often high. In other areas, aspen regrowth after beaver herbivory can be vigorous (Jones *et al*., 2009), and in a juvenile form that beavers avoid (Basey *et al*., 1990).

For the whole of Scotland, 42% of woodland containing ≥ 25% of aspen overlaps with potential beaver woodland (Table 2). There are also high levels of overlap when using the potential core beaver woodland database (37-41% overlap), which represent the areas which are may be more heavily impacted by beaver. Ultimately, beaver may have a large impact on this species and the interaction would need to be closely monitored, and appropriate management applied where necessary.

Table 2. Overlap of potential beaver woodland, and core potential beaver woodland, with aspen woodland. Values are provided for three thresholds of aspen as % of the woodland canopy within an NWSS woodland polygon.

Aspen percentage	Total area (ha)	Overlap with potential beaver woodland [ha (%)]	Overlap with potential core beaver woodland [ha (%)]
≥ 25%	568.5	240 (42%)	209.2 (37%)
≥ 50%	119	49.7 (42%)	47.3 (40%)
≥ 80%	30.8	12.9 (42%)	12.7 (41%)

In northern Scotland, especially Strathspey, European aspen supports a unique biodiversity of dependant plants and animals. It is especially important for lower plants, with 130 species of lichen, 12 mosses and 12 lichenicolous fungi recorded on aspen at Strathspey. Aspen is also important for its associated community of saproxylic insects. The aspen hoverfly (*Hammerschmidtia ferruginea*) is a conservation 'flagship' species for the insect community associated with decaying aspen. This species requires large areas of aspen (i.e. >100-150 mature trees) for populations to survive. There are only eight such aspen woodland patches of suitable size left in Scotland (Rotheray *et al*., 2009). If these are reduced in size then the influx of deadwood into the ecosystem may not be great enough to provide adequate breeding habitat to sustain the populations. The creation of smaller cut stems by beaver is unlikely to be useful as *H. ferruginea* rely on large dead wood > 25 cm in diameter (Rotheray & MacGowan, 2000).

In addition to the impact of beaver on felling aspen and reducing stand size and regeneration there will also be a secondary impact of beaver. *H. ferruginea* and other insects rely for their larval development on the decaying bark of dead aspen. Therefore, the beaver's habit of stripping and feeding on the bark of fallen trees will reduce the abundance of suitable breeding habitat for this important and threatened community.

The majority of the key aspen stands for this community exist in Strathspey, and beaver clearly have the potential to considerably impact these patches (Table 3). An important population also exists outside the Strathspey area in Achany Glen. This stand shows particularly high levels of overlap with potential core beaver woodland. The interaction with these specific stands would need to be closely monitored and appropriate management options applied when necessary.

Table 3. Overlap of potential beaver woodland, and core potential beaver woodland, with aspen woodland in the river Spey catchment.

Total Strathspey aspen area (ha)	Overlap with potential beaver woodland [ha (%)]	Overlap with potential core beaver woodland [ha (%)]
312.7	65.1 (21%)	57.6 (18%)

There is only a small amount, or no overlap between beaver woodland and other woodland habitats of conservation interest that might be impacted by beaver (e.g. montane willow scrub).

3.1.3.4 Annex II and IV species in Scotland

*Green shield-moss (*Buxbaumia viridis*), Annex II - There is a medium likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown.* This rare moss grows on dead wood in humid areas. As beaver are expected to increase the abundance of dead wood in riparian areas, and stabilise water regimes, beaver may increase the habitat for this species. However, beaver may also reduce the amount of shade along watercourses, and reduce the abundance of large dead wood in riparian areas over the long term. The interaction would need to be monitored.

*Slender green feather-moss (*Hamatocaulis (Drepanocladus) vernicosus*), Annex II - There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown* Changes in the water regime within a catchment may alter the nature of the flushes on which *H. vernicosus* survives. Alternatively, the stabilised water regime and increased water table may improve habitat. The interaction would need to be monitored.

Petalwort Petalophyllum ralfsii, *Annex II - There is a very low likelihood that beaver will interact with this species based on levels of potential overlap.* It is only found in a single coastal location not associated with potential beaver woodland.

*Marsh saxifrage (*Saxifraga hirculus*), Annexes II and IV - There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown.* There is no overlap between potential beaver woodland and the current *S. hirculus* distribution. Increased wetland areas caused by beaver may include suitable habitat. *S. hirculus* has not previously been reported as a food item of beaver, but this does not preclude the possibility.

*Slender naiad (*Najas flexilis*), Annexes II and IV - There is a high likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown.* There is a clear overlap between potential beaver distribution and the current *N.flexilis* distribution. However, there is no reported interaction between *N. flexilis* and beaver. Although *N. flexilis* has not been reported as a food item of beaver, this does not preclude the possibility. Although beavers are already present at the Dunkeld–Blairgowrie SAC, the monitoring of the effects of beaver on *N. flexilis* at the site would be difficult. First, it has not been possible to find *N. flexilis* in this water body or the other Dunkeld–Blairgowrie Lochs in recent years. Second, it may be difficult to identify specific effects of beavers in waterbodies that already have pressures of diffuse pollution and invasive non-native species acting on the submerged plant communities.

Although it is impossible to know what effects beavers might have on *N. flexilis* without monitoring data, it should be noted that it has been recorded at 54 lochs since 1980 (there are a further 16 records which are historical or where the data are deficient). A considerable number of the lochs that support it are in the Outer Hebrides, with a few on Colonsay, Coll, Islay and Mull, and therefore in locations distant to mainland Scotland and often without potential beaver woodland habitat. These sites would not be, or are unlikely to be, colonised by beavers.

However, the Dunkeld–Blairgowrie Lochs, White Loch, Fingask Loch, Loch nan Gad, Tangy Loch, Loch Kindar, Lake of Menteith and Loch Bhada Dharaich, all of which are mainland lochs that support *N. flexilis*, may be colonised by beavers in the longer term. There is evidence that other mainland sites (Monk Myre, Lindores Loch, Loch Flemington and Loch Monzievaird) all supported *N. flexilis* in the past, but presently, environmental conditions are believed to be unsuitable for this species at these locations. Based on the work carried out in Knapdale, the beavers appeared to prefer to eat rhizomatous edge/emergent or floating-leaved plant species. *N. flexilis* is a submerged, annual species that spreads by seed and has no rhizome. Although these factors may mean that the risk to *N. flexilis* is reduced, in cases of co-occurrence it is possible that there could be negative effects, should water levels rise and new habitat at appropriate depth be unsuitable for growth or if water quality were to be adversely affected, for example through increased water colour or nutrient concentrations.

*Killarney fern (*Vandenboschia speciosa*), Annexes II and IV – There is no predicted overlap with the sporophyte (D Batty 2008, pers. comm., 4 Jan 2015). The impact of any interaction with beaver is unknown.* There is no reported interaction between *V. speciosa* and beaver. The species occurs as two distinct stages in its life cycle: the sporophyte, which is the more recognisable 'fern' form; and the gametophyte, which resembles a filamentous alga or liverwort. The distribution of the two stages are different; the gametophyte extends to the north coast of mainland Scotland and the sporophyte is restricted to the south-west of Scotland. The sporophyte occurs at a very small number of locations and it is very unlikely that it will be affected by beavers. The gametophyte has been recorded from damp rock crevices in proximity to water, in addition to sites well away from open fresh water. There is a very small possibility that beavers could have an impact upon populations of the gametophyte based upon the potential habitat overlap and the known widespread distribution of the plant. Potential negative impacts would be caused by inundation of existing populations. Conversely, inundation by water might increase local humidity and make conditions more favourable for colonisation by the gametophyte. The proportion of gametophyte populations at risk is likely to be low and such losses are highly unlikely to result in unfavourable conservation status of the *V. speciosa* in Scotland.

Floating water-plantain (Luronium natans)*, Annexes II and IV – There is a medium likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown. L. natans* can utilise a wide variety of water bodies including slow moving and standing water, hence the habitat for the species is likely to increase with beaver activity. Although there is no reported interaction between *L. natans* and beaver, and *L. natans* has not previously been reported as a food item of beaver, this does not preclude the possibility. However, this species is outside its natural range in Scotland.

3.1.3.5 Invasive non-native species in Scotland

In North American, beaver have been known to have both positive and negative effects on invasive non-native species abundance (Lesica & Miles, 2004, Perkins & Wilson, 2005, Parker *et al*., 2007). However, it is unknown what effects beaver will have on invasive species associated with riparian habitat in Scotland. Evidence so far is limited. There is a single report of a beaver feeding on Japanese knotweed (*Fallopia japonica*), a single report of a beaver felling but only partially consuming giant hogweed (*Heracleum mantegazzianum*), and in Germany beaver are thought to feed on Himalayan balsam (*Impatiens glandulifera*) (Jones *et al*., 2011, Campbell *et al*., 2012, Jones *et al*., 2013). *Rhododendron maximum,* a parent of the invasive complex hybrid *Rhododendron ponticum*, has been shown to be a preferred food choice (Dams *et al*., 1995).

No record could be found of an interaction between beaver and many of the invasive aquatic plant species threatening Scotland, such as water primrose (*Ludwigia grandiflora*), fanwort (*Cabomba caroliniana*), large flowered waterweed (*Egeria densa*), floating pennywort (*Hydrocotyle ranunculoides*), New Zealand pygmyweed (*Crassula helmsii*), curly waterweed (*Lagarosiphon major*), and water fern (*Azolla filiculoides*). However, the invasive parrot's feather (*Myriophyllum aquaticum*), and *Elodea* spp. (of which *Elodea nutallii* and *Elodea canadensis* are invasive in the UK) are highly preferred food species for beaver (Allen, 1982, Parker *et al*., 2007). The interaction would need to be monitored – *E. canadensis* is present within parts of Knapdale.

There is a possibility that beaver will increase the dispersal of some invasive species. For instance, beaver herbivory of *E. canadensis* may create numerous smaller fragments of the pondweed. Each of these fragments may go on to act as a propagule for the species. Also, mud and plant material may be used by beaver as part of dam and lodge construction. This behaviour may affect the spread of invasive species (Willby *et al*., 2014).

3.2 Aquatic invertebrates

By creating ponds in stream-dominated areas, beaver impoundment will increase the diversity and abundance of the aquatic invertebrate community at the landscape scale. However, at high dam densities, stream dependent invertebrates may be impacted, as short stream reaches between ponds may differ from stream reaches with no ponds.

3.2.1 Mechanisms of beaver influence

Beaver dams introduce lentic habitat patches into predominantly lotic ecosystems. Within the pond the aquatic invertebrate community changes to reflect the newly created lentic habitat. Shredders and scrapers become less important, while collectors and predators become more important (McDowell & Naiman, 1986). Indeed, beaver may create unique aquatic habitats, such as beaver channels and canals, which support taxa not found in other wetland habitats (Hood & Larson, 2014). Beaver dams also support a high diversity of invertebrates (Rolauffs *et al*., 2001), in particular, the turbulent water flowing over a beaver dam may create rare habitat for lotic species on low gradient stream reaches (Clifford *et al*., 1993). Also, due to the head of water behind dams, stream velocity is increased directly downstream, which can create rare fast flowing habitat on low stream gradients (Smith and Mather, 2013).

Hering *et al.* (2001) thoroughly reviewed the literature on the aquatic invertebrate community in beaver impounded streams in comparison to un-impounded streams. They reported that, on a landscape scale, beaver impoundments have overwhelmingly positive impacts on aquatic invertebrate abundance and diversity. The few exceptions include gravel-preferring species and macro-invertebrate grazers which may be affected by sedimentation within the beaver pond. Caddisflies (Trichoptera) and stoneflies (Plecoptera) may also be negatively impacted due to their preference for fast flowing reaches. However, Rolauffs *et al.* (2001) found that emerging caddisfly density was greater around beaver dams than in lotic stream reaches. Also, Smith *et al.* (1991) found that stonefly abundance returned to above impoundment levels 250 m below an impoundment.

Beaver are expected to increase the diversity of aquatic invertebrates at the landscape scale. However, beaver dams may also impact downstream areas, and furthermore disrupt the river continuum. Therefore it is possible that patches of lotic habitat between beaver impoundments do not support the same communities as lotic habitat on beaver-free catchments. Beaver impoundments may affect the water chemistry, nutrient composition, sediment load, and temperature of downstream stream reaches, and effects may be highly variable (Rosell *et al*., 2005, Fuller & Peckarsky, 2011a). Indeed, different types of impoundment will have different downstream effects. For instance, beaver impoundments with a high head dam and low surface area force water into the ground, causing a greater amount of cool groundwater upwelling, which ultimately cools downstream temperatures. Conversely, low head dams containing ponds with a large surface area will absorb high levels of solar radiation that warm downstream waters. These contrasting effects have different implications for downstream aquatic invertebrates. Water temperature, for example, affects the size of adult mayflies (Ephemeroptera), which has direct implications for their reproductive success (Fuller & Peckarsky, 2011b).

Numerous papers show no change in aquatic invertebrate biodiversity downstream of beaver impoundments in comparison to upstream. However, species abundance and community assemblage may change (McDowell & Naiman, 1986, Margolis *et al*., 2001, Arndt & Domdei, 2011, Adams, 2013, Redin & Sjoberg, 2013). The influence of a beaver impoundment on downstream ecosystems is expected to gradually dissipate with distance. This has been tested in a number of studies. Margolis (2001) showed that the effects of a beaver impoundment on downstream invertebrate assemblages were much reduced 100 m downstream. However, Adams (2013) estimated that beaver dams will impact on crayfish assemblages up to 2 km downstream.

In conclusion, beaver impoundment will increase the diversity and abundance of the aquatic invertebrate community at the landscape scale. However, at high dam densities lotic habitat may be considerably reduced, with subsequent impacts on the invertebrate community. This is important because short stream reaches between impoundments may not resemble un-impounded streams.

3.2.2 Comparison of Castor fiber *and* Castor canadensis

The review paper (Hering *et al*., 2001) used references from both the North American and Eurasian beaver, but attempted to apply references specifically to the European context.

3.2.3 Scottish context

Beavers are broadly thought to be habitat creators for dragonflies (Odonata) due to their ability to create ponds and wetland areas (Harthun, 1999, Roble *et al*., 2009, Schloemer *et al*., 2012). Batty (2015) studied the impacts of beaver activity on the abundance and diversity of dragonflies at Knapdale, Scotland, over a five-year period. Dragonfly diversity and abundance was unaffected by beaver activity. However, the study period was too short to conclude that beaver will not have significant effects over the long term.

3.2.3.1 Annex II species in Scotland

*Freshwater pearl mussel (*Margaritifera margaritifera*), Annexes II (and V) - There is a low likelihood that beaver will interact with this species based on a GIS analysis of levels of potential overlap. The impact of any interaction with beaver is unknown.* The impact of beaver on freshwater pearl mussel (*Margaritifera margaritifera*) populations is debatable. Juvenile *M. margaritifera* cannot survive in beaver ponds due to sedimentation (Rudzite, 2005, Rudzite & Znotina, 2006, Hastie & Toy, 2008, Rudzite & Rudzitis, 2011). However, habitat may also be improved downstream of dams due to a reduced water sediment load and the regulation of stream flow (Campbell, 2006). Abundance of host fish is thought to be a key determinant of juvenile recruitment (Johnson & Brown, 1998). In Scotland the preferred hosts for the parasitic juvenile stages are *Salmo trutta* and/or *Salmo salar* (Clements, 2014). The former is expected to benefit from beaver reintroduction, however the effects on the later are unknown (Kemp *et al*., 2012). No study has yet tested the effects of beaver on *M. margaritifera* populations. However, anecdotally, Hastie & Toy (2008) report on two streams with declining western pearlshell (*Margaritifera falcata*) populations in North America. The pearlshell population in the stream containing beaver impoundments was declining less severely than the stream without beaver impoundments. There also appear to be low levels of concern over any the effects of beavers in areas where there are high levels of overlap (Degerman *et al*., 2009, Popov & Ostrovsky, 2014).

Two main overlap analyses were done. The first used the entire riverine sections within SACs designated for *M. margaritifera* and this suggested that there is a low likelihood of beavers damming 91% of all the SAC river lengths. The second used *M. margaritifera* survey data within these SACs and this suggested that there is a low likelihood of beavers damming 92% of surveyed populations. On 16 out of the 19 SACs, the majority of surveyed populations were in areas predicted to be less likely to be dammed (and for 11 of these SACs, all of the surveyed populations were in areas less likely to be dammed). The remaining river lengths consist of sections where the ability of beavers to dam is unknown, although some of which may be dammable. Data is not currently available to further refine the result. In the event of any wider beaver reintroduction, further monitoring would be required, including how impacts on any migratory host fish species may be affected. It should be noted that this analysis used survey data up until 2010. The analysis should be repeated to check for consistency when more recent data becomes available.

3.3 Terrestrial invertebrates

Beavers have a positive influence on terrestrial invertebrate abundance through a variety of mechanisms such as increasing the supply of dead wood and creating wetlands. Species dependent on trees preferred by beavers would need to be monitored in some areas.

3.3.1 Mechanisms of beaver influence

Beaver may increase terrestrial invertebrate biodiversity on a landscape scale by increasing the abundance of dead wood, providing habitats such beaver meadows, and also by providing beaver-specific structures such as dams and lodges. Seven studies have investigated the impact of beaver on terrestrial invertebrate diversity or species abundance, and all found a positive effect.

Many studies have investigated the impacts of beaver activity on specific species groups. Beaver flooding and herbivory creates an abundance of dead wood that can be utilised by a variety of species. In particular saproxylic beetles may utilise dead, decaying and rotting wood provided by beaver (Saarenmaa, 1978, Zahner *et al*., 2006, Horak *et al*., 2010). The fruit fly *Drosophila virilis* is also thought to be a semi-obligatory commensal with beaver, due to its requirement for rotting bark (Spieth, 1979).

The effects of beaver herbivory may also impact invertebrate abundance. Beaver felled cottonwood (*Populus fremontii* x *P. angustifolia*) trees produce more phenolic glycosides, used for anti-herbivore defence. This in turn attracts the leaf beetle *Chrysomela confluens*, which use these compounds for their own needs (Martinsen *et al*., 1998). Beaver herbivory on cottonwood trees also causes an increase in shoot length, which subsequently leads to an increase in sawfly (Hymenoptera: Symphyta) abundance (Bailey & Whitham, 2006). In addition, the open canopy created by beaver allows the white pine weevil (*Pissodes strobe*) to flourish where previously it had been absent even in the presence of its food source, the white pine (*Pinus strobus*) (McNeel, 1964).

Some invertebrates only utilise beaver-specific habitat. For instance, the beetle *Platypatrobus lacustris* seems to be found specifically around beaver lodges (Goulet, 1965). Also, the endangered Saint Francis satyr butterfly, *Neonympha mitchellii francisci*, is dependent on beaver-created wetlands (Kuefler *et al*., 2008, Bartel *et al*., 2010).

Beavers also support a diverse range of dependent species including fur mites such as *Schizocarpus mingaudi*; helminths such as *Psilotrema castoris*; and ticks such as *Ixodes banksi* (Kollars *et al*., 1995, Bochkov & Dubinina, 2011, Demiaszkiewicz *et al*., 2014). In particular, the beaver beetles (*Platypsyllus castoris* and *Leptinillus validus*) are rare examples of host-dependent beetles (Peck, 2007, Duff *et al*., 2013).

3.3.2 Comparison of Castor fiber *and* Castor canadensis

While the majority of examples have come from the studies on the impacts of *C. canadensis*, there are a number of examples showing the impact of *C. fiber* on terrestrial invertebrates. For instance, many hoverfly larvae feed on decaying wood in boggy habitat. Indeed, the recovery of the endangered hoverfly *Chalcosyrphus eunotus* in Poland has been solely attributed to increasing beaver populations (Soszynska-Maj *et al*., 2010). Also, Dalbeck (2011) discovered that beaver clearings and meadows in Germany contained high levels of grasshopper (Orthoptera: Caelifera) biodiversity, and showed that beaver created habitat was important for grasshopper biodiversity on a landscape scale.

3.3.3 Scottish context

Decaying aspen (see 3.1.3.6) is an important habitat for saproxylic flies, including the rare aspen hoverfly (*H. ferruginea*). Hence, any detrimental impact to the persistence of aspen stands may have knock on impacts on a range of species.

3.3.3.1 Annex II species in Scotland

*Marsh fritillary butterfly (*Euphydryas aurinia*), Annex II – There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). Any interaction with beaver is likely to have a low impact.* There is no overlap between potential beaver woodland and the current *E. aurinia* distribution. The butterfly and its main larval food plant, devil's-bit scabious (*Succisa pratensis*), are found in a wide variety of habitats. No interaction is predicted.

*Round-mouthed whorl snail (*Vertigo genesii*) and Geyer`s whorl snail (*V. geyeri*), Annex II - There is a medium likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown.* There is some overlap between potential beaver distribution and the current *V. genesii* and *V. geyeri* distribution. Based on a sample of records from Blair Atholl and the Black Isle, >70% of the range of each of the two species are in areas where it is predicted that it is less likely beavers will dam. That means <30% of the range are in areas where the likelihood of damming is unknown (some of which may be dammable). However, predicting any interaction is difficult, as it is impossible to know how large a beaver pond may be, and how that might affect local flushes. Changes in the water regime within a catchment may alter the nature of the flushes on which they survive. Alternatively, the stabilised water regime and increased water table may improve their habitat. The interaction would need to be monitored.

*Narrow-mouthed whorl snail (*V. angustior*), Annex II - There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015).* Potential beaver habitat does not overlap with the range of this species in Scotland.

3.4 Fish

Beaver are predicted to have a broadly positive impact on fish biodiversity. This is due to the increased habitat heterogeneity caused by the creation of beaver ponds.

3.4.1 Mechanisms of beaver influence

Reviews of the impacts of beaver on a variety of fish species have been done by Kemp *et al.* (2012) and Collen & Gibson (2001), with further consideration by the Beaver-Salmonid Working Group (2015). A range of possible impacts are possible, in particular since beaver activity will have differing effects on different fish species.

Overall, beaver impoundments replace terrestrial with aquatic habitat, increasing aquatic and wetland habitat abundance. The abundance of lentic habitat is increased, which increases habitat heterogeneity in areas where lotic habitat dominates. The head of water created by dams increases stream velocity downstream. This results in important habitat for lotic-dependent fish species in low-gradient watercourses. Therefore, beaver dams both increase and decrease stream velocity at different points along the stream reach. This fundamental increase in habitat heterogeneity has been shown to have positive impacts on overall fish biodiversity (Hanson *et al*., 1963, Snodgrass & Meffe, 1998, Smith & Mather, 2013). Temporal heterogeneity is also created due to the creation and abandonment of beaver impoundments, and the differing effects of beaver ponds of different ages, with further positive impacts on fish biodiversity (Schlosser & Kallemeyn, 2000). The restoration of degraded water courses through impoundment and increasing the abundance of dead wood will also increase total fish biomass present within a stream reach (Acuna *et al*., 2013). Importantly, although these describe the general impacts of beaver presence on habitat heterogeneity and subsequent impacts on biodiversity, there will be variation in how these impacts may change the abundance of any specific species, positively or negatively (Kemp *et al*., 2012).

3.4.2 Comparison of Castor fiber *and* Castor canadensis

The research on the impacts of Eurasian beaver on fish is limited, both in terms of geographical coverage and the range of species studied. However, the positive effects of increased habitat heterogeneity are expected to be the same.

3.4.3 Scottish context

3.4.3.1 Annex II and IV species in Scotland

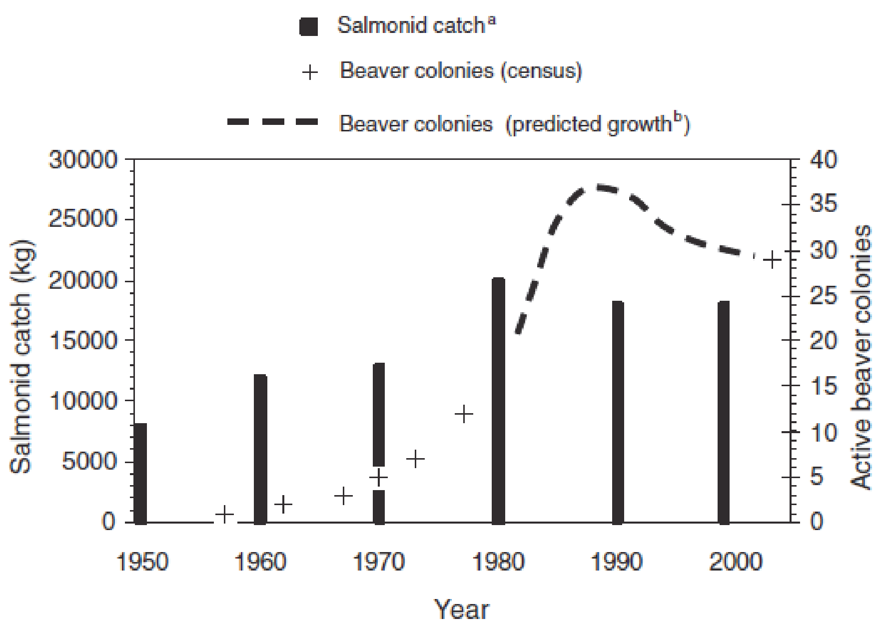
*River lamprey (*Lampetra fluviatilis*), brook lamprey (*Lampetra planeri*), and sea lamprey (*Petromyzon marinus*), Annex II (and V for river lamprey) – Although a GIS analysis of overlap between SACs designated for lamprey and areas less likely to be dammed by beavers was high, impacts of any unpassable dams could extend upstream. The impact of any interaction with beaver is unknown.* All lamprey species migrate upstream at some point in their life cycle. Brook lamprey remain in fresh water for their entire life and will undertake relatively short migrations including between spawning and nursery habitat, and eventually as sexually mature adults to spawning habitat. River and sea lamprey are anadromous species; they migrate to sea before returning to spawn in rivers. Barriers to migrating anadromous fish remain a concern in the United Kingdom and are still implicated in designated site condition assessments as a key reason for poor species distribution. Lamprey are thought to be poor at ascending river obstacles and their migration may be impeded by beaver dams (Maitland, 2003). There is a single observation of a brook lamprey passing a 70 cm high beaver dam (Jensen & Olsen, 2004). However, the degree to which migrations may be hampered remains unclear, and this is particularly important for the anadromous river and sea lamprey.

Ponds created by beaver dams may increase the amount of slow flowing, silty habitat in which the larvae of all three species are often found. However, the deposition of fine silt as a result of beaver dams slowing water velocity may damage lamprey spawning habitat, as river bed interstices become filled and the availability of oxygen reduced.

Overall, Elmeros *et al*. (2003) predicted that there would be no significant impact of beaver on brook lamprey. Just over 90% of watercourse length of SACs designated for lamprey are predicted to be less likely to be dammed by beavers. However, this may under-represent potential impacts (see below).

Atlantic salmon (Salmo salar), *Annex II (and V) – Although a GIS analysis of overlap between SACs designated for* S. salar *and areas less likely to be dammed by beavers was high, impacts of any unpassable dams could extend upstream. The impact of any interaction with beaver is unknown.* The interactions between beaver and salmonids have been extensively reviewed and debated by Kemp *et al.* (2012), Collen & Gibson (2001), and the Beaver-Salmonid Working Group (2015). They conclude that there may be both positive and negative effects of beavers on *S. salar* and that how these interactions will affect the species in Scotland in the future is difficult to predict.

Studies in North America suggest that there is a clear risk that beaver dams will impose a limit to the spawning migration of *S. salar* (e.g. Mitchell & Cunjak, 2007), although the impact this may have at the population level is less clear. The only data that attempts to assess beaver impacts on Atlantic salmon populations in Europe comes from Norway. There a catchment containing 65 km of streams and tributaries was colonised by beaver (Parker and Rønning, 2007). They show a concurrent increase in salmonid (changing to Atlantic salmon after 1960) catch rate with increasing beaver density (Figure 1). However, the result does not take into account the numerous other effects that may have increased Atlantic salmon catch over this period. Also Norwegian salmon catches overall are at historically low levels (Forseth *et al.* 2013).



[a]Catch after 1960 includes salmon only.

[b]Predicted growth is based on an observed population peak on the study area in the late 1980's and the expected form for logistic growth.

Figure 1. The number of occupied beaver colonies and salmonid catch on the main river and tributaries of the lower 65km of the Numedalslågen River, Norway from Parker and Rønning (2007).

92% of the all the watercourse length within SACs designated for *S. salar* are predicted to be less likely to be dammed by beavers. This may under-represent the potential impact of beaver dams on Atlantic salmon populations. If, for instance, a dam is unpassable then all habitat upstream of that dam will be lost to Atlantic salmon. This means that the location of the dam is a critical consideration. However, beaver are less likely to construct dams in the lower, usually wider, areas of river catchments. This is because beavers show less tendency to dam on watercourses >6 m in width (Hartman & Tornlov, 2006). There is also a higher likelihood of dam destruction on larger watercourses during spates.

A key conclusion of the BSWG report (2015) was that dams built on existing structures, such as fish passes or culverts, are more likely to be impassable to fish movement. An analysis of the overlap of areas predicted to be less likely to be dammed (see 2.3) with existing anthropogenic watercourse structures showed that 78% of all culverts, weirs, and fish passes in Scotland were at locations where damming was less likely However, of key importance is the location of impassable dams, and the reduction in accessible habitat that they would cause. Further analysis could be done in the future to highlight which structures risk impeding Atlantic salmon access to key habitats. A research and monitoring program would need to be developed to assess the potential for dams to impede Atlantic salmon movements upstream and downstream, the impact that delayed migration may have, and the survival of Atlantic salmon in impounded areas and below dams (see BSWG (2015) for a full investigation of research requirements). These data should be used in conjunction with juvenile assessments to determine whether beaver presence affects population performance.

Allis shad (Alosa alosa) *and twaite shad* (A. fallax), *Annex II (and V) – There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap.* In Scotland, these anadromous species are mainly associated with the Solway Estuary.

Sturgeon (Acipenser sturio)*, Annex IV – Beavers will have a low impact on this species.* It is not known whether historical records of *A. sturio* caught in UK rivers were vagrants from the continental Europe or a breeding population. However, a restocking project on the Atlantic coast of France, coupled with climate change, may allow a natural colonisation to take place. *A. sturio* migrate to rivers to spawn, however, they do not migrate upstream as far as Atlantic salmon, and spawn in much larger, lower, river reaches than may be dammed by beaver. They do require a hard substrate on which to spawn, and the reduction in sediment load caused by beaver impoundments may help create spawning habitat.

3.5 Amphibians

Beaver positively affect the abundance of many amphibian species, except those dependent on stream habitat. In Scotland, all amphibian species are expected to benefit from beaver created wetlands.

3.5.1 Mechanisms of beaver influence

Studies that investigated the differences between beaver impacted and non-impacted areas were analysed. In eight studies on frogs and toads (Anura), beaver activity was found to have a positive impact on abundance or biodiversity. One study found no impact, and one study found a negative impact. In terms of species studied, 80% of species (n = 19) were positively affected, 17% (n = 4) were unaffected, and 4% (n = 1) were negatively affected.

The meta-analysis highlights numerous positive effects of beaver on frog and toad populations. A number of mechanisms were proposed. The most commonly reported observation was that beavers increase the size and number of lentic zones, an essential breeding habitat for many amphibian species (France, 1997, Coleman Quail, 2001, Metts *et al*., 2001, Cunningham *et al*., 2007, Dalbeck *et al*., 2007, Stevens *et al*., 2007, Aznar & Desrochers, 2008, Karraker & Gibbs, 2009, Dalbeck *et al*., 2014). Indeed, beaver may introduce ponds where few occur, for example in upland areas where streams dominate (Dalbeck *et al*., 2007). Beaver activity may also increase the connectivity between ponds, due to the increased density of lentic habitat, but also due to the creation of canals by beavers (Cunningham *et al*., 2007). Beaver lodges and dams may provide valuable habitat for amphibians that can be used for predator avoidance, larval food and development, or as hibernation sites (Tockner *et al*., 2006, Dalbeck *et al*., 2007, Browne & Paszkowski, 2010, Alvarez *et al*., 2013).

The North American coastal tailed frog (*Ascaphus truei*) does seem to be negatively impacted by the presence of beaver. This is because this species does not inhabit ponds and its tadpoles are specially adapted to turbulent, fast-flowing water (Diller & Wallace, 1999).

Beaver activity was found to have a positive impact on abundance or biodiversity in four studies of salamanders and newts (Caudata). Two studies found no impact, and two studies found a negative impact. In terms of species studied, 30% of species (n = 7) were positively affected, 26% (n = 6) were unaffected, and 43% (n = 10) were negatively affected.

The impact of beaver on newt and salamander species is highly variable. Many species of salamander prefer flowing water and cannot utilise beaver ponds (Metts *et al*., 2001, Cunningham *et al*., 2007, Dalbeck *et al*., 2007). On a landscape scale beaver may reduce the abundance of lotic habitat and replace it with lentic habitat, hence reducing the abundance of habitat for these stream-dependent species. However, there is limited research on whether beaver impoundments degrade lotic species habitat downstream or are barriers to migration, and therefore the effects on lotic species at the whole stream level. Initial data show that, on beaver modified streams, stream-dependent species may be abundant in un-impounded reaches (Cunningham *et al*., 2007).

A higher abundance of predatory fish within beaver ponds may reduce amphibian density. However, Dalbeck (2007) reported that the increase in habitat heterogeneity caused by beaver activity means a key predator (*Salmo trutta*) does not extirpate amphibians from impounded highland streams. In particular it was suggested that the creation of ponds with shallow pond margins containing areas of submerged vegetation and woody debris provide amphibians with protection from predators.

3.5.2 Comparison of Castor fiber *and* Castor canadensis

The majority of studies investigated *C. canadensis*. However, the two studies that investigated the impacts of *C. fiber* both found highly positive influences on amphibian abundance and diversity. In particular, Dalbeck (2007) found that the combined effects of pond creation and beaver herbivory were important for the common midwife toad, *Alytes obstetricans,* due to its requirement for open terrestrial habitats close to lentic habitat.

3.5.3 Scottish context

There are six native species of amphibian in Scotland; the smooth newt (*Lissotriton vulgaris*), palmate newt (*Lissotriton helveticus*), great crested newt (*Triturus cristatus*), common toad (*Bufo bufo*), natterjack toad (*Epidalea calamita*), and common frog (*Rana temporaria*). All species prefer lentic over lotic habitat, and hence should be positively impacted by beaver activity.

3.5.3.1 Annex II and IV species in Scotland

Great crested newt (Triturus cristatus), *Annexes II and IV - There is a high likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). Any interaction with beaver is likely to have a large impact.* Impoundment by beaver will create suitable habitat for *T. cristatus*. Two other species from the genus *Triturus* were shown to heavily utilise older beaver ponds in central Europe (Dalbeck *et al*., 2007). Also, the maintenance of water levels may be beneficial (Smith & Sutherland, 2014). Importantly, *T. cristatus* utilise terrestrial habitat for significant portions of their life cycle, for instance during the post-breeding period, juvenile dispersal, and for hibernation (Malmgren *et al*., 2007, Gustafson *et al*., 2011). Ponds in close proximity to deciduous forest, as would likely be provided by beaver, are important habitat for *T. cristatus* (Gustafson *et al*., 2011). However, mire is a non-preferred habitat and beaver impoundment may also flood hibernation sites, although new ones may become available.

Within the three SACs for great crested newt in Scotland there is a low likelihood that beavers will interact with this species. Turflundie Woods SAC has no potential core beaver woodland. Luce Bay and Sands SAC, in Wigtownshire, is on an area of dune habitat, which is not considered to be potential beaver habitat, and the third, Burrow Head SAC in Wigtownshire, is an area of farmland with gorse scrub and rocky knolls well away from major watercourses and which is also not likely to support beavers.

*Natterjack toad (*Epidalea calamita*), Annex IV - There is a low likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). The impact of any interaction with beaver is unknown.* There is no overlap between potential beaver woodland and the current *E. calamita* distribution in Dumfries and Galloway as it is primarily coastal. Overall, pond creation has been shown to have a positive effect on *E. calamita* populations (Smith & Sutherland, 2014). However, the high levels of invertebrate predators that depredate toad tadpoles may make some beaver ponds unsuitable (Banks & Beebee, 1988).

3.6 Reptiles

Beaver impoundment has a generally positive effect on reptile diversity. The grass snake may be most affected by riparian modification, and this is likely to be positive.

3.6.1 Mechanisms of beaver influence

A number of studies have observed reptiles utilising beaver created habitat. Cottonmouth snakes (*Agkistrodon piscivorus*) have been observed basking on beaver lodges (Graham, 2013), while a variety of terrapins have been observed utilising beaver ponds (Reddoch & Reddoch, 2005). Yagi & Litzgus (2012) found that terrapins exploited new aquatic habitats created by beavers, however flooding also reduced nesting opportunities.

Two studies investigated the usefulness of beaver ponds as habitat for reptiles. Both found that beaver ponds had higher reptile abundance and biodiversity than at un-impounded streams (Russell *et al*., 1999, Metts *et al*., 2001). The older a beaver pond was, the greater the diversity and abundance of reptiles (Russell *et al*., 1999). In particular, the creation of lentic habitat, and of open habitats around ponds due to beaver browsing, was viewed as important for terrapins and lizards respectively. However, the effects on snakes were mixed. While there was a greater diversity of snakes in beaver impacted areas, the abundance of both the worm snake (*Carphophis amoenus*) and the southern ringneck (*Diadophis punctatus*) were much reduced (Metts *et al*., 2001).

There is also one unusual report of live terrapins found with damaged shells caused by rodent gnawing. It was postulated that beaver or porcupine (*Erethizon dorsatum*) were eating the shell of terrapins as a source of calcium (Harding, 1985).

3.6.2 Comparison of Castor fiber *and* Castor canadensis

No literature reports the impacts of *C. fiber* on reptiles.

3.6.3 Scottish context

Reptiles native to Scotland include the adder (*Vipera berus)*, common lizard (*Zootoca vivipara*), and slow worm (*Anguis fragilis*). Recent reports suggest that a grass snake population may also be present, which may expand in response to climate change (*Natrix natrix*). The grass snake is the only species which specialises in freshwater and wetland habitats, and no study has tested the effects of beaver impoundment on this species. An increased abundance of food, such as amphibians, is likely to benefit this species.

3.7 Birds

Beaver have numerous effects on a range of bird species by increasing wetland habitat, providing standing deadwood, creating beaver meadows, increasing the abundance and diversity of prey, and by creating habitat which is rich in structural complexity. This supports an abundant and diverse bird fauna that is greater than may be expected from riparian areas with no beaver activity.

3.7.1 Mechanisms of beaver influence

Studies investigating the impact of beavers on bird biodiversity and abundance were investigated. A total of 30 out of 52 papers showed bird species utilising beaver ponds or beaver created habitat, but did not compare this use to areas not affected by beavers. The remaining 22 studies investigated the differences between beaver impacted and non-impacted areas. Beaver activity was found to have a positive effect on the abundance of a species or overall bird biodiversity in 94% (n=18) of studies, and a negative effect in 6% (n=1) of studies.

The single study to find a negative impact of beaver was an investigation into the abundance of Slavonian grebe (*Podiceps auritus*). Kuczynski *et al* (2012) found that *P. auritus* avoid ‘borrow pits’ (man-made ponds created during highway construction in N. America) that contained beaver (Kuczynski *et al*., 2012). This may be because *P. auritus* prefer ponds with low surrounding forest cover (<33% within 500 m), and hence they prefer habitat less suitable for beaver. However, where sedge beds are not present, *P. auritus* use willow for nesting, and beaver may reduce the abundance of willow in certain situations.

Numerous mechanisms were cited as reasons for increased bird abundance or diversity. The increase in wetland area caused by beaver impoundments is a key determinant of avian biodiversity (Peterson & Low, 1977, Grover & Baldassarre, 1995, Brown *et al*., 1996, Longcore *et al*., 2006). In particular the aquatic characteristics of beaver ponds, such as large shallow water areas, may be particular important for a variety of waterfowl (Anatidae) (Brown *et al*., 1996, Longcore *et al*., 2006).

The gradual edge characteristic of beaver habitat (described in section 3.1.1) may be a key driver of high bird biodiversity. It provides a structurally complex area that may improve nest concealment, reduce predation, increase food production, and ultimately provide a diverse range of ecological niches to be exploited (Edwards & Otis, 1999, Bulluck & Rowe, 2006). The interspersion of different vegetation types seems to be a key component of this habitat, which can provide cover for waterfowl in particular (Beard, 1953, Edwards & Otis, 1999).

The ponds created by beaver dams often flood and kill trees in the riparian zone. This attracts woodpeckers since standing dead wood is an important nesting and feeding habitat (Grover & Baldassarre, 1995, Sikora & Rys, 2004, Tumiel, 2008). Woodpeckers are often classified as ecosystem engineers themselves, due to the use of woodpecker holes by a range of secondary cavity-nesting species (Jones *et al*., 1994, Robles & Martin, 2014). Dead trees and snags are also an important site for raptors (Ewins, 1997), which may also prey on beavers (Rosell *et al*., 1996).

The habitats created by beavers provide a more abundant food supply for birds. Beaver impoundments contain an abundant aquatic assemblage including a diverse range of macroinvertebrates that are an excellent food source for ducks (Danell & Sjoberg, 1982, Brown *et al*., 1996, Longcore *et al*., 2006, Cooke & Zack, 2008). Furthermore, an increased abundance and diversity of fish and amphibians within beaver impoundments provides food for species such as heron (Ardeidae) and kingfisher (Alcedines) (Beard, 1953, Elmeros *et al*., 2004).

Beavers may also facilitate bird abundance in less obvious ways. In areas where ponds are covered with ice and snow for much of the winter it has been observed that beaver physical activity causes the ice to melt earlier in the spring. This can bring benefits to Canada geese (*Branta canadensis*) as it allows them access to an important habitat for an extended period (Bromley & Hood, 2013). It may also bring benefits to a range of species.

Beaver meadows can support diverse vegetation which promotes bird biodiversity (Chandler *et al*., 2009), and may be an essential source of habitat for grassland birds on a landscape scale (Askins *et al*., 2007). Anzar (2008) discovered that beaver meadows had the highest levels of songbird biodiversity when compared to all other adjacent riparian habitats.

In conclusion, beavers create a diverse habitat rich in structural complexity, which supports an avian diversity greater than may be expected from a riparian area unaffected by beavers, including bird species that may not normally be associated with wetlands (Reese & Hair, 1976, Dorset Derby & Prince, 1996). The structurally and temporally heterogeneous habitat created by beaver supports a highly diverse bird fauna on a landscape scale.

3.7.2 Comparison of Castor fiber *and* Castor canadensis

The majority of studies in the meta-analysis focused on *C. canadensis*. However, all studies in Europe also showed a positive impact of *C. fiber* on bird populations. For example, positive impacts have been shown for a variety of birds such as woodpeckers (*Dendrocopos leucotos* and *Picoides tridactylus*), kingfisher (*Alcedo atthis*) and waterfowl (Elmeros *et al*., 2004, Sikora & Rys, 2004, Tumiel, 2008). In particular, beaver are seen as important habitat creators for rustic bunting (*Emberiza rustica*) in Norway where populations are declining (Dale & Hansen, 2013).

3.7.3 Scottish context

Given that beavers are known to create diverse habitats rich in structural complexity, it would be expected that their presence would result in greater avian diversity than may be expected from the existing remnant riparian habitats in Scotland. However, beaver may decrease the structure and/or quality of riparian woodland, hence strictly woodland dependent species may be detrimentally impacted (Livezey, 2009). Although there may be some negative impacts on woodland if tree regeneration is limited by deer grazing, the increase in the amount of standing water and wetland habitat is likely to improve the avian diversity of our riparian zones. If deer grazing is controlled, the increased structural diversity resulting from the cyclical coppicing and regrowth of riparian trees is likely to open niches for species not found in mature closed canopy woodland, for example tree pipits *Anthus trivialis*. The increased shrub layer resulting from the regeneration of tree stools will also create habitat for a range of insectivorous songbirds, particularly warblers.

Inundation of woodland, leading to the death of standing trees, would also create feeding and nesting opportunities for a range of bird species, including raptors and dead wood feeders such as woodpeckers and nuthatch *Sitta europea*. The latter is a naturally colonising species in Scotland whose spread could be enhanced by the presence of beavers.

Examples of scarcer native species that may benefit include marsh harrier *Circus aeruginosus* and bearded tit *Panurus biarmicus*, which have populations currently concentrated in the Tay reedbeds.

3.7.3.1 Schedule 1 species in Scotland

The interaction of beaver with bird species from schedule 1 of the Wildlife and Countryside Act 1981 were assessed (see annex 2). A potential positive impact was predicted for 65% of species assessed, and no interaction was predicted for the remaining 35% of species. Positive impacts on some species may come from an increase in habitat (such as wetland, marsh, riparian meadows, reed beds, etc), and an increase in prey numbers (such as other birds, amphibians, fish, invertebrates, etc). Populations of Slavonian grebe (*Podiceps auritus*) and related species would need to be monitored (see 3.7.1), although Slavonian grebes breed well in Norway alongside a high density of beavers (Aarvak & Oien, 2009).

3.7.3.2 Invasive non-native species

The wetland conditions created by beavers may also assist the spread of invasive non-native species, such as Mandarin duck *Aix galericulata*. This small duck has established seven small populations in Scotland from the Borders to Inverness-shire. It is associated with deciduous woodland next to waterbodies, where it nests in natural cavities or nest boxes put up for other species. The closely related wood duck *A. sponsa* in North America has benefited throughout its range from the expanding North American beaver populations (Folk & Hepp, 2003), which create an ideal forested wetland habitat for the ducks. It is therefore possible that increased populations of beavers in Scotland will also allow the small Mandarin duck population to expand in numbers and range.

3.8 Semiaquatic mammals

Beaver ponds are often used by otters due to the high abundance and diversity of prey found within them. Beaver pond creation and herbivory is also likely to have a large positive influence on water voles.

3.8.1 Mechanisms of beaver influence

Two studies on semi-aquatic mammals were included in our meta-analysis. The first reported a positive impact on North American river otter (*Lontra canadensis*) (Gallant *et al.*, 2009), the second a negative impact on American mink (*Neovison vison*) (Schüttler *et al.*, 2010).

Otter species are likely to benefit from beaver activity. Beavers increase the amount of aquatic habitat, hence increasing suitable otter habitat. The ponds formed are often rich in prey species such as fish, amphibians and invertebrates. Abandoned beaver lodges and bank dens may also provide important shelter for otters (Newman & Griffin, 1994, Swimley *et al.*, 1998, Swimley *et al.*, 1999). Gallant *et al.* (2009) showed that beaver created habitat is an important predictor of North American river otter (*Lontra canadensis*) distribution.

3.8.2 *Comparison of* Castor fiber *and* Castor canadensis

While the majority of the literature focuses on the North American river otter, a number of reports also describe the benefits beavers have on Eurasian/European otter (*Lutra lutra*) (Wlodek *et al*., 1989, Balciauskas & Ulevicius, 1995, Elmeros *et al*., 2003). As the positive mechanisms are associated with pond creation (see section 1.2) and creation of shelter for resting sites, similar effects are expected on both otter species

3.8.3 Scottish context

3.8.3.1 Annex II and IV species in Scotland

Otter (Lutra lutra), *Annexes II and IV - There is a high likelihood that beaver will interact with this species based on levels of potential overlap (NBN Gateway 2015, Stringer et al. 2015). Any interaction with beaver is likely to have a large impact* (see 3.8.2).

3.8.3.2 Other species of conservation importance

European water vole (Arvicola amphibious) - *There is a high likelihood that beaver will interact with this species based on a visual assessment of potential overlap (NBN Gateway 2015, Stringer et al. 2015). Any interaction with beaver is likely to have a high impact.* Water voles have experienced a significant recent population decline throughout the UK (Jefferies, 2003). Beaver presence is likely to result in new and improved habitat for the species. Water voles have a strong preference for slow moving water with abundant aquatic, emergent, and herbaceous bankside vegetation, all features that are characteristic of beaver ponds. A key management technique already used to improve water vole habitat is the thinning of woody riparian vegetation (Field, 2009), which beavers will also do. Evidence for a positive relationship comes from studies of the muskrat (*Ondatra zibethicus*), which is ecologically similar and seems to derive benefit from beaver influenced habitat (Balciauskas & Ulevicius, 1995, McKinstry et al., 1997). The presence of habitat with abundant emergent vegetation is particularly important for water voles to avoid predation by American mink (*Neovison vison*) (Carter & Bright, 2003), and it is ultimately the level of predation by this non-native predator that will determine future population success.

3.8.3.3 Invasive non-native species

It would be expected that American mink would benefit from beaver effects, due to the increase in levels of prey stocks for mink; notably invertebrates, fish, and amphibians (Knudsen, 1962, Balciauskas & Ulevicius, 1995). Mink have also been observed using beaver lodges and burrows (Zurowski & Kammler, 1987). However in South America, where both species are invasive, mink appear to avoid beaver modified habitat (Schüttler *et al*., 2010). This result has also been reported with *C. fiber* and invasive American mink in Russia (Kiseleva, 2008). The interaction would need to be monitored.

3.9 Terrestrial mammals

Beavers will have little influence on the majority of terrestrial mammal species. However, bats may benefit from an increased abundance and availability of food, and better foraging habitat.

3.9.1 Mechanisms of beaver influence

Studies investigating the impact of beavers on terrestrial mammal diversity and abundance were investigated. A total of 25 out of 35 papers described terrestrial mammal species using beavers as prey, beaver ponds, or beaver created habitat, but did not compare this use to areas without beavers. The remaining 10 studies investigated the differences between beaver impacted and non-impacted areas.

Beaver activity was found to have a positive effect on the abundance of a species, or on overall mammal diversity, in 50% (n=5) of studies. No difference was found in 50% (n=5) of studies. No study found a negative impact of beavers on mammal diversity or abundance.

Four of these studies focused on bats, with two finding a positive impact of beaver activity. Nummi *et al.* (2011) showed that beaver created ponds supported a higher abundance of bats than non-beaver ponds. Bats are thought to benefit from beaver activity due to an increase in prey abundance and availability, and improved foraging habitat due a reduction in forest-associated 'clutter' (Ciechanowski *et al*., 2011). When beaver ponds succeed into beaver meadows, any benefits for bats seem to be lost. Bats may also utilise beaver habitat in other ways, for example bats have been found roosting under the exfoliating bark from trees killed by beaver flooding (Menzel *et al*., 2001).

Beavers may increase the abundance of habitat for species dependent on riparian zones, in particular in areas with dry climates. For instance, on the edge of their range, stoats (*Mustela erminea*) and the meadow jumping mouse (*Zapus hudsonius luteus*) heavily utilise beaver created wetlands (Frey & Malaney, 2009, Frey & Calkins, 2014).

Small mammals do not seem to be heavily impacted by beaver activity (Hanley & Barnard, 1999, Suzuki & McComb, 2005). However, a diverse range of small mammals are known to use beaver lodges (Ulevicius & Janulaitis, 2007). A number of other mammal species may also use abandoned beaver lodges or dams as resting sites, such as bobcat (*Lynx rufus*), pine marten (*Martes martes*), fisher (*Martes pennanti*), badger (*Meles meles*), and red fox (*Vulpes vulpes*) (Rosell & Hovde, 1998, Erb *et al*., 2008).

Numerous mammals have been reported to prey on beaver. European predators include wolf (*Canis lupus*), but also less commonly red fox and American mink (Kile *et al*., 1996, Recker, 1997, Niche, 2011). Beaver remains have also been found in lynx (*Lynx lynx*) stomachs (Zunna *et al*., 2011), and pine marten faeces (Rosell & Hovde, 1998), potentially indicating either predation or scavenging. In Latvia beaver are the most important prey species for wolves in the summer months, making up 36% of wolf diet by biomass (Andersone, 1999). It is presumed that some of the smaller predators will only take beaver kits rather than adults.

Beaver herbivory may be beneficial to local ungulate populations. Baker *et al.* (2005) report that regrowth from beaver-felled trees are heavily browsed by red deer (*Cervus elaphus*). Trees felled by beaver and not used may provide food for numerous browsing ungulates (Rosell *et al*., 2005). Beaver meadows are a key habitat for moose (*Alces alces*) in North America (Müller-Schwarze, 2011), also aquatic vegetation within beaver ponds may be a key part of their diet (Rosell *et al*., 2005). However, Nelner & Hood (2011) reported that beaver activity had no influence on large mammal diversity or abundance in either protected areas or agricultural landscapes.

3.9.2 Comparison of Castor fiber *and* Castor canadensis

The majority of the available literature focuses on North America. However, the positive effects for bats have been shown with *C. fiber*. Ciechanowski *et al.* (2011) found a greater abundance of bats using beaver impounded stream reaches in comparison to un-impounded reaches. This was thought to be due to both the extended quantity of smooth open water, but also a reduced tree density and a greater area of open woodland caused by beaver herbivory.

3.9.3 Scottish context

3.9.3.1 Annex IV species in Scotland

The effects of beavers on five bat species which occur in Scotland have been assessed in a Polish study. Many of these species are widespread in Scotland and there is expected to be overlap with potential beaver habitat. The noctule bat (*Nyctalus noctula*), the common pipistrelle (*Pipistrellus pipistrellus*), the soprano pipistrelle (*Pipistrellus pygmaeus*) and Nathusius' pipistrelle (*Pipistrellus nathusii*) were all positively affected by beaver activity. Beaver activity had no impact on the brown long-eared bat (*Plecotus auritus*), and this might be expected as they have little association with watercourses (Ciechanowski *et al*., 2011).

The effect of beavers on Daubenton's bat (*Myotis daubentonii*) may be either positive or neutral. Beavers may create habitat for the species if impoundments have smooth water. Elmeros *et al*. (2003) found an increase in the abundance of Daubenton's bat following beaver impoundment. However, habitat will not be created if smooth water is absent. For instance, Ciechanowski *et al.* (2011) found no impact of beaver on *M. daubentonii*. This may have been due to a layer of duckweed impeding hunting on some of the beaver ponds in the study.

There has been no reported interaction between beaver and the whiskered bat (*Myotis mystacinus*) or Leisler's bat (*Nyctalus leisleri*).

The wildcat (*Felis silvestris*) is another Annex IV species that occurs in Scotland. There are no reports of the species interacting with beavers, and any possible impacts are likely to be minimal and not negative.

4. OVERVIEW

4.1 Results of meta-analysis

Table 4. Results from a meta-analysis of evidence investigating the impacts of beavers on biodiversity.

Species group	Total	Positive	Neutral	Negative
Plants	11(5)	8 (5)	3(0)	0 (0)
A Inverts		See Hering *et al.* (2001)		
T Inverts	7 (2)	7 (2)	0 (0)	0 (0)
Fish		See Kemp *et al.* (2012)		
Frogs & Toads	10 (2)	8 (2)	1 (0)	1 (0)
Salamanders & Newts	8 (1)	4 (1)	2 (0)	2 (0)
Reptiles	2 (0)	1 (0)	1 (0)	0 (0)
Birds	18 (3)	17 (3)	0 (0)	1 (0)
SA Mammals	2 (0)	1 (0)	0 (0)	1 (0)
T Mammals	10 (3)	5 (2)	5 (1)	0 (0)
Total	68 (16)	51 (15)	12 (1)	5 (0)
Percentage		**75% (94%)**	**18% (6%)**	**7% (0%)**

(The number of papers reporting a positive, neutral, or negative influence of beaver on species abundance or biodiversity was totalled. Papers replicating studies using the same species were not included. Results include both beaver species, however numbers within brackets refer to C. fiber *only. Only papers reporting impacts on plant biodiversity are included, impacts on specific plant species abundance are not included due to a lack of consensus in the literature. Please see section 3.1.)*

Table 4 demonstrates that, overall, beaver have been found to have an overwhelmingly positive influence on biodiversity. They have been shown to have a positive impact on the abundance or diversity of a large variety of species. This is due to a range of mechanisms that include:

- Creation of pond habitat and associated changes in water chemistry and bed substrate.
- Changes in water chemistry immediately downstream of beaver ponds.
- Direct creation of important habitat features such as dams and lodges.
- Indirect creation of important habitat features such as standing dead wood after inundation.
- Influx of woody debris into both lentic and lotic environments.
- Habitat created by the response of vegetation to herbivory such as coppiced stands, and juvenile forms containing high levels of anti-herbivory defence chemicals.
- The creation of a unique vegetation structure due to the combination of flooding with tree felling.
- The unique successional stages that result from beaver impoundment such as beaver meadows.

Many of the mechanisms listed here are unique to beavers and hence result in rare or unique habitats. Alongside this unusual ability to create habitat, beavers fundamentally increase habitat heterogeneity through foraging (tree felling) and flooding. As these are uneven across space and time, they provide a key form of intermediate disturbance.

A number of potential negative impacts were also identified in this review. The key examples include the following:

- Beaver cause disturbance, and while disturbance is a fundamental influence on ecological landscapes, it will reduce the extent of old growth riparian woodland communities. This can be a negative impact if this habitat type is rare and a large proportion is impacted, or if ecological continuity is affected. Deer in high abundance may also prevent the regeneration of woodland species, which may lead to localised effects on the quality of some habitat types.
- The creation of lentic habitat may sometimes involve the replacement of lotic habitat. At high dam densities this may be detrimental to lotic obligates as the habitat of stream reaches between impoundments may not be as suitable as those in streams with no, or low density impoundment.
- In specific circumstances, such as at low flow, with high head dams, and where pool depth immediately downstream of the dam is insufficient, fish migration may be impeded. Further research is needed to elucidate the conditions under which this may happen, and how it impacts the populations of affected species.

4.2 Predicted interactions between beaver and habitats and species of conservation interest

There are likely to be positive impacts for a number of species of conservation interest such as otter, water vole, and great crested newt. However, negative interactions may occur when coupled with high deer density for Atlantic hazelwood, aspen, and some other woodland habitats.

Potential beaver habitat overlaps with the habitat of Atlantic salmon and lamprey species, although the impact of any interactions is unclear. For example, the propensity of these species to cross beaver dams under varying conditions is uncertain. Species such as slender naiad may also be affected by beaver activity, although again the likely impact is unclear.

Monitoring would be needed in some areas where beavers occur, and possibly management to limit negative effects and promote positive effects when necessary.

4.3 Achieving Aichi 2020 Biodiversity Targets

Overall, the reintroduction of beaver would contribute to Scotland's commitments to the 2020 Aichi biodiversity targets. Most importantly, beaver reintroduction would result in a range of large, positive impacts on biodiversity, such as helping to prevent the extinction of threatened species (Target 12). However, as well as biodiversity benefits, it has been suggested that the reintroduction of a charismatic species such as beaver would help engage the public with biodiversity, and in the longer term beaver impoundments may contribute in reducing water pollution, and in restoring degraded water courses (Targets 1, 5, & 8). The presence of beavers could help in the provision of ecosystem services to improve water quality, flow regulation, and reduce flooding (Target 14).

However, any reintroduction would have associated risks. For example, without adequate deer management, beaver reintroduction may reduce the quality of riparian woodland in some areas. This may have knock-on impacts on certain species of conservation interest, such as lichen communities on hazel, which may be detrimentally affected (Target 12). The costs and benefits of beaver reintroduction, including additional socio-economic factors, are set out further in Gaywood (2015).

5. DISCUSSION

This review demonstrates that beavers can be expected to have many positive effects on the biodiversity of Scotland. Beavers promote biodiversity through a variety of mechanisms (listed in section 4.2), primarily by increasing habitat heterogeneity, providing a form of intermediate disturbance, and the creation of unique habitats. Beavers may also help restore riparian habitat, as higher water tables and flow regulation widen the riparian zone and promote willow recruitment (Baker, 2003). Beavers may also provide a natural means of restoring incised streams (Pollock *et al*., 2014).

All native species in Scotland evolved alongside beaver. However, the reintroduction of beaver may have detrimental impacts on certain species and habitats, for example linked to the specific requirements of certain aquatic and riparian species and habitats, and the high numbers of deer in parts of Scotland. Threatened species may now rely on habitats in riparian corridors that have become established after beaver extirpation. High deer numbers may affect coppice re-growth, resulting in beaver influenced habitat not resembling historical, evolutionary environments (Baker, 2003, Joys *et al*., 2004). Climate change may also have important implications for the distribution of species in Scotland. For example, reduced rainfall may restrict some lichen communities to riparian areas, hence a greater proportion may be impacted by beaver than in the historical, evolutionary environment. However, beavers may also help to mitigate against the effects of climate change by stabilising flow within watercourses.

Atlantic hazelwood, European aspen and some other woodland habitats would require close monitoring to ensure they are not detrimentally impacted by beavers. These vulnerable species and habitats could be affected, along with species dependent upon them, such as lichens associated with Atlantic hazelwoods. These will, in certain cases, require additional management. In particular, woodland regeneration following beaver activity is possible at low to medium deer densities, but at the high deer densities currently experienced over many parts of Scotland, regeneration could be significantly affected, at least within the narrow, riparian corridors. A coordinated approach to deer and beaver management in such areas would therefore be needed.

If the decision is made to reintroduce beavers more widely in Scotland, an appropriate management strategy would be required to set out how negative impacts can be minimised, and positive impacts promoted (Gaywood, 2015).

6. REFERENCES

Aarvak, T. & Oien, I. J. 2009. Current status and national action plan proposal for the Slavonian grebe. *NOF Rapportserie,* 5, 1-34.

Acuna, V., Ramon Diez, J., Flores, L., Meleason, M. & Elosegi, A. 2013. Does it make economic sense to restore rivers for their ecosystem services? *Journal of Applied Ecology,* 50, 988-997.

Adams, S. B. 2013. Effects of small impoundments on downstream crayfish assemblages. *Freshwater Science,* 32, 1318-1332.

Allen, A.W. 1982. *Habitat suitability index models: Beaver.* U.S. Department of the Interior: Fish and Wildlife Service: OBS-82/10.30.

Alvarez, J. A., Shea, M. A. & Foster, S. M. 2013. *Rana draytonii* (California Red-legged Frog). Association with beaver. *Herpetological Review,* 44, 127-128.

Andersone, Z. 1999. *Beaver: a new prey of wolves in Latvia? Comparison of winter and summer diet of Canis lupus Linnaeus, 1758*, Kluwer Academic/Plenum Publishers.

Arndt, E. & Domdei, J. 2011. Influence of beaver ponds on the Macroinvertebrate benthic community in Lowland Brooks. *Polish Journal of Ecology,* 59, 799-811.

Askins, R. A., Chávez-Ramírez, F., Dale, B. C., Haas, C. A., Herkert, J. R., Knopf, F. L. & Vickery, P. D. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions - Report of the AOU Committee on Conservation. *Auk,* 124, 1-46.

Aznar, J. C. & Desrochers, A. 2008. Building for the future: Abandoned beaver ponds promote bird diversity. *Ecoscience,* 15, 250-257.

Baccus, J. T., Kainer, M. A. & Small, M. F. 2007. Foraging preferences by American beavers, *Castor canadensis* (Rodentia: Castoridae) on central Texas rivers. *Texas Journal of Science,* 59, 243-260.

Bailey, J. K. & Whitham, T. G. 2006. Interactions between cottonwood and beavers positively affect sawfly abundance. *Ecological Entomology,* 31, 294-297.

Baker, B. W. 2003. Beaver (*Castor canadensis*) in heavily browsed environments. *Lutra,* 46, 173-181.

Baker, B. W., Ducharme, H. C., Mitchell, D. C. S., Stanley, T. R. & Peinetti, H. R. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecological Applications,* 15, 110-118.

Baker, B. W., Raul Peinetti, H., Coughenour, M. B. & Johnson, T. L. 2012. Competition favors elk over beaver in a riparian willow ecosystem. *Ecosphere,* 3, 15pp.

Balciauskas, L. & Ulevicius, A. 1995. Semi-aquatic mammal environment correlates in south Lithuanian river valleys. *Ekologija,* 2, 37-44.

Banks, B. & Beebee, T. J. C. 1988. Reproductive success of natterjack toads Bufo calamita in two contrasting habitats. *Journal of Animal Ecology,* 57, 475-492.

Barnes, D. M. & Mallik, A. U. 1996. Use of woody plants in construction of beaver dams in northern Ontario. *Canadian Journal of Zoology,* 74, 1781-1786.

Barnes, D. M. & Mallik, A. U. 2001. Effects of beaver, *Castor canadensis*, herbivory on streamside vegetation in a northern Ontario watershed. *Canadian Field-Naturalist,* 115, 9-21.

Barnes, W. J. & Dibble, E. 1988. The effects of beaver in riverbank forest succession. *Canadian Journal of Botany,* 66, 40-44.

Bartel, R. A., Haddad, N. M. & Wright, J. P. 2010. Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. *Oikos,* 119, 883-890.

Basey, J. M., Jenkins, S. H. & Busher, P. E. 1988. Optimal central-place foraging by beavers: tree-size selection in relation to defensive chemicals of quaking aspen. *Oecologia (Berlin),* 76, 278-282.

Basey, J. M., Jenkins, S. H. & Miller, G. C. 1990. Food selection by beavers in relation to inducible defenses of Populus tremuloides. *Oikos,* 59, 57-62.

Bashinskiy, I. V. The Main Factors of Beaver's Impact on Amphibians in Small River Valleys. 6th International Beaver Symposium, Ivanić-Grad, Croatia, 2012.

Batty, P. 2015. British Dragonfly Society. The Scottish Beaver Trial: Odonata monitoring 2009-2014, final report. *Scottish Natural Heritage Commissioned Report No 785.*

Beard, E. B. 1953. The Importance of Beaver in Waterfowl Management at the Seney National Wildlife Refuge. *The Journal of Wildlife Management,* 17, 398-436.

Beier, P. & Barrett, R. H. 1987. Beaver habitat use and impact in Truckee River Basin, California. *Journal of Wildlife Management,* 51, 794-799.

Bilyeu, D. M., Cooper, D. J. & Hobbs, N. T. 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. *Ecological Applications,* 18, 80-92.

Bochkov, A. V. & Dubinina, H. V. 2011. Mites of the genus Schizocarpus (Acariformes: Chirodiscidae) parasitizing the Eurasian beaver *Castor fiber* (Rodentia: Castoridae) in the Voronezh National Reserve. *Acarina,* 19, 53-66.

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

Carter, S. P. & Bright, P. W. 2003. Reedbeds as refuges for water voles (Ar*vicola terrestris)* from predation by introduced mink (Mu*stela vison)*. *Biological Conservation,* 111, 371-376.

Bromley, C. K. & Hood, G. A. 2013. Beavers (*Castor canadensis*) facilitate early access by Canada geese (*Branta canadensis*) to nesting habitat and areas of open water in Canada's boreal wetlands. *Mammalian Biology,* 78, 73-77.

Brown, D. J., Hubert, W. A. & Anderson, S. H. 1996. Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. *Wetlands,* 16, 127-133.

Browne, C. L. & Paszkowski, C. A. 2010. Hibernation sites of western toads (*Anaxyrus boreas*): characterization and management implications. *Herpetological Conservation and Biology,* 5, 49-63.

Brzyski, J. R. & Schulte, B. A. 2009. Beaver (*Castor canadensis*) impacts on herbaceous and woody vegetation in southeastern Georgia. *American Midland Naturalist,* 162, 74-86.

BSWG 2015. Final Report of the Beaver Salmonid Working Group. Inverness: Prepared for The National Species Reintroduction Forum.

Bulluck, J. F. & Rowe, M. P. 2006. The use of southern Appalachian wetlands by breeding birds, with a focus on Neotropical migratory species. *Wilson Journal of Ornithology,* 118, 399-410.

Campbell, R. D. 2006. What has the beaver got to do with the freshwater mussel decline? A response to Rudzite (2005). *Latvijas Universitates Zinatniskie Raksti,* 710, 159-160.

Campbell, R. D., Harrington, A., Ross, A. & Harrington, L. 2012. Distribution, population assessment and activities of beavers in Tayside. *Scottish Natural Heritage Commissioned Report No. 540.*

Campbell, R. D., Rosell, F., Nolet, B. A. & Dijkstra, V. A. A. 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): Echoes of settlement and reproduction? *Behavioral Ecology and Sociobiology,* 58, 597-607.

Carter S.P. & Bright P.W. 2003. Reedbeds as refuges for water voles (*Arvicola terrestris)* from predation by introduced mink (*Mustela vison)*. *Biological Conservation* 111:371–376.

Chandler, R. B., King, D. I. & DeStefano, S. 2009. Scrub-shrub bird habitat associations at multiple spatial scales in beaver meadows in Massachusetts. *Auk,* 126, 186-197.

Ciechanowski, M., Kubic, W., Rynkiewicz, A. & Zwolicki, A. 2011. Reintroduction of beavers *Castor fiber* may improve habitat quality for vespertilionid bats foraging in small river valleys. *European Journal of Wildlife Research,* 57, 737-747.

Clements, E. 2014. Utilisation of salmonid hosts by glochidia of freshwater pearl mussels in Scotland. *Protecting Scotland's Biodiversity: Monitoring in Action, Edinburgh*.

Clifford, H. F., Wiley, G. M. & Casey, R. J. 1993. Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams. *Canadian Journal of Zoology,* 71, 1439-1447.

Coleman Quail, R. A. 2001. *The importance of beaver ponds to vernal pool breeding amphibians.* State University of New York College of Environmental Science and Forestry 62pp.

Collen, P. & Gibson, R. J. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish: a review. *Reviews in Fish Biology and Fisheries,* 10, 439-461.

Cooke, H. A. & Zack, S. 2008. Influence of beaver density on riparian areas and riparian birds in shrubsteppe of Wyoming. *Western North American Naturalist,* 68, 365-373.

Cunningham, J. M., Calhoun, A. J. K. & Glanz, W. E. 2007. Pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. *Journal of Wildlife Management,* 71, 2517-2526.

Dalbeck, L. 2011. Beaver clearings as a habitat for grasshoppers in forests of the Eifel. *Articulata,* 26, 97-108.

Dalbeck, L. 2012. The Return of the Beaver - a Story of Success in Species Protection. *Zeitschrift des Koelner Zoo,* 55, 167-180.

Dalbeck, L., Janssen, J. & Luise Völsgen, S. 2014. Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*). *Amphibia Reptilia,* 35, 321-329.

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

Dale, S. & Hansen, K. 2013. Population decline in the Rustic Bunting *Emberiza rustica* in Norway. *Ornis Fennica,* 90, 193-202.

Dams, R. J., Barnes, J. A., Ward, G. E., van Leak, D., Guynn, D. C. J., Dolloff, C. A. & Hijdy, M. 1995. Beaver impacts on timber on the Chauga river drainage in south Carolina. *Seventh Eastern Wildlife Damage Management Conference.*

Danell, K. & Sjoberg, K. 1982. Successional Patterns of Plants, Invertebrates and Ducks in a Man-Made Lake. *Journal of Applied Ecology,* 19, 395-409.

Danilov, P., Kanshiev, V. & Fyodorov, F. 2011. *Characteristics of North American and Eurasian beaver ecology in Karelia*.

Danilov, P. I. & Fyodorov, F. V. 2012. A comparison of the engineering activities of the Canadian and the European beaver. *6th International Beaver Symposium, Ivanić-Grad, Croatia.*

Degerman, E., Alexanderson, S., Bergengren, J., Henrikson, L., Johansson, B.-E., Larsen, B. M. & Söderberg, H. 2009. Restoration of freshwater pearl mussel streams. Solna: WWF Sweden.

Demiaszkiewicz, A. W., Lachowicz, J., Kuligowska, I., Pyziel, A. M., Bełzecki, G., Miltko, R., Kowalik, B., Gogola, W. & Gizejewski, Z. 2014. Endoparasites of the European beaver (*Castor fiber* L. 1758) in north-eastern Poland. *Bulletin of the Veterinary Institute in Pulawy,* 58, 223-227.

Diefenbach, D. R. & Owen, R. B., Jr. 1989. A model of habitat use by breeding american black ducks. *Journal of Wildlife Management,* 53, 383-389.

Diller, L. V. & Wallace, R. L. 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in north coastal California. *Journal of Herpetology,* 33, 71-79.

Donkor, N. T. 2007. Impact of Beaver (*Castor canadensis* Kuhl) Foraging on Species Composition of Boreal Forests. *Plant Disturbance Ecology.* Elsevier Inc.

Donkor, N. T. & Fryxell, J. M. 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. *Forest Ecology and Management,* 118, 83-92.

Donkor, N. T. & Fryxell, J. M. 2000. Lowland boreal forests characterization in Algonquin Provincial Park relative to beaver (*Castor canadensis*) foraging and edaphic factors. *Plant Ecology,* 148, 1-12.

Dorset Derby, J. & Prince, H. H. 1996. Influence of beaver on three watersheds in the Houghton Lake area of Michigan. *Michigan Academician,* 28, 375-387.

Duff, A. G., Campbell-Palmer, R. & Needham, R. 2013. The beaver beetle *Platypsyllus castoris* Ritsema (Leiodidae: Platypsyllinae) apparently established on reintroduced beavers in Scotland, new to Britain. *Coleopterist,* 22, 9-19.

Dvorak, J. 2013. Diet preference of eurasian beaver (C*astor fiber* l., 1758) in the environment of Oderske Vrchy and its influence on the tree species composition of river bank stands. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis,* 61, 1637-1643.

Edwards, N. T. & Otis, D. L. 1999. Avian communities and habitat relationships in South Carolina Piedmont beaver ponds. *American Midland Naturalist,* 141, 158-171.

Elmeros, M., Berthelsen, J. P. & Madsen, A. B. 2004. Monitoring of beaver *Castor fiber* in Denmark 1999-2003. *NERI Technical Report No. 489*.

Elmeros, M., Madsen, A. B. & Berthelsen, J. P. 2003. Monitoring of reintroduced beavers (*Castor fiber*) in Denmark. *Lutra,* 46, 153-162.

Erb, J., Coy, P. & Sampson, B. 2008. Fisher and marten demography and habitat use in Minnesota. *Minnesota Department of Natural Resources Summaries of Wildlife Research Findings,* 2007, 366-374.

Erome, G. & Broyer, J. 1984. Analyse de relations castor - vegetation. *Bievre,* 6, 15-63.

Ewins, P. J. 1997. Osprey (*Pandion haliaetus*) populations in forested areas of North America: changes, their causes and management recommendations. *Journal of Raptor Research,* 31, 138-150.

Field, J. 2009. Managing land for water voles. *Gloucestershire Wildlife Trust*

Folk, T. H. & Hepp, G. R. 2003. Effects of habitat use and movement patterns on incubation behavior of female wood ducks (*Aix sponsa*) in southeast Alabama. *Auk,* 120, 1159-1167.

Forseth, T, Fiske, P., Barlaup, B., Gjøsæter, H., Hindar, K. & Diserud, O.H. 2013. Reference point based management of Norwegian Atlantic salmon populations. *Environmental Conservation,* 40, 356–366.

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

Frey, J. K. & Calkins, M. T. 2014. Snow cover and riparian habitat determine the distribution of the short-tailed weasel (*Mustela erminea*) at its southern range limits in arid western North America. *Mammalia,* 78, 45-56.

Frey, J. K. & Malaney, J. L. 2009. Decline of the meadow jumping mouse (*Zapus hudsonius luteus*) in two mountain ranges in new mexico. *Southwestern Naturalist,* 54, 31-44.

Fryxell, J. M. 2001. Habitat suitability and source - Sink dynamics of beavers. *Journal of Animal Ecology,* 70, 310-316.

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

Fuller, M. R. & Peckarsky, B. L. 2011b. Ecosystem engineering by beavers affects mayfly life histories. *Freshwater Biology,* 56, 969-979.

Fyodorov, F. V. & Yakimova, A. E. 2012. Changes in Ecosystems of the Middle Taiga due to the Impact of Beaver Activities, Karelia, Russia. *Baltic Forestry,* 18, 278-287.

Gallant, D., Vasseur, L., Dumond, M., Tremblay, E. & Berube, C. H. 2009. Habitat selection by river otters (*Lontra canadensis*) under contrasting land-use regimes. *Canadian Journal of Zoology,* 87, 422-432.

Gaywood, M. J. (ed.) 2015. Beavers in Scotland: A Report to the Scottish Government. Scottish Natural Heritage, Inverness.

Genney, D. R. 2015. The Scottish Beaver Trial: Lichen impact assessment 2010-2014, final report. *Scottish Natural Heritage Commissioned Report No. 694*.

Gorshkov, Y. A., Gorshkov, D. Y., Easter-Pilcher, A. L. & Pilcher, B. K. 2002. First results of beaver (*Castor fiber*) reintroduction in Volga-Kama National Nature Zapovednik (Russia). *Folia Zoologica,* 51, 67-74.

Goulet, H. 1965. The Habitat of *Platypatrobus* Darlington (Coleoptera: Carabidae). *Psyche: A Journal of Entomology,* 72, 305-306.

Graham, S. P. 2013. How Frequently Do Cottonmouths (*Agkistrodon piscivorus*) Bask in Trees? *Journal of Herpetology,* 47, 428-431.

Grover, A. M. & Baldassarre, G. A. 1995. Bird species richness within beaver ponds in south-central New York. *Wetlands,* 15, 108-118.

Gustafson, D. H., Malmgren, J. C. & Mikusiński, G. 2011. Terrestrial habitat predicts use of aquatic habitat for breeding purposes - A study on the great crested newt (*Triturus cristatus*). *Annales Zoologici Fennici,* 48, 295-307.

Hanley, T. A. & Barnard, J. C. 1999. Food resources and diet composition in riparian and upland habitats for Sitka Mice, *Peromyscus keeni sitkensis*. *Canadian Field-Naturalist,* 113, 401-407.

Hanson, W., Antdr, D. & Campbell, S. 1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Missouri stream. *Am. Midl. Nat.,* 69, 136-149.

Harding, J. H. 1985. Clemmys insculpta (wood turtle). Predation-mutilation. *Herpetological Review,* 16, 30.

Harthun, M. 1999. The influence of the European beaver (*Castor fiber albicus*) on the biodiversity (Odonata, Mollusca, Trichoptera, Ephemeroptera, Diptera) of brooks in Hesse (Germany). *Limnologica,* 29, 449-464.

Hartman, G. 1994. *Ecological studies of a reintroduced beaver (Castor fiber) population.* Swedish University of Agricultural Sciences, Uppsala.

Hartman, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *Journal of Zoology,* 240, 317-325.

Hartman, G. & Tornlov, S. 2006. Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*). *Journal of Zoology (London),* 268, 127-131.

Hastie, L. C. & Toy, K. A. 2008. Changes in density, age structure and age-specific mortality in two western pearlshell (*Margaritifera falcata*) populations in Washington (1995-2006). *Aquatic Conservation,* 18, 671-678.

Hering, D., Gerhard, M., Kiel, E., Ehlert, T. & Pottgiesser, T. 2001. Review study on near-natural conditions of Central European mountain streams, with particular reference to debris and beaver dams: Results of the "REG Meeting" 2000. *Limnologica,* 31, 81-92.

Heurich, M. 2004. Influence of the beaver on the ligneous vegetation along a stream in a central European mountain range. *Beitraege zur Naturkunde in Osthessen,* 40, 23-46.

Hood, G. A. & Bayley, S. E. 2009. A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. *Forest Ecology and Management,* 258, 1979-1989.

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

Horak, J., Vavrova, E. & Chobot, K. 2010. Habitat preferences influencing populations, distribution and conservation of the endangered saproxylic beetle *Cucujus cinnaberinus* (Coleoptera: Cucujidae) at the landscape level. *Eur. J. Entomol.,* 107, 81-88.

Hughes, J. W. & Cass, W. B. 1997. Pattern and process of a floodplain forest, Vermont, USA: Predicted responses of vegetation to perturbation. *Journal of Applied Ecology,* 34, 594-612.

Hyvönen, T. & Nummi, P. 2008. Habitat dynamics of beaver *Castor canadensis* at two spatial scales. *Wildlife Biology,* 14, 302-308.

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

Jefferies, D. J. 2003. The Water Vole and Mink Survey of Britain 1996-1998 with a history of the long-term changes in the status of both species and their causes. *The Vincent Wildlife Trust.*

Jensen, J. K. & Olsen, O. G. 2004. Observations of the ability of brook lamprey *Lampetra planari planeri* to pass small dams in streams. *Flora og Fauna,* 110, 56-57.

Johnson, P. D. & Brown, K. M. 1998. Intraspecific life history variation in the threatened Louisiana pearlshell mussel, Margaritifera hembeli. *Freshwater Biology,* 40, 317-329.

Johnston, C. A. & Naiman, R. J. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology,* 1, 47-57.

Johnston, C. A. & Naiman, R. J. 1990. Browse selection by beaver: effects on riparian forest composition. *Canadian Journal of Forest Research,* 20, 1036-1043.

Jones, A., Halley, D., Gow, D., Branscombe, J. & Aykroyd, T. 2011. Welsh Beaver Assessment Initiative Report: An investigation into the feasibility of reintroducing European Beaver (*Castor fiber*) to Wales. Wildlife Trusts Wales, UK.

Jones, C. G., Lawton, J. H. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos,* 69, 373-386.

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

Jones, S., Gow, D., S.L., J. & Campbell-Palmer, R. 2013. The battle for British Beavers. British Wildife.

Joys, A. C., Fuller, R. J. & Dolman, P. M. 2004. Influences of deer browsing, coppice history, and standard trees on the growth and development of vegetation structure in coppiced woods in lowland England. *Forest Ecology and Management,* 202, 23-37.

Karraker, N. E. & Gibbs, J. P. 2009. Amphibian production in forested landscapes in relation to wetland hydroperiod: A case study of vernal pools and beaver ponds. *Biological Conservation,* 142, 2293-2302.

Kemp, P. S., Worthington, T. A., Langford, T. E. L., Tree, A. R. J. & Gaywood, M. J. 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries,* 13, 158-181.

Kile, N. B., Nakken, P. J., Rosell, F. & Espeland, S. 1996. Red fox, *Vulpes vulpes*, kills a European Beaver, *Castor fiber*, kit. *Canadian Field-Naturalist,* 110, 338-339.

Kindschy, R. R. 1985. Response of red willow to beaver use in southeastern Oregon. *Journal of Wildlife Management,* 49, 26-28.

Kiseleva, N. V. 2008. Distribution of the mink in the mountain forest of the Chelyabinsk region. *Izvestiya Chelyabinskogo Nauchnogo Tsentra,* 1, 82-86.

Knudsen, G. J. 1962. Relationship of beaver to forests, trout and wildlife in Wisconsin. *Technical Bulletin Number 25.* Madison 1, Wisconsin: Wisconsin Conservation Department.

Kollars, T. M., Jr., Durden, L. A., Keirans, J. E. & Oliver, J. H., Jr. 1995. First records of *Haemaphysalis* (Aboimisalis) *chordeilis*, *Ixodes* (Ixodes) *brunneus*, and *Ixodes* (Pholeoixodes) *banksi* (Acari: Ixodidae) from Missouri. *Journal of Entomological Science,* 30, 511-512.

Kuczynski, E. C., Paszkowski, C. A. & Gingras, B. A. 2012. Horned grebe habitat use of constructed wetlands in Alberta, Canada. *Journal of Wildlife Management,* 76, 1694-1702.

Kuefler, D., Haddad, N. M., Hall, S., Hudgens, B., Bartel, B. & Hoffman, E. 2008. Distribution, population structure and habitat use of the endangered Saint Francis Satyr butterfly, *Neonympha mitchellii francisci*. *American Midland Naturalist,* 159, 298-320.

Kuijper, D. P. J., Jedrzejewska, B., Brzeziecki, B., Churski, M., Jedrzejewski, W. & Zybura, H. 2010. Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieza Primeval Forest, Poland. *Journal of Vegetation Science,* 21, 1082-1098.

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

Lesica, P. & Miles, S. 2004. Beavers indirectly enhance the growth of Russian olive and tamarisk along eastern Montana rivers. *Western North American Naturalist,* 64, 93-100.

Livezey, K. B. 2009. Range expansion of barred owls, Part II: facilitating ecological changes. *American Midland Naturalist,* 161, 323-349.

Lochmiller, R. L. 1979. Use of beaver ponds by southeastern woodpeckers in winter. *Journal of Wildlife Management,* 43, 263-266.

Longcore, J. R., McAuley, D. G., Pendelton, G. W., Bennatti, C. R., Mingo, T. M. & Stromborg, K. L. 2006. Macroinvertebrate abundance, water chemistry, and wetland characteristics affect use of wetlands by avian species in Maine. *Hydrobiologia,* 567, 143-167.

Maitland, P. S. 2003. Ecology of the River, Brook and Sea Lamprey. Peterborough: Conserving Natura 2000 Rivers Ecology Series No. 5. English Nature.

Malmgren, J. C., Andersson, P. A. & Ekdahl, S. 2007. Modelling terrestrial interactions and shelter use in great crested newts (*Triturus cristatus*). *Amphibia Reptilia,* 28, 205-215.

Margolis, B. E., Raesly, R. L. & Shumway, D. L. 2001. The effects of beaver-created wetlands on the benthic macroinvertebrate assemblages of two Appalachian streams. *Wetlands,* 21, 554-563.

Marshall, K. N., Thompson Hobbs, N. & Cooper, D. J. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B: Biological Sciences,* 280.

Martell, K. A., Foote, A. L. & Cumming, S. G. 2006. Riparian disturbance due to beavers (*Castor canadensis*) in Alberta's boreal mixedwood forests: implications for forest management. *Ecoscience,* 13, 164-171.

Martinsen, G. D., Driebe, E. M. & Whitham, T. G. 1998. Indirect interactions mediated by changing plant chemistry: Beaver browsing benefits beetles. *Ecology,* 79, 192-200.

McCall, T. C., Hodgman, T. P., Diefenbach, D. R. & Owen Jr, R. B. 1996. Beaver populations and their relation to wetland habitat and breeding waterfowl in Maine. *Wetlands,* 16, 163-172.

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

McKinstry, M. C., Caffrey, P. & Anderson, S. H. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal of the American Water Resources Association,* 37, 1571-1577.

McKinstry, M. C., Karhu, R. R. & Anderson, S. H. 1997. Use of active Beaver, *Castor canadensis*, lodges by Muskrats, *Ondatra zibethicus*, in Wyoming. *Canadian Field-Naturalist,* 111, 310-311.

McMaster, R. T. & McMaster, N. D. 2000. Vascular flora of beaver wetlands in western Massachusetts. *Rhodora,* 102, 175-197.

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

McNeel, W., Jr. 1964. Beaver Cuttings in Aspen Indirectly Detrimental to White Pine. *The Journal of Wildlife Management,* 28, 861-863.

Menzel, M. A., Carter, T. C., Ford, W. M. & Chapman, B. R. 2001. Tree-roost characteristics of subadult and female adult evening bats (Nycticeius humeralis) in the Upper Coastal Plain of South Carolina. *American Midland Naturalist,* 145, 112-119.

Metts, B. S., Lanham, J. D. & Russell, K. R. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the Upper Piedmont of South Carolina. *American Midland Naturalist,* 145, 54-65.

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

Mitchell, C. C. & Niering, W. A. 1993. Vegetation change in a topogenic bog following beaver flooding. *Bulletin of the Torrey Botanical Club,* 120, 136-147.

Mitchell, S. C. & Cunjak, R. A. 2007. Stream flow, salmon and beaver dams: Roles in the structuring of stream fish communities within an anadromous salmon dominated stream. *Journal of Animal Ecology,* 76, 1062-1074.

Moore, B. D., Sim, D. A. & Iason, G. R. 2013. The Scottish Beaver Trial: Woodland monitoring 2011. *Scottish Natural Heritage Commissioned Report.*

Müller-Schwarze, D. 2011. The Beaver: Its Life and Impact, Second Edition. 228.

Naiman, R. J., Johnston, C. A. & Kelley, J. C. 1988. Alteration of North American streams by beaver: The structure and dynamics of streams are changing as beaver recolonize their historic habitat. *Bioscience,* 38, 753-762.

NBN Gateway 2015. Data courtesy of the National Biodiversity Network Gateway with thanks to all the data contributors. <http://data.nbn.org.uk> Interactive map (Accessed Jan. 2015). The NBN and its data contributors bear no responsibility for the further analysis or interpretation of this material, data and/or information.

Nelner, T. B. & Hood, G. A. 2011. Effect of agriculture and presence of American beaver *Castor canadensis* on winter biodiversity of mammals. *Wildlife Biology,* 17, 326-336.

Newman, D. G. & Griffin, C. R. 1994. Wetland use by river otters in Massachusetts. *Journal of Wildlife Management,* 58, 18-23.

Niche, K.-A. 2011. Carnivores as predators of beavers (*Castor fiber* et and *Castor canadensis*). *Beitraege zur Jagd- und Wildforschung,* 36, 619-632.

Nolet, B. A., Hoekstra, A. & Ottenheim, M. M. 1994. Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. *Biological Conservation,* 70, 117-128.

Nordén, B., Ryberg, M., Götmark, F. & Olausson, B. 2004. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation,* 117, 1-10.

Nummi, P. & Holopainen, S. 2014. Whole-community facilitation by beaver: Ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24, 623–633.

Nummi, P., Kattainen, S., Ulander, P. & Hahtola, A. 2011. Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation,* 20, 851-859.

Obidziński, A., Orczewska, A. & Cieloszczyk, P. 2011. The impact of beavers' (*Castor fiber* L.) lodges on vascular plant species diversity in forest landscape. *Polish Journal of Ecology,* 59, 63-73.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation,* 81, 221-231.

Parker, H. & Rønning, Ø. C. 2007. Low potential for restraint of anadromous salmonid reproduction by beaver *Castor fiber* in the Numedalslågen River Catchment, Norway. *River Research and Applications,* 23, 752-762.

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

Peck, S. B. 2007. Distribution and biology of the ectoparasitic beetles *Leptinillus validus* (Horn) and *L. aplodontiae* Ferris of North America (Coleoptera: Leiodidae: Platypsyllinae). *Insecta Mundi,* 0003, 1-7.

Perkins, T. E. & Wilson, M. V. 2005. The impacts of *Phalaris arundinacea* (reed canarygrass) invasion on wetland plant richness in the Oregon Coast Range, USA depend on beavers. *Biological Conservation,* 124, 291-295.

Peterson, S. R. & Low, J. B. 1977. Waterfowl Use of Uinta Mountain Wetlands in Utah. *The Journal of Wildlife Management,* 41, 112-117.

Pinto, B., Santos, M. J. & Rosell, F. 2009. Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. *Canadian Journal of Zoology,* 87, 317-325.

Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N. & Volk, C. 2014. Using beaver dams to restore incised stream ecosystems. *BioScience,* 64, 279-290.

Pollock, M. M., Naiman, R. J., Erickson, H. E., Johnston, C. A., Pastor, J., Pinay, G., Jones, C. G. & Lawton, J. H. 1995. *Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins*. In: Linking species & ecosystems. Chapman & Hall.

Popescu, V. D. & Gibbs, J. P. 2009. Interactions between climate, beaver activity, and pond occupancy by the cold-adapted mink frog in New York State, USA. *Biological Conservation,* 142, 2059-2068.

Popov, I. Y. & Ostrovsky, A. N. 2014. Survival and extinction of the southern populations of freshwater pearl mussel Margaritifera margaritifera in Russia (Leningradskaya and Novgorodskaya oblast). *Hydrobiologia,* 735, 161-177.

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

Ray, H. L., Ray, A. M. & Rebertus, A. J. 2004. Rapid establishment of fish in isolated peatland beaver ponds. *Wetlands,* 24, 399-405.

Recker, W. 1997. Rare cause of death of the beaver, *Castor fiber*. The mink, *Mustela* (*Lutreola*) *vison*, as a predator of beaver dams. *Saugetierkundliche Mitteilungen,* 39, 87.

Reddoch, J. M. & Reddoch, A. H. 2005. Consequences of beaver, *Castor canadensis*, flooding on a small shore fen in Southwestern Quebec. *Canadian Field-Naturalist,* 119, 385-394.

Redin, A. & Sjoberg, G. 2013. Effects of beaver dams on invertebrate drift in forest streams. *Sumarski List,* 137, 597-607.

Reese, K. P. & Hair, J. D. 1976. Avian species diversity in relation to beaver pond habitats in the Piedmont region of South Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, 437-447.

Rikkinen, J. 2003. New resinicolous ascomycetes from beaver scars in western North America. *Annales Botanici Fennici,* 40, 443-450.

Roble, S. M., Carle, F. L. & Flint, O. S., Jr. 2009. Dragonflies and Damselflies (Odonata) of the Laurel Fork Recreation Area, George Washington National Forest, Highland County, Virginia: Possible Evidence for Climate Change. *Virginia Museum of Natural History Special Publication,* 16, 365-399.

Robles, H. & Martin, K. 2014. Habitat-Mediated Variation in the Importance of Ecosystem Engineers for Secondary Cavity Nesters in a Nest Web. *PLoS ONE,* 9, e90071.

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

Rood, S. B., Kalischuk, A. R., Polzin, M. L. & Braatne, J. H. 2003. Branch propagation, not cladoptosis, permits dispersive, clonal reproduction of riparian cottonwoods. *Forest Ecology and Management,* 186, 227-242.

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

Rosell, F. & Hovde, B. 1998. Pine Marten, Martes martes, as a Eurasian Beaver, *Castor fiber*, lodge occupant and possible predator. *Canadian Field-Naturalist,* 112, 535-536.

Rosell, F., Parker, H. & Kile, N. B. 1996. Causes of mortality in beaver (*Castor fiber* & canadensis). *Fauna (Oslo),* 49, 34-46.

Rotheray, E. L., MacGowan, I., Rotheray, G. E., Sears, J. & Elliott, A. 2009. The conservation requirements of an endangered hoverfly, *Hammerschmidtia ferruginea* (Diptera, Syrphidae) in the British Isles. *Journal of Insect Conservation,* 13, 569-574.

Rotheray, G. E. & MacGowan, I. 2000. Status and breeding sites of three presumed endangered Scottish saproxylic syrphids (Diptera, Syrphidae). *Journal of Insect Conservation,* 4, 215-223.

Rudzite, M. 2005. Assessment of the condition of freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus 1758) populations in Latvia. *Latvijas Universitates Zinatniskie Raksti,* 691, 121-128.

Rudzite, M. & Rudzitis, M. 2011. The populations of the freshwater pearl mussel *Margaritifera margaritifera* in Natura 2000 site nature reserve "Melturu sils". *Environmental and Experimental Biology,* 9, 37-41.

Rudzite, M. & Znotina, V. 2006. An answer to Campbell. *Latvijas Universitates Zinatniskie Raksti,* 710, 161-163.

Runyon, M. J., Tyers, D. B., Sowell, B. F. & Gower, C. N. 2014. Aspen restoration using beaver on the northern yellowstone winter range under reduced ungulate herbivory. *Restoration Ecology,* 22, 555-561.

Russell, K. R., Moorman, C. E., Edwards, J. K., Metts, B. S. & Guynn Jr, D. C. 1999. Amphibian and reptile communities associated with beaver (*Castor canadensis*) ponds and unimpounded streams in the Piedmont of South Carolina. *Journal of Freshwater Ecology,* 14, 149-158.

Saarenmaa, H. 1978. The occurrence of bark beetles (Col., Scolytidae) in a dead spruce stand flooded by beavers (*Castor canadensis* Kuhl). *Silva Fennica,* 12, 201-216.

Schloemer, S., Dalbeck, L. & Hamm, A. 2012. The influence of the beaver (*Castor fiber)* on the dragonfly-fauna (Odonata) of the Northern Eifel (West Germany). *6th International Beaver Symposium, Ivanić-Grad, Croatia.*

Schlosser, I. J. & Kallemeyn, L. W. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology,* 81, 1371-1382.

Schüttler, E., Ibarra, J. T., Gruber, B., Rozzi, R. & Jax, K. 2010. Abundance and habitat preferences of the southernmost population of mink: Implications for managing a recent island invasion. *Biodiversity and Conservation,* 19, 725-743.

Sikora, A. & Rys, A. 2004. Distribution, abundance and habitat preferences of the white-backed woodpecker *Dendrocopos leucotos* in the regions of Warmia and Masuria. *Notatki Ornitologiczne,* 45, 253-262.

Skinner, Q. D., Speck, J. E., Jr., Smith, M. & Adams, J. C. 1984. Stream water quality as influenced by beaver within grazing systems in Wyoming. *Journal of Range Management,* 37, 142-146.

Smith, J. M. & Mather, M. E. 2013. Beaver dams maintain fish biodiversity by increasing habitat heterogeneity throughout a low-gradient stream network. *Freshwater Biology,* 58, 1523-1538.

Smith, M. E., Driscoll, C. T., Wyskowski, B. J., Brooks, C. M. & Cosentini, C. C. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. *Canadian Journal of Zoology,* 69, 55-61.

Smith, R. K. & Sutherland, W. J. 2014. *Amphibian conservation: Global evidence for the effects of interventions*, Exeter, Pelagic Publishing.

Snodgrass, J. W. & Meffe, G. K. 1998. Influence of beavers on stream fish assemblages: Effects of pond age and watershed position. *Ecology,* 79, 928-942.

Soszynska-Maj, A., Soszynski, B. & Klasa, A. 2010. Distribution and ecology of the saproxylic hoverfly *Chalcosyrphus euontus* (Loew, 1873) (Diptera: Syrphidae) in Poland. *Fragmenta Faunistica (Warsaw),* 52, 191-195.

Spieth, H. T. 1979. The virilis group of Drosophila and the beaver *Castor*. *American Naturalist,* 114, 312-316.

Stevens, C. E., Paszkowski, C. A. & Foote, A. L. 2007. Beaver (*Castor canadensis*) as a surrogate species for conserving anuran amphibians on boreal streams in Alberta, Canada. *Biological Conservation,* 134, 1-13.

Stringer, A. P., Blake, D. & Gaywood, M. J. 2015. A geospatial analysis of potential Eurasian beaver (*Castor fiber)* colonisation following reintroduction to Scotland. *Scottish Natural Heritage Commissioned Report No. 875.*

Suzuki, N. & McComb, B. C. 2005. Associations of small mammals and amphibians with beaver-occupied streams in the Oregon Coast Range. *Northwest Science,* 78, 286-293.

Suzuki, N. & McComb, W. C. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon Coast Range. *Northwest Science,* 72, 102-110.

Swimley, T. J., Brooks, R. P. & Serfass, T. L. 1999. Otter and beaver interactions in the Delaware Water Gap National Recreation Area. *Journal of the Pennsylvania Academy of Science,* 72, 97-101.

Swimley, T. J., Serfass, T. L., Brooks, R. P. & Tzilkowski, W. M. 1998. Predicting river otter latrine sites in Pennsylvania. *Wildlife Society Bulletin,* 26, 836-845.

Taylor, B. R., Macinnis, C. & Floyd, T. A. 2010. Influence of rainfall and beaver dams on upstream movement of spawning Atlantic salmon in a restored brook in Nova Scotia, Canada. *River Research and Applications,* 26, 183-193.

Taylor, G. B. 1999. Impacts of beaver (*Castor canadensis carolinensis*) on riparian ecosystems in the Chauga river drainage. *NCASI Technical Bulletin,* 2, 534.

Terwilliger, J. & Pastor, J. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. *Oikos,* 85, 83-94.

Tockner, K., Klaus, I., Baumgartner, C. & Ward, J. V. 2006. Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy). *Hydrobiologia,* 565, 121-133.

Tumiel, T. 2008. Abundance and distribution of the three-toed woodpecker in the Puszcza Knyszynska forest in 2005-2007. *Notatki Ornitologiczne,* 49, 74-80.

Ulevicius, A. & Janulaitis, M. 2007. Abundance and species diversity of small mammals on beaver lodges. *Ekologija,* 53, 38-43.

Urban, J., Suchomel, J. & Dvořák, J. 2008. Contribution to the knowledge of woods preferences of European beaver (*Castor fiber* L. 1758) in bank vegetation on non-forest land in the forest district Soutok (Czech Republic). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis,* 56, 289-294.

Willby, N. J., Perfect, C. & Law, A. 2014. The Scottish Beaver Trial: Monitoring of aquatic vegetation and associated features of the Knapdale lochs 2008-2013. *Scottish Natural Heritage Commissioned Report No. 688.*

Wimmer, C. Use of coniferous trees by beavers. 4th European Beaver Symposium, Freising, Germany, 2006.

Wlodek, K., Lapinski, W., Gielo, M., Sobolewski, H. & Rosler, A. 1989. Expansion des Fischotters Lutra lutra (L., 1758) in Polen. *Martin-Luther-Universitaet Halle-Wittenberg Wissenschaftliche Beitraege*, 44-54.

Wright, J. P., Jones, C. G. & Flecker, A. S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia,* 132, 96-101.

Yagi, K. T. & Litzgus, J. D. 2012. The effects of flooding on the spatial ecology of spotted turtles (*Clemmys guttata*) in a partially mined peatland. *Copeia*, 179-190.

Zahner, V., Hanöffer, S., Schurli, C. & Müller, S. 2006. Beaver induced structure change along a stream in Bavaria and its influence on fish fauna and an indicator beetles. *4th European Beaver Symposium, Freising, Germany.*

Zunna, A., Ozolins, J., Stepanova, A., Ornicans, A. & Bagrade, G. 2011. Food habits of the lynx (*Lynx lynx*) in Latvia based on hunting data. *Beitraege zur Jagd- und Wildforschung,* 36, 309-317.

Zurowski, W. & Kammler, J. 1987. American mink (*Mustela vison* Schreber, 1777) in beavers sites. *Przeglad Zoologiczny,* 31, 513-521.

Zwolicki, A. 2006. Impact of the canopy gaps made by beavers on the forest undergrowth herb structure in Bory Tucholskie, North-Poland. 4th European Beaver Symposium, Freising, Germany.

ANNEX 1: FULL RESULTS OF META-ANALYSIS WITH CITATIONS

Species/ group	Positive	Neutral	Negative
Willow	(Bilyeu *et al*., 2008, Marshall *et al*., 2013)	(Kindschy, 1985, Beier and Barrett, 1987, Nolet *et al*., 1994)	(Heurich, 2004, Baker *et al*., 2005, Fyodorov and Yakimova, 2012, Dvorak, 2013)
Aspen	(Rood *et al*., 2003, Runyon *et al*., 2014)		(Beier and Barrett, 1987, Johnston and Naiman, 1990, Barnes and Mallik, 2001, Heurich, 2004, Martell *et al*., 2006, Fyodorov and Yakimova, 2012, Dvorak, 2013)
Plant biodiversity	[8 - (Wright *et al*., 2002, Bonner *et al*., 2009, Bartel *et al*., 2010) [(5) - (Hughes and Cass, 1997, McMaster and McMaster, 2000, Zwolicki, 2006, Obidziński *et al*., 2011, Law *et al*., 2014)	(3 - (Mitchell and Niering, 1993, Donkor and Fryxell, 1999, Brzyski and Schulte, 2009)(0)	0 (0)
Terrestrial inverts	[7 - (McNeel, 1964, Goulet, 1965, Martinsen *et al*., 1998, Bailey and Whitham, 2006, Bartel *et al*., 2010)][(2)- (Dalbeck, 2012, Fyodorov and Yakimova, 2012)]	0	0
Frogs & toads	[8 - (France, 1997, Metts *et al*., 2001, Cunningham *et al*., 2007, Stevens *et al*., 2007, Karraker and Gibbs, 2009, Popescu and Gibbs, 2009)] [(2) - (Dalbeck *et al*., 2007, Bashinskiy, 2012)]	[1 - (Metts *et al*., 2001)] (0)	[1 - (Suzuki and McComb, 2005)] (0)
Salamanders & newts	[4 - (France, 1997, Suzuki and McComb, 2005, Cunningham *et al*., 2007) [(1) - (Dalbeck *et al*., 2007)]	[2 - (Metts *et al*., 2001, Suzuki and McComb, 2005)] (0)	[2 - (Metts *et al*., 2001, Suzuki and McComb, 2005)] (0)
Reptiles	[1 - (Metts *et al*., 2001)] (0)	[1 - (Yagi and Litzgus, 2012) (0)	0 (0)
Birds	[17 - (Beard, 1953, Peterson and Low, 1977, Lochmiller, 1979, Diefenbach and Owen, 1989, Grover and Baldassarre, 1995, McCall *et al*., 1996, McKinstry *et al*., 2001, Folk and Hepp, 2003, Bulluck and Rowe, 2006, Longcore *et al*., 2006, Aznar and Desrochers, 2008, Cooke and Zack, 2008, Bromley and Hood,	0 (0)	[1 - (Kuczynski *et al*., 2012)] (0)

	2013, Nummi and Holopainen, 2014)] [(3) - (Elmeros *et al*., 2004, Sikora and Rys, 2004, Tumiel, 2008)]		
Semi-aquatic mammals	[1 - (Gallant *et al*., 2009)] (0)	0 (0)	[1 - (Schüttler *et al*., 2010)] (0)
Terrestrial mammals	[5 - (Frey and Malaney, 2009, Nummi *et al*., 2011, Frey andCalkins, 2014)] [(2) - (Ulevicius and Janulaitis, 2007, Ciechanowski *et al*., 2011)]	[5 - (Hanley and Barnard, 1999, Suzuki and McComb, 2005, Nelner and Hood, 2011)] [(1) - (Elmeros *et al*., 2004)]	0 (0)

ANNEX 2: POTENTIAL INTERACTION OF PROTECTED BIRD SPECIES WITH BEAVER

Non-marine birds listed on Schedule 1 of the Wildlife & Countryside Act 1981 and their potential interactions with beaver:

Species	Common Name	Potential Interaction
Circus cyaneus	Hen harrier	Increased prey abundance - other birds
Haliaeetus albicilla	White-tailed eagle	Increased prey abundance - other birds and fish
Milvus milvus	Red kite	No clear interaction
Anas querquedula	Garganey	Habitat creation - wetland
Anser anser	Greylag goose	Habitat creation - wetland
Aythya marila	Scaup	Habitat creation - wetland
*Cygnus columbianus**	Bewick's swan*	Habitat creation - wetland
Cygnus cygnus	Whooper swan	Habitat creation - wetland
Melanitta nigra	Common scoter	Habitat creation - wetland
Charadrius dubius	Little ringed plover	Habitat creation - wetland
Charadrius morinellus	Dotterel	No clear interaction
*Larus melanocephalus**	Mediterranean gull*	Habitat creation - wetland
*Larus minutus**	Little gull*	Habitat creation - wetland
Calidris temminckii	Temminck's stint	Habitat creation - wetland
Limosa limosa	Black-tailed godwit	Habitat creation - wetland
Numenius phaeopus	Whimbrel	Habitat creation - wetland
Philomachus pugnax	Ruff	Habitat creation - wetland
Tringa glareola	Wood sandpiper	Habitat creation - wetland
Tringa nebularia	Greenshank	Habitat creation - wetland
Tringa ochropus	Green sandpiper	Habitat creation - wetland
Alcedo atthis	Kingfisher	Habitat creation - wetland
*Upupa epops**	Hoopoe*	Habitat creation - wetland
*Falco rusticolus**	Gyr falcon*	No clear interaction
Falco subbuteo	Hobby	Increased prey abundance - dragonflies and bats
Coturnix coturnix	Quail	No clear interaction
Tetrao urogallus	Capercaillie	No clear interaction
Gavia arctica	Black-throated diver	No clear interaction
Gavia stellata	Red-throated diver	Habitat creation - wetland
Crex crex	Corncrake	Habitat creation - beaver meadows
Porzana porzana	Spotted crake	Habitat creation - wetland
Plectrophenax nivalis	Snow bunting	No clear interaction
Pyrrhocorax pyrrhocorax	Chough	No clear interaction
Carpodacus erythrinus	Rosefinch	No clear interaction
Loxia spp	Crossbills	No clear interaction
*Serinus serinus**	Serin*	No clear interaction
Lanius collurio	Red-backed shrike	Increased prey abundance - dragonflies & amphibians
Luscinia svecica	Bluethroat	Habitat creation - wetland
Phoenicurus ochrurus	Black redstart	No clear interaction
Panurus biarmicus	Bearded tit	Habitat creation – wetland - reedbeds
Parus cristatus	Crested tit	Habitat creation - dead standing trees, cavity dweller

*Regulus ignicapillus**	Firecrest*	No clear interaction
*Sylvia undata**	Dartford warbler*	No clear interaction
Turdus illiacus	Redwing	No clear interaction
Turdus pilaris	Fieldfare	No clear interaction
*Ardea purpurea**	Purple heron*	Habitat creation - wetland
Botaurus stellaris	Bittern	Habitat creation - wetland - reedbeds
Platalea leucorodea	Spoonbill	Habitat creation - wetland
Jynx torquilla	Wryneck	Habitat creation - dead standing trees, cavity dweller
Podiceps auritus	Slavonian grebe	Habitat creation - wetland
Podiceps nigricollis	Black-necked grebe	Habitat creation - wetland
Nyctea scandiaca	Snowy owl	No clear interaction

*No recorded nesting in Scotland and seem very unlikely to do so.

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