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REVIEW

The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK

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ABSTRACT

1. In Scotland, UK, beavers became extinct about 400 years ago. Currently, two wild populations are present in Scotland on a trial basis, and the case for their full reintroduction is currently being considered by Scottish ministers. Beavers are widely considered 'ecosystem engineers'. Indeed, beavers have large impacts on the environment, fundamentally change ecosystems, and create unusual habitats, often considered unique. In this review, we investigate the mechanisms by which beavers act as ecosystem engineers, and then discuss the possible impacts of beavers on the biodiversity of Scotland.
2. A meta-analysis of published studies on beavers' interactions with biodiversity was conducted, and the balance of positive and negative interactions with plants, invertebrates, amphibians, reptiles, birds, and mammals recorded.
3. The meta-analysis showed that, overall, beavers have an overwhelmingly positive influence on biodiversity. Beavers' ability to modify the environment means that they fundamentally increase habitat heterogeneity. As beavers are central-place foragers that feed only in close proximity to watercourses, their herbivory is unevenly spread in the landscape. In addition, beaver ponds and their associated unique successional stages increase habitat heterogeneity both spatially and temporally. Beavers also influence the ecosystems through the creation of a variety of features 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 that is rich in structural complexity.
4. In Scotland, a widespread positive influence on biodiversity is expected, if beavers are widely reintroduced. For instance, beaver activity should provide important habitat for the otter *Lutra lutra*, great crested newt *Triturus cristatus* and water vole *Arvicola amphibious*, all species of conservation importance.
5. Beavers are most likely to have detrimental impacts on certain woodland habitats and species of conservation importance, such as the Atlantic hazelwood climax community and aspen *Populus tremula* woodland. A lack of woodland regeneration caused by high deer abundance could lead to habitat degradation or loss. These are also of particular importance due to the variety of associated dependent species of conservation interest, such as lichen communities in Atlantic hazelwoods.

INTRODUCTION

The reintroduction of a species is often used as a tool to improve the conservation status of the focal species. However, it may also be used as a tool to improve the overall species richness of the release area, to increase habitat quality, or to improve ecosystem functioning (NSRF 2014).

Beavers *Castor fiber* and *Castor canadensis* are herbivorous rodents (Rodentia) of riparian areas. They are widely considered ecosystem engineers: species that create, modify or maintain habitats (Jones et al. 1994). This is due, in part, to their extraordinary ability to fell large trees and their ability to dam watercourses (Wright et al. 2002, Müller-Schwarze 2011).

In Scotland, UK, the case for reintroducing beavers is currently being considered by Scottish ministers, following 20 years of study (Gaywood 2015). Currently, two wild populations are present in Scotland on a trial basis, and the case for their full reintroduction is currently being considered by Scottish ministers. The reintroduction of an ecosystem engineer may have profound consequences for the ecosystem and landscape in the release area. Importantly, the effects of beavers in the modern landscape may be different from those in the past environment (Moore et al. 1999). This is because the distributions of some species and habitats are now much more restricted than when beavers were last widespread, frequently as a result of human pressures. In addition, woodland remnants that have persisted in riparian areas have often become a more important habitat for woodland species, and the abundance of large ungulates is now likely to be much higher than previously recorded. These factors mean that the modern Scottish landscape does not resemble the past environment, and that the reintroduction of an ecosystem engineer may have negative effects on some habitats or species.

The aim of this review is to assess whether the reintroduction of beavers to Scotland would have a broadly positive or negative overall impact on biodiversity. Habitats and species of conservation concern are identified that may particularly benefit from, or may be vulnerable to, beaver reintroduction. We use a meta-analysis to review comprehensively the effects of beavers on biodiversity and species abundance. This is accompanied by a review of the mechanisms that lead beavers to influence biodiversity. We use the meta-analysis and review to identify Scottish species and habitats that may be positively or detrimentally impacted by beavers, following reintroduction.

METHODS

Castor fiber and *Castor canadensis*

It is frequently reported that North American beavers *Castor canadensis* have either a greater propensity or a greater ability to build dams than Eurasian beavers *Castor fiber* (Müller-Schwarze 2011, Kemp et al. 2012). The only evidence for this was found in the Russian north-west, where invasive North American beavers and Eurasian beavers could be directly compared. Early data suggested that there were differences in dam-building behaviour. However, beavers have now expanded into more comparable, adjacent areas, and no difference in dam-building behaviour has been observed (Danilov et al. 2011). The authors suggest that previous results were based on comparing beavers living in different habitats. Therefore, literature from both species is utilised in this paper. The Eurasian beaver *Castor fiber* is being considered for reintroduction to Scotland.

Meta-analysis

The online data bases 'Scopus' and 'Zoological Record' were searched for literature relating to the two beaver species in July 2014. All English-language literature identified as a result of using the search terms '*Castor fiber*', '*Castor canadensis*', and '*Castor* spp' was archived. The results were then searched for references in which the impacts of beavers on particular species groups (e.g. amphibians) were investigated.

Studies were categorised as explicitly showing a positive, neutral, or negative effect of beavers on species diversity, abundance or both. The effect was then evaluated, and only papers that included a statistical test of the effect, a suitable control, or both, were retained for further analysis. For example, a study in which areas affected by beavers were compared with those unaffected would be considered to have a suitable control.

We considered presenting the total number of species positively or negatively affected by beaver activity. However, with this approach, certain papers dealing with a high diversity of species (such as those from the southern USA) would dominate the analysis, and hence potentially bias any result. Conversely, if papers were simply counted as reporting an overall positive, neutral, or negative effect, then the result would be biased towards species that have been the subject of more research. The latter approach was used; however, to reduce the bias, studies in which previously described interactions were repeated were not included. This means that some reported effects are much better supported by the literature than others. In total, 49 studies were included in the meta-analysis, with some studies included within more than one taxonomic group. Full details of every paper used in the meta-analysis and a description of each interaction are included in Appendix S1.

Extensive reviews have already been performed for two of the species groups (aquatic invertebrates and fish; Collen & Gibson 2001, Hering et al. 2001, Kemp et al. 2012). A repetition of this extensive work was judged to be unnecessary, hence summary of the results of those reviews are presented here. The plant meta-analysis revealed a difference of opinion on the impact of beavers on some tree species, but a consensus when investigating the effects on biodiversity. Both are reported here in the text, but only the effects on biodiversity are reported in the table (Table 1).

Predicting beaver interactions in the Scottish context

The meta-analysis findings, together with the expert judgement of specialists (partly based on experience gained from

Table 1. Results from a meta-analysis of evidence investigating the impacts of beavers on biodiversity. The total number of papers in which a positive, neutral, or negative influence of beavers on species abundance or biodiversity is shown. Papers replicating studies using the same species were not included. Results include both beaver species. However, numbers within parentheses refer to *Castor fiber* only. Only papers in which impacts on plant biodiversity are reported are included, impacts on specific plant species abundance are not included due to a lack of consensus in the literature. A full explanation of interactions is provided in Appendix S1

Species group	Total	Positive	Neutral	Negative
Plants	10 (4)	7 (4)	3(0)	0 (0)
Aquatic invertebrates	See Hering et al. (2001)			
Terrestrial invertebrates	5 (2)	5 (2)	0 (0)	0 (0)
Fish	See Kemp et al. (2012)			
Frogs and toads	10 (2)	8 (2)	1 (0)	1 (0)
Salamanders and newts	8 (1)	4 (1)	2 (0)	2 (0)
Reptiles	2 (0)	1 (0)	1 (0)	0 (0)
Birds	17 (4)	15 (3)	0 (0)	2 (1)
Mammals	11 (3)	6 (2)	4 (1)	1 (0)
Total	63 (16)	46 (14)	11 (1)	6 (1)
Percentage		73% (88%)	17% (6%)	10% (6%)

field-based projects run in Scotland, Gaywood 2015), were used to try to predict what may happen if beavers are reintroduced widely throughout Scotland. The potential interactions between beavers and relevant terrestrial and freshwater habitats and species of European conservation importance were estimated. The species considered were those listed in Annexes II and IV of the Habitats Directive and occurring in Scotland, all non-marine birds listed on Schedule 1 of the Wildlife & Countryside Act 1981, and a small number of other species of particular conservation importance. It was not possible to assess the hundreds of other species and habitats of conservation concern, for example, the UK Biodiversity Action Plan and Scottish Biodiversity List species. Some of these species may need further consideration in the event of any future, or wider, beaver reintroduction.

REVIEW OF THE IMPACTS OF BEAVERS ON BIODIVERSITY

Habitats and associated plants

MECHANISMS OF BEAVER INFLUENCE

The ability of beavers to fell very large trees is remarkable, and perhaps only equalled by that of elephant species (Elephantidae). This ability, alongside the propensity of beavers for constructing structures such as dams and lodges, means that they have a larger impact on local ecosystems than many other herbivores (Rosell et al. 2005).

In the meta-analysis, we found 10 studies that reported the effects of beaver activity on plant biodiversity, and specifically effects on aquatic macrophytes, herbaceous (vascular) terrestrial plants, and trees. Seven studies reported a positive effect and three a neutral effect on biodiversity. A combination of beaver flooding and herbivory may produce distinctive riparian habitats. The transition from aquatic to terrestrial areas may be characterised by flooded emergent vegetation (Grover & Baldassarre 1995, Brown et al. 1996, Ray et al. 2001), 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 variety of habitats, ultimately resulting in high levels of plant diversity. Since dams tend to be established irregularly along a watercourse, and because beavers are central-place foragers (Fryxell & Doucet 1991), the impacts of beavers are not consistent along a watercourse. Hence, landscapes that contain beavers have a patchwork mosaic of different levels of beaver influence, and are structurally diverse at many scales. There is also the further influence of temporal heterogeneity caused by the multiple successional pathways that may develop from beaver ponds (Naiman et al. 1988). 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 returned to a terrestrial state, a beaver meadow may form. Plant succession within beaver meadows is slower than after 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 to lotic habitat. The timescale 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 that can remain stable for centuries (Naiman et al. 1988).

Beavers prefer to feed on tree species such as willow *Salix* spp. and aspen *Populus* spp. Herbivory of preferred species promotes the abundance of non-preferred species, altering the species composition of the plant community (Donkor & Fryxell 2000). However, there seem to be a number of mechanisms that ensure preferred species are rarely extirpated. For example, aspen and willow can show rapid regrowth after beaver browsing (Jones et al. 2009), and aspen regrowth may be in a juvenile form avoided by beavers (Basey et al. 1990). In contrast, willows invest in rapid compensatory growth after herbivory, although this regrowth may be more palatable to beavers (Veraart et al. 2006). This suggests that preferred species may have evolved responses to beaver herbivory. In addition, the felling of large trees opens the canopy, allowing higher light levels at ground level, and 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 *Alnus* spp. due to their preference for wet, marshy soils (Donkor & Fryxell 2000, Marshall et al. 2013).

In certain situations, beaver herbivory has been predicted to have negative effects on overall biodiversity. Beavers have been shown to prefer to feed on certain tree species. However, this preference may change depending on the abundance of different species in the environment. For instance, in the Biesbosch in the Netherlands, beavers were reintroduced into an environment dominated by willows. Beavers were observed to select species other than willows. It was suggested that this increased the diversity of their diet, and allowed them to avoid dietary deficiencies (Nolet et al. 1994). This selective herbivory of the less common species was predicted to decrease tree biodiversity over the long term.

On temporal and landscape scales, beaver herbivory is variable. Beaver settlement may not be permanent and there may be a variety of reasons for territory abandonment, such as the depletion of resources in the area. After abandonment, there may be many years before recolonisation, allowing plant species time to recover (Fryxell 2001). On a landscape scale, beavers browse predominantly in close proximity to water (<10 m), exhibit tree size selectivity with distance to water, and are central-place foragers, which results in gradients of herbivory pressure along watercourses (Jenkins 1980, Fryxell & Doucet 1991, Hood & Bayley 2009). These mechanisms help to create a dynamic equilibrium, preventing preferred species extirpation (Donkor 2007).

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

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

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

The meta-analysis and literature review suggests that beavers may have a range of positive benefits on plant biodiversity in Scotland. However, their impact on preferred species may be a concern. For instance, European aspen *Populus tremula* has a restricted range in Scotland, and is a highly preferred species of beavers. Despite the ability of aspen to regrow rapidly, the local loss of *Populus termuloides* has been reported in close proximity (30 m) to some beaver impoundments (Martell et al. 2006), and also on 4–5% of stream reaches within beaver-occupied habitat (Beier & Barrett 1987). However, both the reduction in overstory density and the transport into watercourses of felled branches (that may act as propagules for *Populus balsamifera*) may increase aspen recruitment on a wider scale (Rood et al. 2003, Runyon et al. 2014).

An unknown factor is the influence of beavers on the age class structure of affected woodlands. Old woodland with large trees is important for woodland-associated communities, such as lichens, and large dead wood is important for saproxylic insects. In Scotland, aspen woodlands and Atlantic hazelwoods harbour particularly important communities. If beaver herbivory shifts the age-structure of these woodlands towards younger growth, this may have detrimental effects on overall biodiversity (Gaywood 2015).

Numerous tree species can be coppiced and produce suckers. Indeed, it has been argued that the reintroduction of beavers into Scotland would increase the diversity of aspen age classes throughout the landscape, with subsequent positive impacts on biodiversity (Jones et al. 2009). However, deer (*Cervus elaphus*, *Capreolus capreolus*, and some further non-native Cervidae) may prevent regrowth, depending on the amount of browsing and the tree species that is browsed (Kuijper et al. 2010, Runyon et al. 2014). For instance, willow can regrow vigorously when deer density is at medium to low levels, particularly as the raised water tables created by beaver impoundments can greatly improve willow recruitment (Jones et al. 2009, Marshall et al. 2013). When ungulate browsing is high, willow regrowth may be restricted to hedge height (Baker et al. 2005).

By the end of the 5-year Scottish Beaver Trial at Knapdale in mid-Argyll, 26% of beaver-browsed tree stumps were showing regrowth. Regrowth was not equal between species. For instance, very poor re-sprouting was observed on alder, although overall impacts on this species were low. Ash *Fraxinus excelsior* and willow showed vigorous re-sprouting, suggesting that species differ in their ability to respond to beaver browsing. 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). This highlights how high deer density could reduce the regrowth of beaver-browsed woodland.

Invertebrates

MECHANISMS OF BEAVER INFLUENCE

Beaver impoundments convert lotic habitats into lentic habitats. Within the ponds, the aquatic invertebrate community changes to reflect the newly created lentic habitat. Under such circumstances, shredders and scrapers become less abundant, while collectors and predators become more abundant (McDowell & Naiman 1986). Beavers may also create unique aquatic habitats, such as channels and canals, which support taxa that are not found in other wetland habitats (Hood & Larson 2015). Beaver dams can support a high diversity of invertebrates (Rolauffs et al. 2001). In particular, the turbulent water flowing over a beaver dam, and the increased stream velocity directly downstream of a dam due to the head of water behind dams, may both create rare habitat for lotic species on low-gradient stream reaches (Clifford et al. 1993, Smith & Mather 2013).

Hering et al. (2001) thoroughly reviewed the literature on the aquatic invertebrate community in beaver-impounded streams and un-impounded streams. They reported that, on a landscape scale, beaver impoundments have positive impacts on aquatic invertebrate abundance and diversity. The few exceptions include gravel-preferring species and macro-invertebrate grazers that may be affected by sedimentation within the beaver pond. Caddisflies (Trichoptera) and stoneflies (Plecoptera) may also be negatively affected due to their preference for fast-flowing reaches.

Beavers are therefore expected to increase the diversity of aquatic invertebrates at the landscape scale. However, beaver dams may also influence downstream areas and disrupt the river continuum. Therefore, it is possible that patches of lotic habitat between beaver impoundments will 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 reaches, and effects may be highly variable (Rosell et al. 2005). 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 large surface areas 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 2011).

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, Arndt & Domdei 2011, Redin & Sjoberg 2013). The influence of a beaver impoundment on downstream ecosystems is expected to dissipate gradually with distance. For instance, the effects of a beaver impoundment on downstream invertebrate assemblages has been shown to be much reduced 100 m downstream of the beaver dam (Margolis et al. 2001). In addition, stonefly abundance has been shown to return to above-impoundment levels 250 m below an impoundment (Smith et al. 1991). However, crayfish species assemblages have been affected up to 2 km downstream from beaver dams (Adams 2013).

Beavers may increase terrestrial invertebrate biodiversity by increasing the abundance of dead wood, by providing habitats such beaver meadows, and by providing beaver-specific structures such as dams and lodges. Five studies have investigated the impact of beavers on terrestrial invertebrate diversity or species abundance, and all found a positive effect (Appendix S1). In particular, saproxylic beetles may utilise dead, decaying, and rotting wood resulting from beaver flooding and herbivory (Saarenmaa 1978, Zahner et al. 2006, Horak et al. 2010).

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

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. This may affect some important lotic obligates in Scotland, such as the freshwater pearl mussel *Margaritifera margaritifera*. Juvenile *Margaritifera margaritifera* cannot survive in beaver ponds due to sedimentation (Rudzite 2005). However, habitat may be improved downstream of dams due to a reduced water sediment load and the regulation of stream flow (Campbell 2006). The 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 stage of *Margaritifera margaritifera* are brown trout *Salmo trutta* and Atlantic salmon *Salmo salar* (Hastie & Young 2001). The former is expected to benefit from beaver reintroduction, although the effects on the latter are unknown, and so the implications for *Margaritifera margaritifera* are unclear (Kemp et al. 2012).

Fish

MECHANISMS OF BEAVER INFLUENCE

Reviews of the impacts of beavers on a variety of fish species are provided by Kemp et al. (2012) and Collen and Gibson (2001). A variety of possible influencing mechanisms have been identified, and it is likely that beaver activity will have differing effects on different fish species.

Overall, beaver impoundments replace terrestrial habitat with aquatic habitat, thereby 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 a dam 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; this has further positive impacts on fish biodiversity (Schlosser & Kallemeyn 2000). Restoring degraded watercourses through impoundment and increasing the abundance of dead wood also increases total fish biomass present within a stream reach (Acuna et al. 2013). Importantly, although this describes the general impacts of beaver activity on habitat heterogeneity and subsequent impacts on biodiversity, there will be variation in how these impacts influence, positively and negatively, the abundance of any single species (Kemp et al. 2012).

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

Through increases in habitat heterogeneity, beavers are likely to influence fish biodiversity positively in Scotland. However, previous reviews identify a number of species that may be either positively or negatively affected by beaver activity, and the cumulative effects of different mechanisms are unknown. For instance, lamprey *Lampetra* spp. and *Petromyzon marinus* and Atlantic salmon *Salmo salar* may be unable to pass certain dams at certain times; however, beaver activity may also improve water quality and food abundance. Ultimately, multiple mechanisms will interact, with unknown repercussions on population performance (Collen & Gibson 2001, Kemp et al. 2012, BSWG 2015).

Amphibians

MECHANISMS OF BEAVER INFLUENCE

In the meta-analysis, we considered the frogs and toads (Anura), and newts and salamanders (Caudata) separately, due to common differences in habitat requirements. A positive impact of beaver activity on the abundance or diversity of frogs and toads was found in eight studies. One study found no impact, and one study found a negative impact.

The meta-analysis highlights numerous positive effects of beavers on frog and toad populations. A number of mechanisms were proposed including increasing the size, number, and diversity of lentic zones, which provides essential breeding habitat for many amphibian species (Cunningham et al. 2007, Stevens et al. 2007). Indeed, beavers 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, for larval food provision and development, or as hibernation sites (Karraker & Gibbs 2009, Browne & Paszkowski 2010, Alvarez et al. 2013). Only lotic obligates were negatively affected by beaver activity (see Appendix S1).

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

Beaver activity was found to have a positive impact on abundance or biodiversity in four studies of salamanders and newts. Two studies found no impact, and two studies found a negative impact. The impact of beavers on newt and salamander species is variable. Many species of salamander prefer flowing water and cannot utilise beaver ponds (Metts et al. 2001, Dalbeck et al. 2007). On a landscape scale, beavers 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 unimpounded reaches (Cunningham et al. 2007).

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

There are six native species of amphibian in Scotland. All species prefer lentic habitat over lotic habitat, and hence should be positively impacted by beaver activity. In particular, impoundment by beaver may create suitable habitat for *Triturus cristatus*, as two other species from the genus *Triturus* were shown to utilise older beaver ponds heavily in central Europe (Dalbeck et al. 2007).

Reptiles

MECHANISMS OF BEAVER INFLUENCE

A number of researchers 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). The older a beaver pond was, the greater the diversity and abundance of reptiles (Russell et al. 1999).

In two studies, the usefulness of beaver ponds as habitat for reptiles was investigated. One showed that beaver ponds had higher reptile abundance and biodiversity than unimpounded streams (Metts et al. 2001). 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. Yagi and Litzgus (2012) found that terrapins exploited new aquatic habitats created by beavers; however, flooding also reduced nesting opportunities.

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

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

Birds

MECHANISMS OF BEAVER INFLUENCE

Thirty of 47 papers showed that bird species use beaver ponds or beaver-created habitat, but this use was not compared with the use of areas not affected by beavers. In the remaining 17 studies, the differences between beaver-impacted and non-impacted areas were investigated. Beaver activity was found to have a positive effect on the abundance of a species or on overall bird biodiversity in 88% (n = 15) of studies, and a negative effect in 12% (n = 2) of studies.

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). In particular, the aquatic characteristics of beaver ponds, such as large shallow-water areas, may be particularly important for a variety of waterfowl (Anatidae; Brown et al. 1996, Longcore et al. 2006).

The gradual edge characteristic of beaver habitat (see 'Habitats and associated plants') 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 (Picinae), 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 (Robles & Martin 2014). Dead trees and snags are also important for raptors (Ewins 1997).

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 (Longcore et al. 2006, Cooke & Zack 2008, Nummi & Holopainen 2014). Furthermore, an increased abundance and diversity of fish and amphibians within beaver impoundments provides food for species such as herons (Ardeidae) and kingfishers (Alcedines; Beard 1953, Elmeros et al. 2003).

Beavers may facilitate increases in bird abundance in less obvious ways. In places where ponds are covered with ice for much of the winter, it has been observed that beaver activity causes the ice to melt earlier in the spring. This brings 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 benefit a range of other 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). Aznar and Desrochers (2008) discovered that beaver meadows had the highest levels of songbird biodiversity when compared to all other adjacent riparian habitats.

In two studies, a negative association between birds and beavers was found. Kuczynski et al. (2012) found that Slavonian grebes *Podiceps auritus* avoid 'borrow pits' (man-made ponds created during road construction) that contained beavers. This may be because *Podiceps auritus* prefer ponds with low surrounding forest cover (<33% within 500 m), and hence they prefer habitat less suitable for beavers. However, where sedge beds are not present, *Podiceps auritus* use willow for nesting, and beavers may reduce the abundance of willow in certain situations. Whitethroat *Sylvia communis* abundance was also observed to decline at local levels after beaver reintroduction into Denmark (Elmeros et al. 2003).

In summary, 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). The structurally and temporally heterogeneous habitat created by beavers supports a highly diverse bird fauna on a landscape scale.

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

The meta-analysis shows that, given that beavers are known to create diverse habitats rich in structural complexity, their presence is likely to result in a greater avian diversity than may be expected from the existing remnant riparian habitats in Scotland. A potentially detrimental mechanism is the change in age structure of riparian woodland; hence bird species strictly dependent on old woodland may be detrimentally affected (Livezey 2009). This may be further exacerbated if tree regeneration is limited by deer grazing. If deer grazing can be controlled, the increased structural diversity resulting from the cyclical coppicing and regrowth of riparian trees by beavers is likely to open niches for species not found in mature closed-canopy woodland, for example tree pipits *Anthus trivialis*. The increased shrub layer 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, dead wood feeders such as the nuthatch *Sitta europea*, and woodpeckers.

Mammals

MECHANISMS OF BEAVER INFLUENCE

Studies investigating the impact of beavers on mammalian diversity and abundance were investigated. In 25 of 36 papers, mammalian species were described as using beavers as prey, or utilising beaver ponds, or other beaver-created habitat, but this was not compared to areas without beavers. In the remaining 11 studies, differences were investigated 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 mammalian species diversity, in 55% ($n = 6$) of these 11 studies. No difference was found in 36% ($n = 4$) of the studies. In a single study, a negative impact of beaver meadows on bat species diversity was found.

Four studies within the meta-analysis were focused on bats; in two, a positive impact of beaver activity was found. 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 due to improved foraging habitat due a reduction in woodland density (Ciechanowski et al. 2011). Bats may also utilise beaver habitat in other ways, for example, by roosting under the exfoliating bark of trees killed by beaver flooding (Menzel et al. 2001). When beaver ponds succeed into beaver meadows, any benefits for bats seem to be lost, as meadows are poorer bat habitat than adjacent riparian habitats (Brooks 2009).

Otter species (Lutrinae) are likely to benefit from beaver activity. Through impoundment, beavers increase the amount of suitable aquatic 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 such as the North American river otter *Lontra canadensis* (Newman & Griffin 1994, Swimley et al. 1999). Gallant et al. (2009) showed that beaver-created habitat is an important predictor of North American river otter distribution.

Small terrestrial mammals do not seem to be impacted by beaver activity (Hanley & Barnard 1999, Suzuki & McComb 2004). However, a diverse range of small mammals are known to use beaver lodges (Ulevicius & Janulaitis 2007).

Beavers may influence large mammals, as creators of habitats, sources of prey, and because trees felled by beavers may provide food for numerous browsing ungulates (Baker et al. 2005, Rosell et al. 2005). However, Nelner and Hood (2011) reported that beaver activity had no influence on large mammal diversity or abundance in either protected areas or agricultural landscapes, although they did conclude that beavers were important for maintaining water levels in agricultural wetlands, and therefore ecological heterogeneity.

IMPLICATIONS FOR SCOTTISH BIODIVERSITY

The beneficial effects of beavers on mammalian diversity and abundance are likely to be seen in Scotland. Effects on otters and bats are the examples best supported by the literature. In addition, beaver presence is likely to result in new and improved habitat for the European water vole *Arvicola amphibious*. 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. However, predation of water voles by the non-native American mink *Neovison vison* has been a major factor in the extinction of water voles in many Scottish main river stems and tributaries to date. Therefore, the apparent avoidance of beaver-modified habitat by mink reported from Patagonia (Schüttler et al. 2010) and Russia (Kiseleva 2008) is interesting and, if this pattern is translated to Scotland, could have important implications for the future strategic management of mink.

Invasive non-native species

Beavers have been known to have both positive and negative effects on invasive non-native species abundance (Perkins & Wilson 2005, Parker et al. 2007). In Scotland, beaver herbivory may reduce invasive non-native species abundance. For instance, *Rhododendron maximum*, a parent of the invasive complex hybrid *Rhododendron ponticum*, the invasive parrot's feather *Myriophyllum aquaticum*, and *Elodea* spp. (including *Elodea nutallii* and *Elodea canadensis* which are invasive in the UK) are food species for beavers (Allen 1982, Dams et al. 1995, Parker et al. 2007), although it seems unlikely that beavers would exert a controlling influence on these plants. However, herbivory may also increase the dispersal of some invasive species. For instance, beaver herbivory of *Elodea canadensis* may create numerous smaller fragments of the pondweed. Each of these fragments may act as a propagule for the species (Willby et al. 2014).

The wetland conditions created by beavers may also provide habitat for invasive non-native species, such as the Mandarin duck *Aix galericulata*, as beaver ponds are a preferred habitat of the closely related wood duck *Aix sponsa* in North America (Folk & Hepp 2003).

OVERVIEW

Results of meta-analysis

The results of the meta-analysis (Table 1) demonstrate that, overall, beavers have an overwhelmingly positive influence on biodiversity. Beavers influence biodiversity by increasing habitat heterogeneity. The process of pond creation and subsequent rescindment creates an abundance of temporal habitat diversity, providing a variety of successional stages. Hence, a mosaic of beaver impoundments at different stages throughout a landscape, combined with beaver herbivory that is unevenly spread in both time and space, is expected to provide a high level of abundance of habitat heterogeneity, and hence biodiversity. Other ways in which beavers may have a positive impact on the abundance or diversity of a large variety of species 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 of woody plant species 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 these are unique to beavers and hence result in rare or unique habitats. 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. In Scotland, there are likely to be positive impacts for a number of species of conservation interest such as otters, water voles, and great crested newts. However, a number of potential negative impacts were also identified during this review, with potential implications for Scotland. These include the following:

- Beavers cause disturbance, and while disturbance is a fundamental influence on ecological landscapes, it may reduce the extent of old-growth riparian woodland communities, or shift the age structure of a woodland towards younger growth. This can be a negative impact if old-growth woodland is rare and if a large proportion is impacted, or if ecological continuity is affected. Two habitat types of conservation importance that fulfil these criteria in Scotland are aspen woodland and Atlantic hazelwood. 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 often involves 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 beaver impoundments or with a low density of impoundments.
- Overall impacts on certain fish species are unknown, in particular on Atlantic salmon and species of lamprey. While many positive and negative mechanisms have been proposed, further research is needed to elucidate the overall impacts on populations of affected species.

CONCLUSIONS

This review demonstrates that beavers, if widely reintroduced, can be expected to have many positive effects on the biodiversity of Scotland. Beavers promote biodiversity through a variety of mechanisms, primarily by increasing habitat heterogeneity and creating unique habitats. Beavers may also help restore riparian habitat and provide a natural means of restoring incised streams (Pollock et al. 2014).

All native species in Scotland evolved alongside beavers. However, the reintroduction of beavers may have detrimental impacts on certain species and habitats. Threatened species may now rely on habitats in riparian corridors that have become increasingly important refuges for them since beaver extirpation. High deer density may affect tree regrowth in some areas, resulting in beaver-influenced habitat not resembling any past environment (Baker et al. 2005). 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, so that a greater proportion of these communities may be impacted by beavers than in the past 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 where they overlap with potential beaver habitat to assess any potential impacts (Gaywood 2015). These vulnerable species and habitats also harbour a number of important dependent species, such as lichens associated with Atlantic hazelwoods. In certain cases, these will 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. A co-ordinated 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 how positive impacts can be promoted.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article the publisher's web-site.

Appendix S1. Details of the meta-analysis with mechanisms and references as summarised in Table 1.