Beavers: the original engineers of Britain's fresh waters

Kelsey Wilson, Alan Law, Martin Gaywood, Paul Ramsay and Nigel Willby

Beavers have had a profound effect on the wetlands of Knapdale Forest, Argyll, since their release 11 years ago. Roy Waller/Alamy Stock Photo

Beavers are agents of change. In modern-day Britain, it feels somewhat surreal to encounter a landscape profoundly altered by something other than humans, yet this would once have been the norm across much of the Northern Hemisphere. The loss of megafauna, and the biota and ecological processes that depend on their activities, is something that we now recognise as a hallmark of the Anthropocene. While Britain has had a slower start than some mainland European countries, beaver reintroduction is now gathering traction, motivated by prospects of habitat enhancement, natural flood management and wider biodiversity benefits. Beaver numbers in some regions of the country have reached levels which 20 years ago would have seemed unimaginable. Responding to the recent rise in licences for beaver reintroduction issued by Natural England, Patrick Barkham even joked in *The Guardian* that beavers have replaced croquet lawns as the must-have accessory for English country estates.

So, what will the expansion of beavers mean for freshwater habitats in Britain? To what extent are the benefits of beavers observed elsewhere likely to be replicated in our heavily modified landscapes after a 400-year absence, and what do we still need to know? First, we provide a brief update on the status of beavers in Britain and some background on their biology and behaviour.

A potted recent history

The Eurasian Beaver *Castor fiber* is a charismatic native mammal that was once widespread throughout Britain, but was most likely hunted to extinction by the 1600s. Beavers were officially returned in 2009, following a long debate that resulted in a five-year trial-reintroduction project at Knapdale Forest, in the west of Scotland – the Scottish Beaver Trial (SBT). The complex tale of how beavers became reacquainted with British waters has featured in previous issues of *British Wildlife* (Gaywood *et al.* 2008; Jones *et al.* 2013), but a brief update is overdue. Tayside is now the stronghold of beavers in Britain following escapes from private collections, coupled with unauthorised releases of animals on the rivers Tay and Earn, suspected to date back

Beaver-engineered stream channel on private land in Tayside. This was formerly a straightened channel 1m wide. Nigel Willby

Beaver-generated fine-scale habitat complexity, Tayside. Anyone can make a pond, but there is only one way to make a beaver pond. Nigel Willby

to the early 2000s. A 2017/18 survey estimated 114 active territories (approximating to 319–547 animals) dispersed across Tayside's fresh waters (Campbell-Palmer *et al.* 2018). This population has trebled since 2012 and appears to be spreading westwards, with satellite territories now appearing in the Forth catchment and Trossachs. In England, small, licensed populations are now established or imminent in at least ten counties, mostly as part of enclosed trial projects. Some of these date back to the early 2000s, the largest (and only officially sanctioned) free-living population in England comprising around 13 territories on the River Otter, Devon (Brazier *et al.* 2020). In Wales, the feasibility of officially bringing beavers back is being investigated, and several small enclosed populations already exist on private estates.

Since May 2019, beavers in Scotland have been listed as a European Protected Species, a status celebrated by conservationists but not welcomed by all. In parts of rural Tayside, beaver activity can conflict with lowland farming and therefore translocation or lethal control is permitted under licence. Tayside beavers have been translocated to Knapdale to reinforce that population and to boost its genetic diversity, but they are also in demand for ongoing or proposed trials in various parts of England. The River Otter Beaver Trial runs until the end of August 2020, after which the government will decide on the future status of beavers in England.

Beaver biology and engineering

The two species of beaver, North American *Castor canadensis* and our native Eurasian Beaver, are large, semi-aquatic, crepuscular rodents, in which order they are beaten for size only by the South American Capybara *Hydrochoerus hydrochaeris*. They live in family groups usually comprising two breeding monogamous adults, their offspring from the previous year(s), known as yearlings and subadults, and their kits. Unlike other rodents, beavers breed only once a year, in late spring, typically producing two to four kits, which emerge from their lodge or burrow in the summer. The offspring usually stay in their family group for up to two years, before dispersing around the period April–June. Beavers are very social animals and have a dominance hierarchy based on age. They mostly communicate through scent-marking and deposit a pungent glandular substance called castoreum (historically used in perfumes and food flavourings) at the edge of their territories to warn off rivals. Territory sizes vary widely (0.5–20km) with habitat quality, but typically average 3–4km of riverbank or lakeshore.

Although beavers themselves are often elusive, the signs of their activity are unmistakable and are usually concentrated in, or adjacent to, riparian woodlands. Beavers are strictly herbivorous and, when on land, forage mostly within 30m of the riverbank or lakeshore. They form well-worn trails inland from the water's edge, where they gnaw and fell broadleaf trees, often then stripping the bark and leaves. For shelter they build impressive lodges, using sticks, vegetation and mud, or burrow into soft banks, as well as digging networks of canals to provide access to wooded areas for feeding. Beavers also graze on aquatic and riparian vegetation, especially in the summer, leaving middens of discarded material. Unstripped branches are cached underwater to be used in winter when food is sparse or inaccessible. The beavers will sometimes feed on cereal or vegetable crops if a territory borders arable farmland.

While beavers are best known for their dam-building abilities, this behaviour is far from ubiquitous. Dams are built in order to raise and stabilise water levels, providing a submerged lodge or burrow entrance, ready access to resources and safety from land-based predators. Dam densities, composition and heights, and the area inundated, vary hugely with topography: in smaller streams there may be in excess of 10 dams/km, with structures often 1–1.5m tall, while on lakes and lowland rivers dams are scarcer and lower in height, but may potentially be longer and can impound valley wetlands (Gurnell 1998). In some locations, dams may simply not be required.

The ponds formed upstream of beaver dams are colonised by plants, aided by propagules carried downstream, imported by beavers and other biota, or from a pre-existing wetland seedbank (beavers may rework systems that they occupied decades or even centuries earlier). The key to the ecological interest of a beaver pond is ongoing maintenance of dam and lodge, fluctuating water levels, canal-digging, grazing of plants and collapse or windblow of drowned trees, which adds to the jumble of felled or fallen dead wood. Ultimately, after anything from three to 30 years, neglect of a dam, loss of water and successional processes combine to create a beaver meadow. Beaver ponds are gloriously complex places with sometimes bizarre juxtapositions of species and microhabitats quite unlike anything else, but they would be far less interesting, and much like any other pond, if beavers simply constructed their dam and then swam away.

The end result is that beaver activities collectively promote habitat heterogeneity, which is a cornerstone of biodiversity. In ecological restoration, a common priority and criterion for success is enhanced heterogeneity. Some might call this patchiness, others complexity, but, whatever the definition, the intrinsic 'messiness' of large grazing animals is a great source of heterogeneity. Our wetlands have long since lost the large animals that used to create such heterogeneity (e.g. moose, beaver). Horses and cattle are passable substitutes in the right places and in the right amounts, but are now mostly fenced out to safeguard them or to reduce diffuse pollution and bank erosion.

An increasing obsession with order and control has undoubtedly been to the detriment of the great diversity of organisms that rely on disturbance and weak competition, many of which have declined in recent decades following eutrophication and the cessation of traditional management. As beavers excel when it comes to creating 'untidy' landscapes (perhaps one thing that all parties in the beaver debate would agree on), their activities can have important cascading effects on freshwater biota.

Ecological impacts

Aquatic vegetation

Beavers affect aquatic vegetation in two ways: first, through inundation and creation of less shaded habitat by damming; and, secondly, by eating it. The first is what beavers are renowned for, but the second is arguably of equal or greater ecological importance.

Unshaded, shallow water with periodic disturbance tends to suit aquatic plants, but the added benefits of beaver dams are still striking. In southern Sweden, the difference in plant composition between adjacent patches, an indicator of fine-scale heterogeneity, was 17% higher in beaver ponds than in other adjacent non-beaver wetlands, while plant species richness was 33% higher in beaver ponds (Willby *et al.* 2018). Fifty percent more species were restricted to beaver ponds in this region than were restricted to other wetlands, with ruderal species the main beneficiaries (Law *et al.* 2019). Beavers are clearly able to create novel freshwater habitats which are not easily replicated: anyone can make a pond, but there is only one way to make a beaver pond.

A major element in the enduring interest of beaver habitats is that the animals feed heavily on aquatic vegetation during the growing season. Beavers are usually referred to as choosy generalists: they will eat most plants but not quite everything. Being large and territorial, they have the potential to exert a strong impact on the composition of surrounding vegetation communities within a few seasons. By selecting large, fleshy or rhizomatous plants they benefit smaller, less competitive ruderal species, commonly leading to an increase in plant diversity. Repeated monitoring in Knapdale during the SBT, for example, revealed declines in Great Fen-sedge

Cladium mariscus and Common Club-rush *Schoenoplectus lacustris* of 81% and 39%, respectively (Willby *et al.* 2014). Elsewhere, marked reductions were documented in Bogbean *Menyanthes trifoliata* and Yellow Flag *Iris pseudacorus* over an eight-year period as a result of grazing, accompanied by a trebling of plant species richness (Law *et al.* 2014a). At Knapdale, beavers also fed readily on the leaves of White Water-lily *Nymphaea alba*, displaying a clear preference for larger leaves, as well as uprooting rhizomes (Law *et al.* 2014b).

Invertebrates

When a stream is dammed, the invertebrates that are more reliant on highly oxygenated running water (such as *Baetis* mayflies and Elmidae riffle beetles) are quickly replaced by those associated with slow-moving, warm shallow water with high volumes of organic debris and extensive vegetation. These include dragonflies and damselflies, diving beetles, water boatmen and backswimmers. The fauna varies spatially within a beaver pond, depending on proximity to the dam, areas of disturbance, and successional stage, although colonisation is rapid. An often overlooked outcome of habitat-engineering by beavers is the increase in invertebrate abundance, especially of generalist diptera (e.g. Dixidae, chironomids), which is likely to benefit terrestrial consumers (carabid beetles, spiders, and species at higher trophic levels). Law *et al.* (2016) found that average invertebrate abundance was three times higher in beaver ponds compared with unmodified streams. Following damming, other beaver activities continue to influence the suitability of the aquatic habitat for invertebrates. Beaver-dug channels (which may be up to 300m long), for example, have been shown to increase wetland perimeter by 575%, providing key edge habitat for some species (Hood & Larson 2015). Dams and lodges add further to habitat heterogeneity through provision of greater amounts of coarse woody debris and entrapped sediment (France 1997).

Many studies reveal lower invertebrate-species richness in beaver-created habitats compared with pre-existing or nearby streams: the fauna of running-water habitats tends locally to be richer, and damming may have a negative impact on some specialist riverine taxa, including those of conservation importance. Further scrutiny, however, shows that, as with plants, the novel habitats generated by beavers hold species not shared with other habitats. This means that landscapes containing a mosaic of unmodified and beaver-created habitats support increased biodiversity. For instance, Law *et al.* (2016) found that, overall, aquatic invertebrate richness was 28% higher in a Tayside landscape containing beaver-engineered features than in the same landscape without these features. The scale at which effects are measured is therefore important.

Vertebrates

Beavers have the ability to create havens for other animal species. Beaver ponds are ideal habitats for endangered amphibians, their shallow and well-vegetated waters providing excellent conditions for spawning, as well as an abundance of invertebrates on which to feed (Osipov *et al.* 2018; Dalbeck *et al.* 2020). Damming, digging and the felling of trees create microhabitats that fish can utilise to avoid predators (Wathen *et al.* 2019), while various age classes of fish will also benefit from the proliferation of invertebrate prey and habitat diversification.

Great Fen-sedge (top) and White Water-lily (bottom) were among the aquatic plants favoured by the Knapdale beavers during the Scottish Beaver Trial. Nigel Willby

View of a lochan in Tayside, with fringing emergent vegetation in August 2003 (left) and August 2012 (right). The arrows indicate the same group of trees in each photograph. The decrease in conifers in the background is due to commercial forestry, not beaver activity (Law *et al.* 2014). Nigel Willby

There are frequently concerns that fish of high economic importance to Britain, such as Atlantic Salmon *Salmo salar* and Sea Trout *Salmo trutta*, may, under certain circumstances, be unable to ascend beaver dams to access spawning grounds (see Kemp *et al.* 2012 for a review on this topic). Yet recent research in Norway has demonstrated that both of these species can successfully traverse beaver dams on their journey upstream (Malison & Halley 2020). Further research on the full range of fish species and age classes that utilise beaver ponds is required in order to understand this dynamic relationship.

The gently sloping banks, shallow water, exposed wet mud, diverse vegetation and abundance of invertebrates make beaver ponds ideal habitat

Dubh Loch: an untidy case study

Dubh Loch (pronounced 'doo loch' and translating as black lake), in Knapdale Forest, is one of the longest and most intensively monitored beaver sites in Britain and an excellent example of the engineering prowess of this species. Within months of being reintroduced to Loch Coille-Bharr (33ha) in 2009, the beaver family had moved to the connected and much smaller Dubh Loch (0.4ha). The animals dammed the small outflow, raising the water level by >1m, which flooded a substantial area and increased the size of the loch four-fold.

There were profound alterations to the distribution and biomass of aquatic plants following the arrival of beavers, with some plants quick to colonise the shallow areas, suggesting the pre-existence of a long-lasting seedbank. The overall plant-species richness has increased (last surveyed in 2018), and the relatively homogenous stands of vegetation that previously existed have been replaced by a kaleidoscope of alternating soggy, inundated and dry patches. The site continues to evolve. There has been a reduction in tree canopy associated with the death and subsequent windblow of drowned trees but, with ongoing declines in dam integrity and water levels falling from their peak in 2011, birch *Betula* and willow *Salix* which had seemed dead have been returning to leaf in recent years, and emergent vegetation is expanding. In April 2020, there were also reports that beavers had begun to repair the Dubh Loch dam; ongoing disturbances at different scales, and cycles of occupation, abandonment and reoccupation are what make beaver-created wetlands unique.

Aerial view of the Dubh Loch, Knapdale, in (a) 2008 pre-beaver, (b) 2015 with extensive inundated areas, and (c) 2018 showing the development of the beaver meadow. The pontoon at the top of pictures (b) and (c) was built in 2013 by Forestry and Land Scotland to cater for increasing visitor numbers. Google Earth (a); Alan Law (b and c)

Left: Dubh Loch dam in May 2014, 4.5 years after construction: dams age quickly and become leaky without maintenance and new material. Top right: patchiness in emergent plant stands (Soft Rush *Juncus effusus*, Bottle Sedge *Carex rostrata* and Branched Bur-reed *Sparganium erectum*) amid fallen and windblown trees (May 2013). Bottom right: dense beds of Broad-leaved Pondweed *Potamogeton natans* and White Water-lily established in the fourth season after damming in former birch woodland (May 2013). Nigel Willby

for some waders and waterbirds. In Finland, Teal *Anas crecca* produce larger broods on beaver ponds (Nummi *et al.* 2018), while Green Sandpipers *Tringa ochropus* were almost six times more abundant after sites were flooded by beavers (Nummi & Holopainen 2014). Bats, too, utilise beaver ponds widely, attracted by the abundance of emerging invertebrates (Ciechanowski *et al.* 2011). A combination of snow tracking and camera trapping in Finland allowed Nummi *et al.* (2019) to show that mammal richness was 83% higher in beaver-created wetlands than in non-beaver wetlands, with Moose *Alces alces*, Otter *Lutra lutra* and Pine Marten *Martes martes* all benefiting strongly. Although little research has been conducted to date, the expectation from reviewing the evidence (Stringer & Gaywood 2016) is that beaver ponds in Britain will provide new and important habitat for vertebrates of conservation importance such as Otter, Water Vole *Arvicola amphibius*, Daubenton's Bat *Myotis daubentonii* and Great Crested Newt *Triturus cristatus*. Work is now required to validate these expectations.

Beyond the water's edge: riparian woodland

Over millions of years of co-evolution, trees have adapted to the pressure of grazing herbivores. In response to felling by beavers, trees such as willow and Hazel *Corylus avellana* readily sprout new shoots from cut stumps in a coppice-like response, which allows the tree to regenerate naturally. Beavers share riparian woodlands with other large, herbivorous mammals known also to alter forests – deer. Deer often browse small saplings before they can reach maturity or strip the bark on those that do. In Scotland, recent evidence suggests that deer are threatening forest regeneration, with a third of woodlands now deemed in 'poor condition' owing to deer impacts (Burton *et al.* 2018). Initial findings from the SBT documented heavy deer browsing on resprouted beaver-cut stems at Knapdale (Iason *et al.* 2014). Twenty riparian-woodland beaver sites are being monitored by the University of Stirling in Tayside and Knapdale as part of a research project on interactions between beavers and deer. This work will reveal the short-term and long-term outcomes of these interactions and their potential cascading, ecosystem-level consequences for Britain's woodlands. Final results are expected in 2022.

As well as influencing forest regeneration, beaver activity also alters the composition of riparian vegetation. Beavers are selective, often preferring willows and Aspen *Populus tremula* while avoiding Black Alder *Alnus glutinosa*, and generally choosing stems of 2–8cm in diameter (Haarberg & Rosell 2006). Their diet, however, reflects the availability and diversity of species in the local habitat, which can be highly site-specific. Results from the SBT showed that beavers fed on a total of six tree species, including large quantities of Downy Birch *Betula pubescens*, but that willows and Rowan *Sorbus aucuparia* were strongly favoured (Iason *et al.* 2014). Foraging intensity also varies within the riparian zone, depending on how stems of the preferred size and species are distributed. Beavers tend to take more numerous, smaller stems closer to the water and fewer, larger stems as distance from the water increases (Haarberg & Rosell 2006).

The active selection of trees of specific species and sizes, and at particular distances from water, can drive change over larger scales. Short-term studies in Norway suggested that beaver activity can result in diversification of woodland into mixed species, ages, heights and diameters at various distances from the water's edge (Haarberg & Rosell 2006). On the other hand, a longer-term investigation in Russia that monitored beaver foraging and woodland composition over 50 years revealed a complete shift in forest composition towards a more homogenous woodland, with an increase in the abundance of trees at the low end of beaver preference (Goryainova *et al.* 2014). Ultimately, the foraging preferences of beavers, possibly reinforced by other herbivores, could potentially transform some riparian woodlands.

Beavers also raise some challenges for woodland conservation that should not be overlooked. Knapdale beavers, for example, have developed a taste for Hazel, the key component of Atlantic hazelwood which also supports an internationally important oceanic-lichen community. Furthermore, the beavers' well-known penchant for Aspen may not help some rarer flies, including the Aspen Hoverfly *Hammerschmidtia ferruginea*, that specialise on dead mature Aspen. Such challenges are not, however, insurmountable and, ironically, beavers have served to raise the profile of these habitats and their biota, along with the need to protect and restore them (Stringer & Gaywood 2016).

The future

Beavers are the only native mammal reintroduced to Britain in modern times. This represents a brave step which provokes contrasting emotions, but one that clearly has much to offer for freshwater and riparian ecosystems. We conclude by considering some future perspectives and needs.

Expanding the evidence base

Beavers are part of a toolbox of measures for managing or restoring wetlands. Like any tool, they are better for some jobs than for others and are most suitable when outcomes can be flexible and focused on processes, rather than being

When foraging farther from water, beavers will typically harvest fewer, larger tree stems. Nature Picture Library/Alamy Stock Photo

A beaver-cut willow stem with newly sprouted regenerative leafy shoots in Tayside. Kelsey Wilson

highly prescribed. We now have a good general understanding of beavers' effects on some biota through case studies, but the transferability of these to a wider range of contexts is only now starting to become clear as beaver trials around Britain report their findings. Adopting some basic monitoring standards and applying these over the large number of new or recent small-scale trials would help to build a coherent evidence base across a wide range of land uses and types. Similarly, there is scope to widen the range of taxa studied, especially vertebrates. Ongoing PhD projects at Southampton and Exeter Universities will help to fill the gap in relation to the responses of fish to beaver dams in Britain, and work has recently begun at University College London to measure bird responses to habitat-engineering by beavers.

Demonstrating multiple benefits

We have intentionally focused here on freshwater biodiversity, but research at Stirling and Exeter Universities, in addition to reviews commissioned and run by Scottish Natural Heritage (SNH) (Gaywood 2015; Stringer & Gaywood 2016), increasingly demonstrate the multiple environmental benefits from habitat-engineering by beavers. These extend to flow attenuation and improved downstream water quality due to fine-sediment and nutrient storage (Law *et al.* 2016; Puttock *et al.* 2017), indicating clear potential for beavers to contribute to natural flood management and reduction of diffuse pollution. Mitigation by beavers of drought impacts is attracting increasing attention in the USA and may well prove to be a benefit of increased relevance in the UK. The potential positive socio-economic role of beavers in contributing to cultural and other ecosystem services has also been highlighted (Gaywood 2015). Demonstrating the wider environmental benefits of beavers beyond simply biodiversity gain, important though that is, will make the case for their reintroduction more persuasive.

Long-term studies

Our current understanding of beavers in Britain is inevitably limited, and based largely on short-term projects or extrapolated from mainland European and North American studies. Where they are established, however, beavers are well known to have cycles of occupation, abandonment and reoccupation that may span a period ranging from a few years to many decades. Time will tell how these cycles apply when British beaver populations are expanding and where animals face strong gradients in habitat quality and territory connectivity, which may regulate their dispersal within and beyond their present distribution. As beaver populations expand, modelling studies that link population dynamics and habitat characteristics over large scales will be increasingly valuable as a means of predicting the effects of beavers and identifying where management may be needed (Gaywood 2015).

Resolving conflicts

In sensitive locations, such as drainage or transport infrastructure, beavers can have disruptive effects and will require management, as they do elsewhere in Europe and North America. Under the present circumstances, conflicts with agriculture are also likely to need managing, especially where there is damming, burrowing and risk of embankment failure in lowland areas. There are several decades or more of experience with such matters in other European countries from which we can continue to learn. In Scotland, SNH, in consultation with a range of stakeholder organisations, has developed a management framework for beavers centred on the use of approved practical mitigations. The status quo, however, is changing. In England, for instance, the Environmental Land Management Scheme will soon replace current agri-environment schemes as the basis for payments to farmers for delivering public goods. This may increase willingness to accommodate the consequences of beavers in some areas, given suitable rewards. Justifying these rewards will require evidence of ecological and other benefits, but beavers should not disappoint.

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References

Brazier, R. E., *et al.* 2020. River Otter Beaver Trial: Science and Evidence Report. https://bit.ly/2ByMAll

Burton, V., *et al.* 2018. Green gold to wild woodlands: understanding stakeholder visions for woodland expansion in Scotland. *Landscape Ecology* 34: 1–21.

Campbell-Palmer, R., Puttock, A., Graham, H., Wilson, K. A., Schwab, G., Gaywood, M. J., & Brazier, R. E. 2018. Survey of the Tayside area beaver population 2017–2018. Scottish Natural Heritage. Commissioned Report No. 1013.

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(4): 737–747.

Dalbeck, L., Hatchel, M., & Campbell-Palmer, R. 2020. A review of the influence of beaver *Castor fiber* on amphibian assemblages in the floodplains of European temperate streams and rivers. *Herpetological Journal* 30: 135–146.

France, R. L. 1997. The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. *Canadian Journal of Zoology* 75(7): 1009–1013.

Gaywood, M. J. (ed.). 2015. *Beavers in Scotland – A report to the Scottish Government*. Scottish Natural Heritage, Inverness. 204pp.

Gaywood, M. J., Batty, D., & Galbraith, C. 2008. Reintroducing the European Beaver in Britain. *British Wildlife* 19: 381–391.

Goryainova, Z., Katsman, E., Zavyalov, N., Khlyap, L., & Petrosyan, V. 2014. Evaluation of tree and shrub resources of the Eurasian beaver (*Castor fiber* L.) and changes in beaver foraging strategy after resources depletion. *Russian Journal of Biological Invasions* 5(4): 242–254.

Gurnell, A. M. 1998. The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography* 22(2): 167–189.

Haarberg, O., & Rosell, F. 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. *Journal of Zoology* 270(2): 201–208.

Hood, G. A., & Larson, D. G. 2015. Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology* 60(1): 198–208.

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

Jones, S., Gow, D., Lloyd Jones., A., & Campbell-Palmer, R. 2013. The battle for British beavers. *British Wildlife* 24: 381–392.

Kemp, P. S., Worthington, T. A., Langford, T. E., Tree, A. R., & Gaywood, M. J. 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish and Fisheries* 13(2): 158–181.

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

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

Law, A., McLean, F., & Willby, N. J. 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. *Freshwater Biology* 61(4): 486–499.

Law, A., Levanoni, O., Foster, G., Ecke, F., & Willby, N. J. 2019. Are beavers a solution to the freshwater biodiversity crisis? *Diversity and Distributions* 25(11): 1763–1772.

Malison, R. L., & Halley, D. J. 2020. Ecology and movement of juvenile salmonids in beaver-influenced and beaver-free tributaries in the Trøndelag province of Norway. *Ecology of Freshwater Fish* (in press). DOI: 10.1111/eff.12539

Nummi, P., & Holopainen, S. 2014. Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24(5): 623–633.

Nummi, P., Suontakanen, E., Holopainen, S., & Väänänen, V. 2018. The effect of beaver facilitation on Common Teal: pairs and broods respond differently at the patch and landscape scales. *Ibis* 161(2): 301–309.

Nummi, P., Liao, W. F., Huet, O., Scarpulla, E., & Sundell, J. 2019. The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Global Ecology & Conservation* 20: e00701.

Osipov, V., Bashinskiy, I., & Podshivalina, V. 2018. Influence of the activity of the Eurasian beaver *Castor fiber* (Castoridae, Mammalia) on the ecosystem biodiversity of small rivers in the forest–steppe zone. *Biology Bulletin* 45(10): 1139–1148.

Puttock, A., Graham, H. A., Cunliffe, A. M., Elliott, M., & Brazier, R. E. 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Science of the Total Environment* 576: 430–443.

Stringer, A. P., & Gaywood, M. J. 2016. The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland. *Mammal Review* 46(4): 270–283.

Wathen, G., Allgeier, J. E., Bouwes, N., Pollock, M. M., Schindler, D. E., & Jordan, C. E. 2019. Beaver activity increases habitat complexity and spatial partitioning by steelhead trout. *Canadian Journal of Fisheries and Aquatic Sciences* 76(7): 1086–1095.

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.

Willby, N. J., Law, A., Levanoni, O., Foster, G., & Ecke, F. 2018. Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373(1761): article no 2017.0444. https://doi.org/10.1098/rstb.2017.0444

Kelsey Wilson, Alan Law and **Nigel Willby** are all based at the University of Stirling. Kelsey is a second-year PhD student working on interactions between beavers and deer, with an MSci based on beaver research in Knapdale and Tayside. Alan is a lecturer working on freshwater ecosystems, with a PhD on the ecological effects of beavers. Nigel is a Professor of Freshwater Science and since 2003 has run a research programme on the ecological effects of beavers. **Martin Gaywood** is Species Projects Manager at SNH and has worked on beaver reintroduction since 2000. **Paul Ramsay** has hosted beavers (and researchers) on his estate since 2002 and documented their effects.