Using ecosystem engineers as tools in habitat restoration and rewilding: beaver and wetlands

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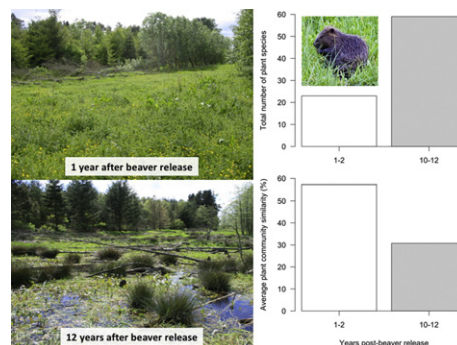[b] Scottish Natural Heritage, Great Glen House, Inverness IV3 9NW, Scotland, UK
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HIGHLIGHTS

- Restoration attempts often fail, but may benefit from utilising ecosystem engineers.
- Impacts of beaver released onto drained pasture were studied for 12 years.
- Beaver increased habitat heterogeneity and plant richness at plot and site scales.
- Ecosystem engineers can contribute significantly to meeting common restoration goals.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Potential for habitat restoration is increasingly used as an argument for reintroducing ecosystem engineers. Beaver have well known effects on hydromorphology through dam construction, but their scope to restore wetland biodiversity in areas degraded by agriculture is largely inferred. Our study presents the first formal monitoring of a planned beaver-assisted restoration, focussing on changes in vegetation over 12 years within an agriculturally-degraded fen following beaver release, based on repeated sampling of fixed plots. Effects are compared to ungrazed exclosures which allowed the wider influence of waterlogging to be separated from disturbance through tree felling and herbivory. After 12 years of beaver presence mean plant species richness had increased on average by 46% per plot, whilst the cumulative number of species recorded increased on average by 148%. Heterogeneity, measured by dissimilarity of plot composition, increased on average by 71%. Plants associated with high moisture and light conditions increased significantly in coverage, whereas species indicative of high nitrogen decreased. Areas exposed to both grazing and waterlogging generally showed the most pronounced change in composition, with effects of grazing seemingly additive, but secondary, to those of waterlogging.

Our study illustrates that a well-known ecosystem engineer, the beaver, can with time transform agricultural land into a comparatively species-rich and heterogeneous wetland environment, thus meeting common restoration objectives. This offers a passive but innovative solution to the problems of wetland habitat loss that complements the value of beavers for water or sediment storage and flow

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attenuation. The role of larger herbivores has been significantly overlooked in our understanding of freshwater ecosystem function; the use of such species may yet emerge as the missing ingredient in successful restoration.

1. Introduction

Agricultural activity has impacted most natural ecosystems, often at the expense of their biological and physical diversity (Foley et al., 2005; Strayer and Dudgeon, 2010). Protecting surviving examples of rare or threatened ecosystems is vital, but re-creation or restoration of degraded systems may also boost resilience and further enhance ecosystem functioning (Naeem, 2006). Freshwaters are inextricably linked to the most fundamental aspects of human life (Strayer and Dudgeon, 2010), yet are often overexploited, polluted, physically modified, invaded or otherwise degraded (Dudgeon et al., 2006), with >50% of wetland area destroyed during the 20th century (Millennium Ecosystem Assessment, 2005). Furthermore, freshwaters, despite covering <1% of Earth's surface, support disproportionately high biodiversity, including around 12% of the world's known animal species (Collen et al., 2014; Gleick, 1998). Additionally, these systems can act as carbon sinks (Kayranli et al., 2010), or, by enhancing storage and slowing release of water, can both attenuate flooding and alleviate water shortages (Burchsted et al., 2014). It is recognised that freshwaters can be at least partially restored through human intervention, for example, by re-meandering or adding large woody material to rivers (Palmer et al., 2014), creating ponds (Williams et al., 2008), raising the water table on peatlands by ditch blocking (González and Rochefort, 2014), reducing nutrient pressures through point source control (Phillips et al., 2005), restoring riparian buffer zones to reduce diffuse nutrient loading (Krause et al., 2008) or manipulating trophic cascades in lakes (Jeppesen et al., 2012). However, despite a wealth of case studies and practical expertise, efforts to return freshwater systems to an undisturbed state are frequently frustrated by inadequate knowledge of historical reference conditions, a lack of biodiversity response, unrealistic goals and confounding stressors (Moss, 2015; Palmer et al., 2014). Consequently, restoration projects often fail to meet expectations, in-spite of the considerable resources allocated to their planning, execution and monitoring.

A complementary option for restoring ecologically degraded systems is to re-establish species that are noted for their ecosystem engineering activities (Nienhuis et al., 2002; Pollock et al., 2014), and which were most likely a key element of undisturbed reference conditions, but whose populations have been depleted through human activity (e.g. hunting or habitat loss). An obvious candidate for restoring wetlands is the beaver, widely regarded as a classic ecosystem engineer (Jones et al., 1994) due to their habit of constructing dams along small water courses (Hartman and Tornlov, 2006), and for selectively foraging trees (Haarberg and Rosell, 2006; Raffel et al., 2009) and herbaceous plants (Law et al., 2014). Despite being critically reduced or hunted to extinction populations of both North American (*Castor canadensis* Kuhl) and Eurasian (*Castor fiber* L.) beaver have recovered partly following legal protection in the early 20th century (Halley and Rosell, 2002), coupled with public anti-trapping sentiment and decreased demand for pelts (Müller-Schwarze and Sun, 2003). Numerous reintroductions, other types of conservation translocation and introductions, followed by natural dispersal, have greatly aided this recovery. The main stimuli for recent reintroductions have been a public and associated political desire to restore a species extirpated by humans coupled with the capacity of beaver to restore ecosystem function, habitat dynamics and heterogeneity (Halley and Rosell, 2002). There is thus a rapidly developing interest in the use of beaver as restoration agents in both dryland and temperate environments (Gibson et al., 2015; Pollock et al., 2014),

with beaver reintroductions increasingly being regarded as an integral component of the wider restoration of river corridors (Burchsted et al., 2014). Moreover, in parallel, several recent reviews have called for improved long-term monitoring of experimental 'rewilding' projects more generally, to better understand and quantify the consequences of novel reintroductions and to pre-empt potential human-wildlife conflicts (Lorimer et al., 2015; Svenning et al., 2015).

Beaver alter their habitat in various ways, including grazing and tree felling, but most fundamentally via construction of dams. These are constructed from felled wood, stones and mud placed perpendicular to water flow, thereby raising and stabilising water levels, reducing exposure to terrestrial predators and increasing access to resources in flooded areas (Rosell et al., 2005). By transforming erosional streams into depositional pond environments and raising the adjacent water table beaver dams have pronounced effects on both aquatic and terrestrial biota and their trophic interactions, as well as to hydrology and water biogeochemistry (Correll et al., 2000). Associated changes in biodiversity have been demonstrated for plants, invertebrates, amphibians, fish, mammals and birds (Cunningham et al., 2007; McDowell and Naiman, 1986; Nummi and Holopainen, 2014; Schlosser and Kallemeyn, 2000; Stringer and Gaywood, 2016; Wright et al., 2002).

Effects of beaver on the local environment (see Rosell et al. (2005) for a review) should extend to both natural and human-dominated landscapes (Hood and Larson, 2014) and it is perhaps understandable that the major focus in restoration-oriented studies has been on their hydrological and geomorphic effects, with ecological benefits usually assumed rather than evidenced. However, biodiversity response is a key indicator of restoration effectiveness. The relative importance of different beaver activities (e.g. tree felling, grazing, dam building, canal digging) in wetland restoration is also unclear, constraining efforts to emulate effects through direct intervention, or to forecast ecological trajectories and beneficiaries of beaver-aided restoration. This omission reflects the difficulties in predicting long-term territory occupancy by beaver, collecting suitable pre-settlement baseline data and experimentally controlling foraging. Our study offers an in-depth perspective of the ecological effects of dam building, felling and grazing by beaver introduced explicitly for restoration purposes, based on long-term monitoring. We focus on changes in vegetation and ask specifically; i) how plant species richness and composition is modified by direct beaver-induced disturbance or indirectly through water level rise, and ii) if beaver are a suitable tool for restoring agriculturally-degraded wetlands.

2. Material and methods

2.1. Site and beaver stocking

The study took place on a 525 ha private estate, situated near Blairgowrie in eastern Scotland, (56°37′32.81″N, 3°13′36.72″W), lying at an elevation of 220 m. The area receives approximately 820 mm of rain annually, with a mean annual temperature of 8.4 °C (Meteorological Office UK, 2015). The study site comprised an enclosed 13 ha area of grassland plus stands of small deciduous trees, predominantly willow (*Salix* L. spp.), alder (*Alnus* Mill. spp.) and a limited component of aspen (*Populus tremula* L.), that were planted in 1993 (Fig. 1a). The study area occupies a neutral valley fen that was drained in the 1800s to create pasture for livestock. A spring-fed drainage ditch of depth 0.1–0.3 m, bisects the site running from east to west and is fed by several peripheral drains.

Fig. 1. An overview of the study site (a) – aerial photography from August 2006 ("Google Maps," 2006), (b) October 2012 ("Bing Maps," 2012) with the white box indicating the area covered in image (c) (drone image flown June 2015). The drone image highlights the reduction in tree cover and increased standing water area. Solid white lines indicate dams (with their identity number); dashed white lines indicate beaver-created canals. Exclosures are represented by red boxes (not drawn to scale) with text representing grazing treatment; PU = permanently ungrazed and IU = initially ungrazed.

A pair of Eurasian beaver were released in to the study area in summer 2002 as part of a demonstration project to assess their wetland restoration potential. The male died in December 2003 and was replaced in November 2004 with successful breeding first occurring in 2006. During 2006–7 and on occasions thereafter some animals evaded the enclosing fence and dispersed within the wider estate but from 2007 onwards at least four beaver were found annually within the main study area. Effects of habitat engineering by these beaver on flow, water chemistry and aquatic invertebrates are covered in Law et al. (2016).

2.2. Methods

Vegetation surveys were carried out in August 2003, 2004, 2012 and 2014 using fixed plots of 1 m × 1 m. To control for the effects of beaver grazing, three large exclosures, each of 100 m², and situated 50–100 m apart, were erected in March 2003 (Fig. 1c). These were sited in areas suitable for use by beaver, but the vegetation enclosed was completely protected from beaver herbivory and showed no evidence of disturbance by beaver when exclosures were first established. Exclosures were constructed from Rylock-type stock fencing 0.9 m high anchored into the substrate by metal rods and stapled to 2 m long larch posts.

The fence height and mesh size allowed continued access by herbivores such as roe deer, rabbits and small rodents. Areas within exclosures are referred to as 'ungrazed' and areas outwith exclosures as 'grazed' in the context of beaver. Grazed areas could also be affected by additional forms of disturbance by beaver, for example directly by trampling or canal-digging, and indirectly by altered light or nutrient availability. In grazed treatments 8 plots were assigned to each of the four outer edges of each exclosure (Fig. 1c) (32 plots surrounding each exclosure). A further 32 plots were established within each exclosure giving a total of 192 plots surveyed per year. Plots were located outwith the immediate perimeter (1 m buffer) of each exclosure to avoid possible trampling effects associated with surveys or exclosure construction. In each plot the coverage (%) of all plant species was recorded by two surveyors to the nearest 5%. Direct measurements of soil moisture, using a Delta-T soil moisture meter with SM150 probe attached, were initiated in 2008 when the extent of open water habitat in summer was still limited and similar to that at the outset of the study. Over the study period the years 2004, 2008 and 2012 were among the 5 wettest growing seasons (April to August) since weather data recording began in 1957, whilst 2003, 2006 and 2013 received only 60–75% of the long term average growing season rainfall (Meteorological Office UK, 2015). There was a

slight positive but non-significant trend ($r^2 = 0.017$; $p = 0.68$) in growing season precipitation over the period 2002–2014.

Exclosures 1 and 2 did not remain beaver-proof throughout the study due to felled trees collapsing on the fencing in 2006 allowing beaver to access the exclosures before they could be repaired; only exclosure 3 remained intact and beaver-proof throughout the study. Rather than discard the data from exclosures 1 and 2 we dismantled these two exclosures and monitored this unplanned change in treatment to corroborate the other treatment effects. The study was thus divided into two time periods; 1–2 years and 10–12 years post beaver release, each with permanently grazed, initially ungrazed (exclosures 1 and 2) and permanently ungrazed (exclosure 3) treatments. Each time period also encompassed an abnormally wet and dry year. We pooled years in this way for clarity of presentation rather than treating them individually and because trial analyses indicated strong contrasts between periods but only minor differences within them (Supplementary Material, Fig. S1). The initial time period, though not quite a strict baseline, refers to data from a time period with low potential for impact by beavers due to the short duration of occupancy and the low number of animals present at that time (Willby et al., 2014). The areas first sampled in 2003 were also at this time qualitatively very similar to other parts of the study area in which beaver were inactive and to comparable areas of the wider estate from which beavers were absent.

2.3. Exploratory and statistical analyses

Plant species richness was expressed as the number of plant species per plot. For each grazing treatment the effect of time since release (categorical data) on richness was tested using a generalised mixed effects model with Poisson family link function. No patterns were detected when model Pearson residuals were extracted and plotted against fitted values. Sample-based accumulation curves (Colwell et al., 2004) were generated to compare species accumulation rates in different treatments per time period, with total species estimated using the chao1 function (Vavrek, 2011).

Unconstrained ordination was conducted using non-metric multidimensional scaling (NMDS) on a Bray-Curtis dissimilarity index (BCI) generated from a log-transformed species cover × sample matrix for each grazing treatment. Using the function 'adonis' within the vegan library (Oksanen et al., 2017) a permutational multivariate analysis of variance was used to test for differences in species composition between time periods, based on a BCI matrix and 999 permutations. Ellipses (defined by the 95% confidence interval) were fitted around centroids based on plot dissimilarity scores derived from the NMDS to contrast species composition and fine scale heterogeneity per time period. The size of ellipse reflects species turnover between plots within each time period. The homogeneity of dispersion of plots for each time period was calculated using the betadisper R function and tested using the anova function (Oksanen et al., 2017). Species indicative of each time period per treatment were derived using the Indval R function (Roberts, 2016) which identifies 'indicator' species from their fidelity for, and occupancy of a particular group. In this case significant indicator species were those indicative of either the 1–2 year or 10–12 year time periods.

To interpret potential environmental drivers of change in vegetation the species composition was synthesised into a cover-weighted mean Ellenberg indicator score per plot for moisture, light and nitrogen using the Ellenberg scores for British plants (Hill et al., 1999). Increasing plot scores for moisture, light and nitrogen imply a shift towards a moisture tolerant, light demanding or nitrophilic flora respectively. Derived Ellenberg values or model residuals did not conform to parametric assumptions through standard transformations (log10, arcsine, logit, square-route), therefore potential differences in derived Ellenberg values between time periods were tested using the Kruskal-Wallis one-way analysis of variance test.

All statistical analyses and graphics were produced using RStudio version 1.0.136 (http://www.rstudio.com/), with the additional packages; plyr (Wickham, 2011), reshape2 (Wickham, 2007), AER (Kleiber and Zeileis, 2008), fossil (Vavrek, 2011), vegan (Oksanen et al., 2017), lme4 (Bates et al., 2015) and labdsv (Roberts, 2016).

3. Results

3.1. Environmental modifications

Beaver-induced changes were exemplified by an increase in open water and complete or partial loss of tree canopy in some parts of the study area (Figs. 1, 2). Beaver constructed a 3 m long dam (dam 1) at the eastern edge of the site in 2002 raising the stream level by c. 0.7 m. Prior to first breeding in 2006 the overall extent of habitat modification was relatively modest (Fig. 1a) and centred mostly on tree felling. A further four major dams were constructed over the 12-year study period upstream of this first dam (Fig. 1c), ranging from 0.7–110 m long and 0.4–1 m high, with a total length of dam of 195 m. These dams impounded a total area of 0.4 ha of open water during wet months, as well as waterlogging formerly well drained areas nearby. In addition beaver excavated 500 m of canal.

Average soil moisture within the three exclosures (or in two cases former exclosures) increased from 34% in 2008 to 93% in 2012 and 70% in 2014. Similar moisture levels were recorded outwith exclosures; 42%, 91% and 75% in 2008, 2012 and 2014 respectively. Differences in soil moisture within versus outwith exclosures were non-significant in all years of measurement (Kruskal Wallis test; $p < 0.4$) Potential effects

Fig. 2. An overview of the study site 1 year post release (spring 2003) (a) and 12 years post release (early summer 2014) (b). Photos were taken facing looking WSW from mid way along dam 2.

of increased soil moisture caused by beaver dams therefore applied to all areas regardless of their accessibility to beaver.

3.2. Species richness

After 1–2 years of beaver presence a low and similar number of species per plot were found in all grazing treatments (Fig. 3). However, 10–12 years after beaver release all grazing treatments exhibited significantly greater species richness, increasing by an overall average of 46% (59%, 33% and 45% for permanently ungrazed, initially ungrazed and permanently grazed respectively). The observed species richness increase was similar across treatments and there is therefore no indication of grazing or waterlogging having a more pronounced effect on alpha diversity.

From 2003 to 2014 192 fixed plots were surveyed in each of four years (total = 768 plots) in which a total of 64 herbaceous species were recorded. In years 1–2 a total of 23 species were recorded across all plots compared to 59 in years 10–12. When species richness is viewed in terms of the cumulative number of species, treatment effects also become apparent. Similar to mean species richness (Fig. 3), the cumulative species richness was greater 10–12 years post beaver release for all treatments (Fig. 4), indicating the site-wide influence of waterlogging due to dam construction. However, those plots additionally exposed to grazing for a short and long period (initially ungrazed and permanently grazed treatments (Fig. 4B and C)) had a greater species accumulation rate than plots that were ungrazed (Fig. 5A). The cumulative number of species per treatment increased by 109% (from 11 to 23 species), 187% (from 15 to 43 species) and 148% (from 23 to 57 species) in permanently ungrazed, initially ungrazed and permanently grazed treatments respectively, with an overall average increase across all treatments of 148%. Most species accumulation curves reached an asymptote indicating effective and complete sampling of each time period × treatment combination. The only exception were plots that had been grazed for 12 years where doubling the number of plots sampled would have yielded an estimated additional 8 species.

3.3. Species composition and heterogeneity

After 10–12 years post beaver release the composition of vegetation in each treatment had shifted significantly (all p values <0.001) as shown by the change in the position of the centroids in Fig. 5. However, the relative dissimilarity between treatments was unchanged

after 10–12 years. The change in vegetation composition is highlighted by the identity and quantity of significant indicator species in the different time periods based on the IndVal analysis, with many more indicator species being associated with the 10–12 years post release period, including those characteristic of shallow, fertile wetlands e.g. *Juncus effusus*, *Stellaria alsine*, *Glyceria fluitans* and *Rorippa nasturtium-aquaticum*, which replace a species-poor flora dominated by *Urtica dioica* and *Holcus mollis* plus terrestrial weeds (Fig. 6, with full list for permanently and initially ungrazed in Supplementary Material Fig. S2). The use of Ellenberg indicator scores for plants underlines the type of changes in plant community composition (Fig. 7), with both moisture tolerant and light demanding species increasing significantly in cover and nitrophiles decreasing between the two survey periods regardless of treatment. These changes reflect the shift in habitat character of the study area from lightly wooded agricultural pasture to wetland, as illustrated in Figs. 1 and 2.

As well as compositional changes over time the heterogeneity of the vegetation, as reflected in the dispersion of samples from each centroid, also increased significantly (all p values <0.001) for all treatments. This is indicated in Fig. 5 by the relative size of each ellipsis. The mean dispersion distance from each centroid increased by 65%, 93% and 54% compared to 1–2 years post release levels for permanently ungrazed, initially ungrazed and permanently grazed treatments respectively, with an overall average increase in heterogeneity of 71%. This indicates a reduction in the proportion of plots with shared species, consistent with the greater cumulative number of species recorded in all treatments (Fig. 4) and the increased scatter in light and moisture Ellenberg indicator scores shown in Fig. 7, especially for grazed treatments.

4. Discussion

The quality and quantity of freshwater ecosystems is declining globally (Dudgeon et al., 2006), despite their importance to society and the disproportionately high biodiversity they support (Bunn, 2016). Methods of protection, restoration or creation often rely on long-term coordinated management and interventions which can be expensive, and have uncertain outcomes. Our study illustrates that releasing a well-known ecosystem engineer, the beaver, a largely 'passive' management approach, can transform land impacted by agricultural drainage and tree planting into a more species-rich and heterogeneous wetland environment. Whilst demonstration projects in which animals are constrained to a greater or lesser degree within sub-optimal habitat
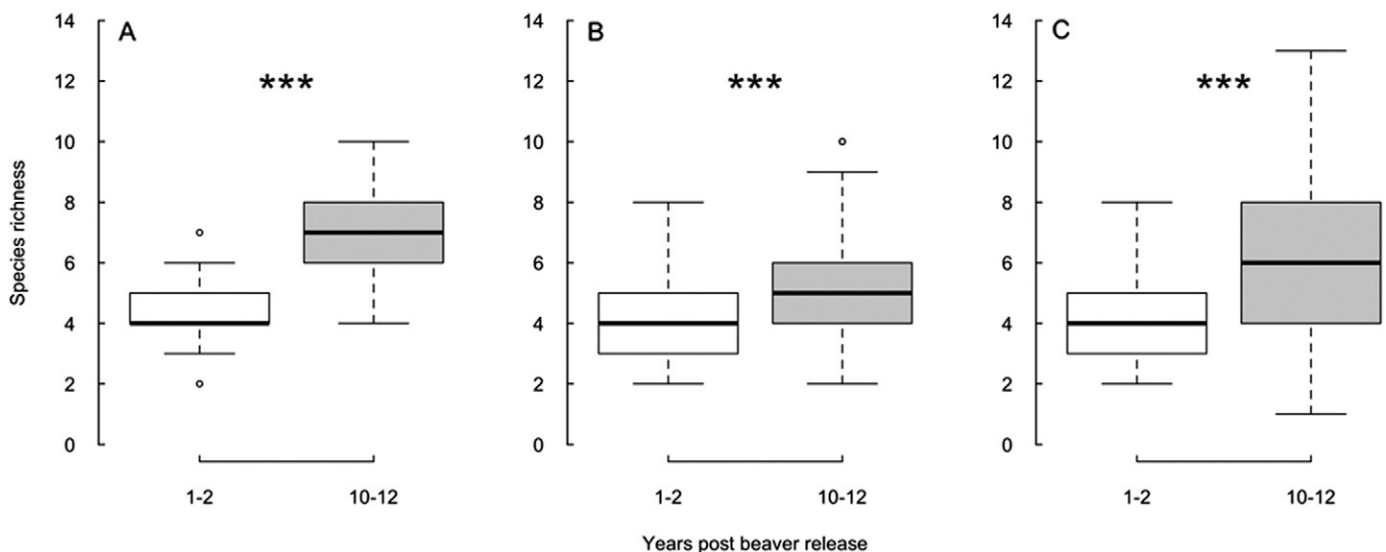

Fig. 3. Species richness for 1–2 (white boxes) and 10–12 years post beaver release (grey boxes) per grazing treatment; (A) permanently ungrazed, (B) initially ungrazed and (C) permanently grazed. ***p < 0.001.
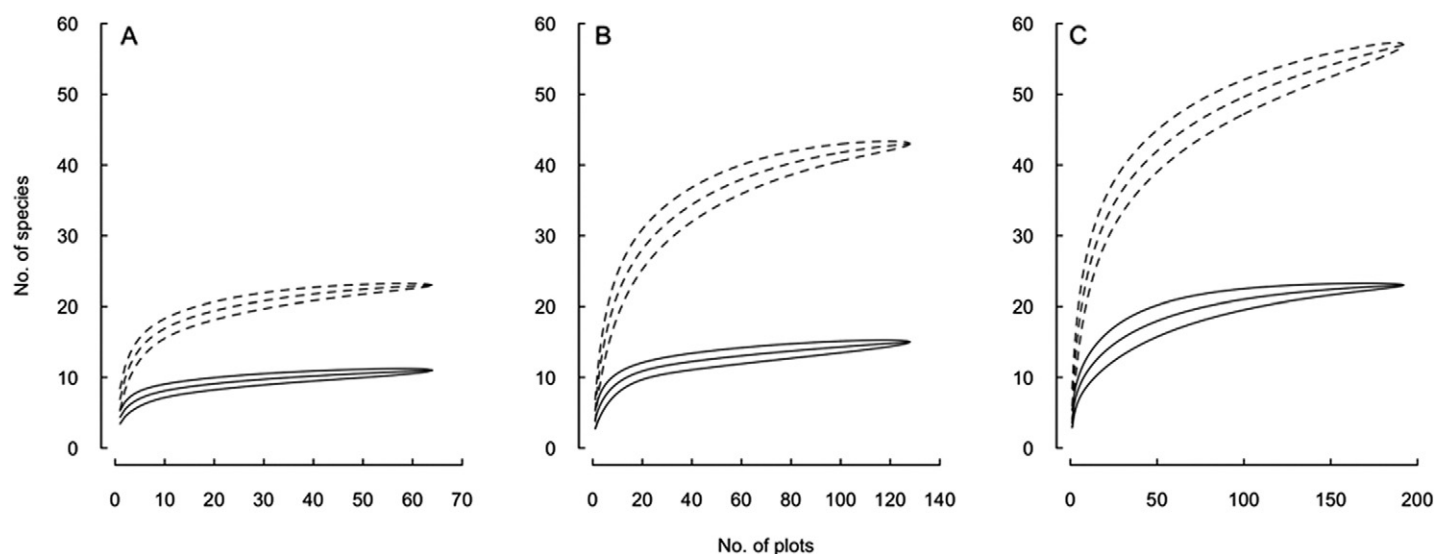
Fig. 4. Species accumulation based on the number of plots sampled for 1–2 (solid line) and 10–12 years post beaver release (dashed line) per grazing treatment; (A) permanently ungrazed, (B) initially ungrazed and (C) permanently grazed. 95% confidence intervals are shown around each treatment line.

represent a non-natural situation the habitat engineering features we observed are typical of natural conditions (Wright et al., 2002; Zavyalov, 2014), as well as being similar to other enclosed populations (Puttock et al., 2017), and can therefore be considered valuable and informative.

4.1. Beaver-induced changes to the environment, plant species richness and composition

Dam construction increased soil moisture across the study site, as evidenced from direct measurement and through change in plant composition, whilst unenclosed areas were additionally subject to grazing and other forms of direct disturbance by beavers. Consequently, beaver-created or modified wetlands have high or variable light penetration (from direct removal or flooding-induced recession of the tree canopy or taller understorey herbs) and elevated soil moisture (from dam creation) (Johnston et al., 1995; Naiman et al., 1994; Wright et al., 2002). This was reflected in the plant Ellenberg moisture and light scores (Fig. 2). The ponds behind beaver dams are often enriched in major ions and nutrients due to prolonged retention of surface runoff (Naiman et al., 1994; Puttock et al., 2017), characteristics which extended to our study site (Law et al., 2016). However, despite terrestrial areas becoming waterlogged through impoundment of the stream network, the cover of nitrophilous plants decreased throughout our study.

This may reflect a combination of increased leaching of nutrients from soil and their storage in pond sediments or aquatic vegetation (Law et al., 2016), or decreased nutrient availability through a reduction in decomposition rates in rewetted soils (Richert et al., 2000). The use of Ellenberg indicator scores appears to be a valuable tool to infer drivers of change in the absence of direct abiotic measurements (which will vary temporally and may therefore be poorly represented by discontinuous monitoring) and where plants are identified to the species level.

Mean richness per plot and cumulative richness were significantly higher after 10–12 years compared to 1–2 years post beaver release across all treatments. The increase in plot scale richness was small relative to the low initial richness of ~4 species per plot 1–2 years post release, reflecting the challenges of restoring severely degraded fens to a species rich condition in areas of intensive agriculture (Klimkowska et al., 2010). We propose that the general increase in soil wetness experienced across the study site was the primary driver of the elevated plot and site-scale richness. This was achieved through a reduction in the cover of the tall dominant understorey species *Urtica dioica* L. in permanently ungrazed plots from an average of 30% to 5%, thus permitting establishment of light-demanding herbs and grasses (Fig. 2). Plots that were grazed since the start of the study however had the greatest cumulative species richness suggesting that disturbance by grazing and waterlogging had additive effects. For both 1–2 and 10–12 years post
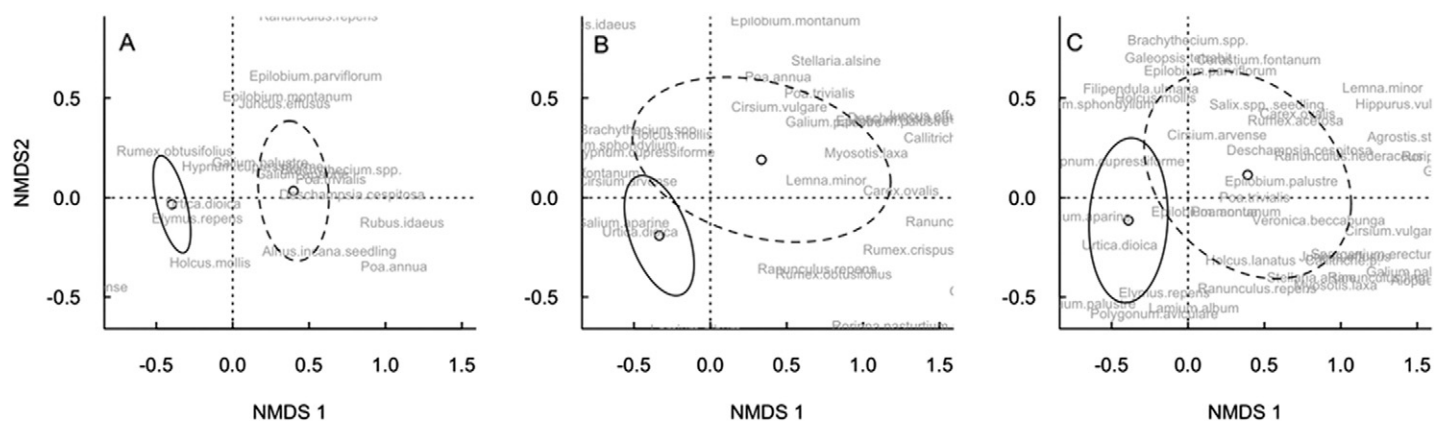

Fig. 5. Non-metric multidimensional scaling (NMDS) of log transformed plant species data displaying the composition within (A) permanently ungrazed, (B) initially ungrazed and (C) permanently grazed treatments for 1–2 (solid ellipsis) and 10–12 (dashed ellipsis) years post beaver release. Ellipses represent the standard deviation (95% CI) of plot scores, grouped by time period. Species NMDS scores are plotted in grey. All stress values <0.15.
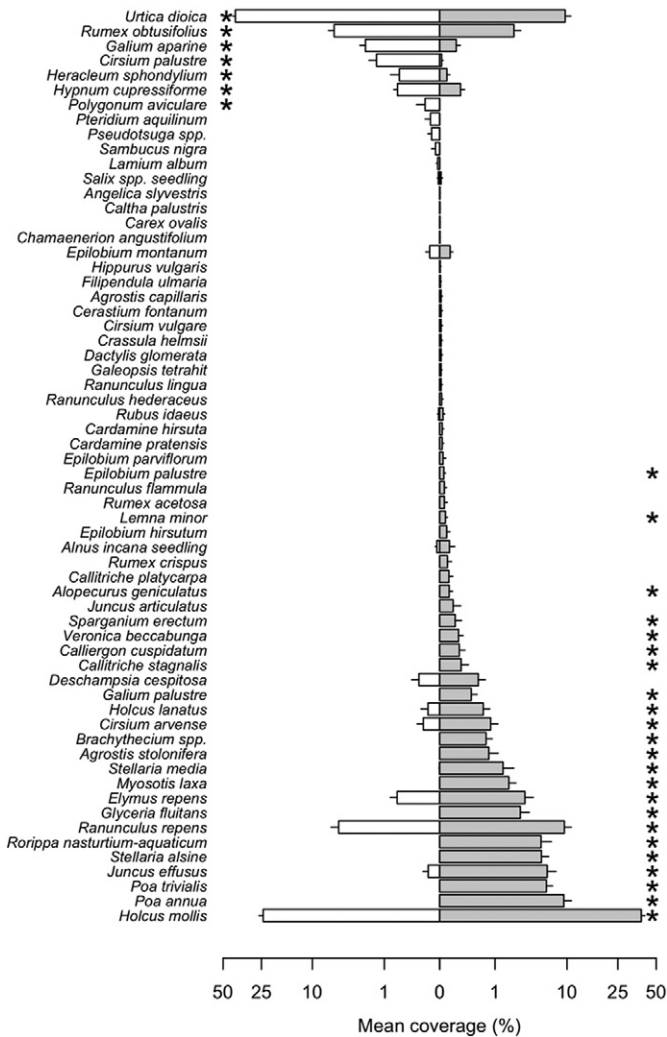
Fig. 6. The change in mean coverage (± 1 SE) of each plant species where present from 1 to 2 (white bars) and 10 to 12 (grey bars) years post beaver release for permanently grazed plots, ranked by the difference between each time period. Species that were significant indicators (*p* < 0.05) of either time period, based on IndVal scores, are indicated by asterixes.

Fig. 7. Summary of weighted Ellenberg scores based on species composition are displayed for; (a) moisture, (b) light and (c) nitrogen, for 1–2 (white boxes) and 10–12 years post beaver release (grey boxes). *p < 0.05, **p < 0.01, ***p < 0.001.

release the variance in plant composition between plots (arising from differences in richness, identity and cover of species) was greater in grazed treatments and the relative increase in either heterogeneity or cumulative richness over the study duration was strongest in the presence of grazing. Law et al. (2014) report a trebling of species richness in an established wetland after nine years of beaver activity and in the absence of hydrological changes. Changes in soil moisture (via nearby dam construction) and grazing, coupled with canal-digging and tree felling, thus created a fine-scale mosaic of patches experiencing different intensities and types of disturbance.

Overlaps occurred between plant composition in all grazing treatments indicating that disturbance by beaver increased beta diversity through recruitment of new species combined with reduced coverage, but rarely elimination of existing species (Supplementary Material Fig. S2). For example, common terrestrial taxa such as *U. dioica* and *Rumex obtusifolius* L. which are tolerant of intermittent winter flooding (Grime et al., 1988) were still present 10–12 years post release, but at lower coverage. Wetland species were, however, most strongly associated with grazed plots suggesting that some additional form of disturbance on top of waterlogging is required to accelerate the transition to a wetland flora. Beneficiaries of waterlogging combined with beaver grazing included *Myosotis laxa* Lehm., *Veronica beccabunga* L. and
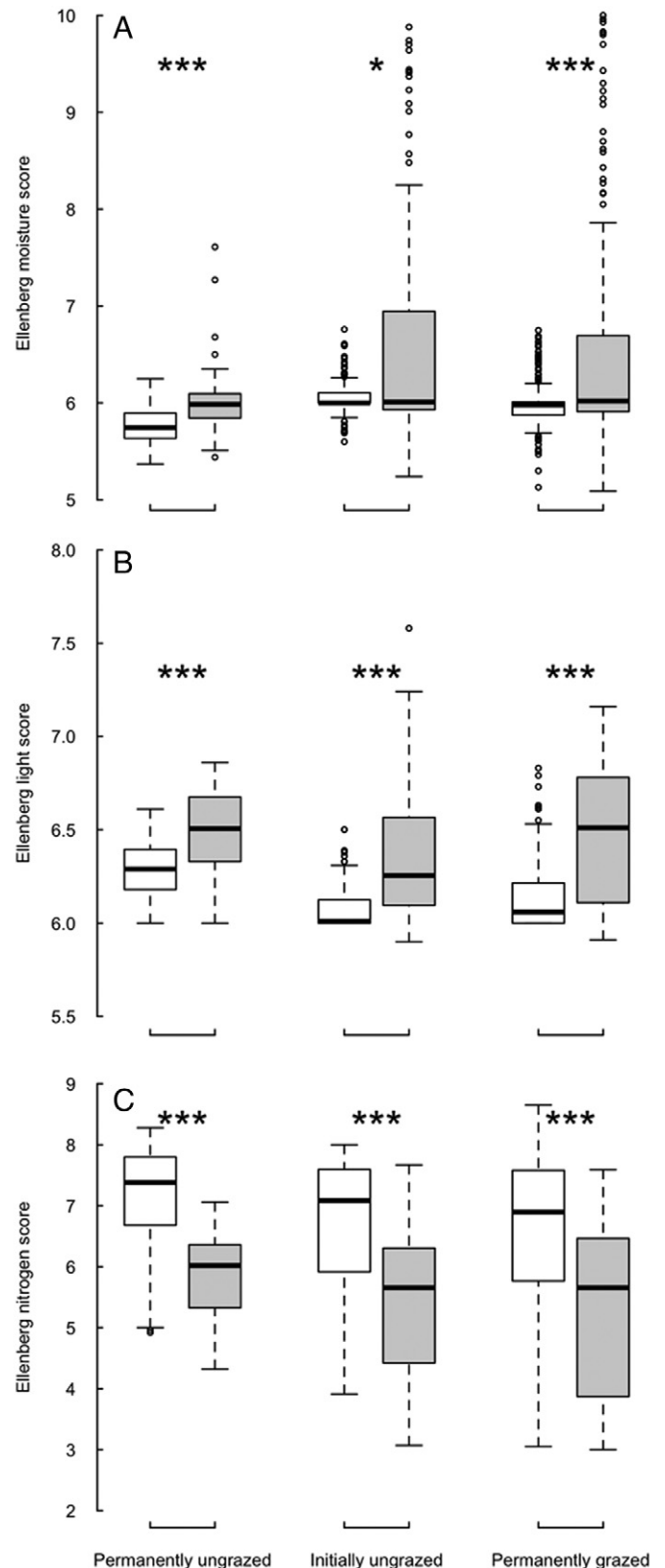
Rorippa nasturtium-aquaticum L. which are also commonly associated with fertile river and pond margins grazed by livestock (Rodwell, 2000). Grazing of wetlands by domestic livestock (Jones et al., 2011)

and beaver (Law et al., 2014) favours small ruderal species and is probably necessary to release them from dominance by larger rhizomatous species that would occur with rewetting alone, especially in more fertile environments (Timmermann et al., 2006). In our study grazing for 6–8 or 10–12 years had similar effects compared to the ungrazed treatment which suggests that beyond some minimum duration the length of grazing activity is not critical provided that rewetting has remained in place.

After 1–2 years of beaver-induced disturbance, including construction of dams (increasing soil moisture), felling of trees and grazing (altering tree abundance and light availability), ruderal, terrestrial species, such as *Galium aparine* L. and *Heracleum sphondylium* L., persisted in grazed plots. After 8–12 years of access to beavers grazed plots supported a noticeably higher cumulative species richness (Fig. 4) compared to their ungrazed counterparts (Fig. 5). This could reflect variations in the intensity of habitat engineering linked to the numbers of animals present but it also seems likely that a lag exists between beaver release and observed positive effects on vegetation which is possibly compounded in agricultural environments by elevated fertility (Lamers et al., 2014). This suggests that judgement of beaver effects is best postponed until potential colonisation lags have elapsed. Decadal scale delays in response to environmental change have been observed previously in lakes (Sand-Jensen et al., 2016), grasslands (Isbell et al., 2013) and wetlands (Moreno-Mateos et al., 2012) as a result of agricultural legacies. In a freshwater context the length of the response lag will likely depend on geographic location, connectivity to propagule sources (both in situ and external), site productivity and beaver occupation time and population density. Re-wetting as a method of restoration may provide similar results in terms of physical wetland creation, however it is the ongoing disturbance of various beaver behaviours (e.g. grazing, maintenance and construction of dams and canals, felled or fallen trees, discarded wood and water plants) that make these wetlands unique (Fig. 1c).

Changes to terrestrial, aquatic and riparian ecosystems by beaver in more natural environments are well documented, yet teasing apart the relative influence of grazing and hydrology and how these influences interact or change with time is challenging. This reflects the difficulties of predicting the location and duration of beaver territory occupancy, collecting adequate baseline data and experimentally controlling for foraging. In this respect artificially contained beaver populations within demonstration projects offer clear advantages provided animals are not at unnaturally high densities. In our study exclosures were originally intended as a strict control for beaver effects. However, they could not control for water level rise which, due to the extent of one dam (dam 2), was unexpectedly pervasive, and ultimately, in two out of three cases, also proved vulnerable to tree felling; future studies might therefore need to utilise nearby beaver-free sites to achieve strict controls which should be monitored in parallel to a study site both before and after beaver release. Nevertheless, by intensive sampling of fixed plots at high spatial resolution on multiple occasions over a decadal timescale our work offers the first detailed study of the effects of a planned beaver-assisted wetland restoration on plant richness and composition and the mechanisms that underpin this. Our findings emphasise the importance of stress from waterlogging and disturbance from grazing; we cautiously consider that the waterlogging component of beaver activity has a greater overall impact on vegetation composition and heterogeneity than grazing, but that there is an important additive effect when both occur.

4.2. Implications

After 12 years of habitat engineering by beaver the study site was almost unrecognisable from its initial state, with a mosaic of aquatic, semi-aquatic and terrestrial habitat patches having formed, evidenced by parallel changes in plot- and site-scale plant richness and composition. Not only is engineering by beaver thus beneficial to conserving

and promoting a range of freshwater biota, including plants (this study) and invertebrates (Law et al., 2016), but the increased richness and diversity in an intensively modified landscape will likely also improve ecosystem function and resilience. For example, increased biodiversity has been observed to render communities of aquatic macroinvertebrates (Menezes et al., 2010) and macrophytes (Lorenz et al., 2012) more robust to environmental change.

As part of the tool kit for restoring degraded wetlands or generating new habitats, habitat engineering by beaver is a passive method requiring little continuous management and is a potentially low-cost option. It offers an alternative for land managers and conservationists who typically have to resort to mowing or low intensity livestock grazing in the absence of large native aquatic herbivores, and management of water level regimes (Schrautzer et al., 2016). However, the effectiveness of beaver as ecosystem engineers depends on availability of small-sized palatable trees (e.g. willow, birch and aspen), and therefore indirectly the extent of livestock grazing and other land management practices (Gibson and Olden, 2014; Small et al., 2016). Potentially, depending on their legal status or proximity to superior habitat, or other sensitive features, beaver may also require enclosing (cost of fencing) or some initial basic modification to existing habitat (e.g. a small pond, tree planting) to deter escape or dispersal. Moreover, whilst an essentially passive management approach at a local scale, beaver presence is not free of cost; impacts on some aspects of the natural or human environment may be considered detrimental, requiring management or compensation, even if there are overall net benefits to biodiversity and ecosystem services (Gaywood 2015).

Any decision to formally reintroduce beaver more widely, whether for habitat restoration or other motives, that may stem from smaller scale trials, must acknowledge all stakeholders in a catchment from the outset (e.g. farmers, foresters, residents, anglers, managers of infrastructure), and recognise that beavers will increase and disperse more widely, potentially then requiring future surveillance and management of the population (Campbell-Palmer et al., 2016). Reintroduction is a significant step in terms of its requirements, e.g. advice, resources, techniques, risk assessment, monitoring and licensing etc. (IUCN/SSC, 2013), but we can learn greatly from well monitored smaller scale trials.

Our findings must be considered within the context of the type of study site and the specific objective of re-creating a wetland on agricultural land, rather than managing or enhancing an existing wetland. In our study the regional species pool was most likely diminished through a long history of agricultural land use and associated drainage, thus restricting the supply of suitable propagules from external sources (Lamers et al., 2014; Williams et al., 2008). Ancient seed banks may therefore have contributed to the current plant composition, as documented in studies of emergent plants within beaver ponds (Ray et al., 2001). This may favour the use of beaver as a tool for restoring former wetlands because gradual rewetting combined with disturbance via foraging, trampling and canal digging will favour regeneration from a relict seed bank. By contrast, introducing beaver to already species-rich, heterogeneous wetland environments may have less universally positive outcomes. Even in this study, the outcome of beaver activity likely deviates from the type of fen vegetation that existed prior to drainage (albeit centuries after extinction of native beaver). This suggests that use of beaver in modern landscapes may be more compatible with rewilding philosophy where the endpoint is fluid and unscripted and the focus is on benefits of renewed ecosystem function or processes (e.g. water storage, enhanced water quality, biodiversity support), rather than classic restoration thinking where a community converges towards a predefined target via a predictable trajectory. Expectations in areas of intensive agriculture must also be tempered by realism as positive impacts on biodiversity may take many years to develop (Klimkowska et al., 2010) and will likely depend on geographic location, topographic characteristics, connectivity to external propagule sources, site fertility and beaver density and duration of occupancy (Law et al., 2014), in

addition to the complex socio-economic considerations of cost versus benefit.

5. Conclusions

Beaver have been reintroduced or their populations reinforced in many countries for a combination of economic, ethical and ecological reasons, as well as having naturally recolonised large areas. Their potential use as agents of stream and wetland restoration is rapidly gaining traction among conservation bodies, water resource managers and private landowners as part of a shift towards landscape-scale thinking and related process-based passive management (rewilding). The potential for beaver dams to contribute to natural flood management as part of a suite of measures has already been demonstrated (Law et al., 2016; Puttock et al., 2017). However, ecological effects of beavers in 'novel' environments also need documenting if interventions are to proceed on the basis of evidence rather than trial and error. Our results show that beaver not only alter their environment at a coarse scale, but also enhance plant heterogeneity at a scale that would be too fine to replicate through human intervention. Beaver are, however, not a 'magic bullet', and their ability to restore degraded wetlands, at least in terms of their biodiversity, may not become evident for some time – a decade or more perhaps. Pre-emptive engagement to limit conflicts between beaver and stakeholders in agricultural catchments must also be seen as an integral part of any broader scale beaver-aided wetland restoration initiative, and conservation translocation guidelines need to be applied to ensure relevant biological, socio-economic and legal considerations are addressed (IUCN/SSC, 2013; National Species Reintroduction Forum, 2014).

Restored wetlands perform important functions of general societal value, such as water storage and carbon sequestration, beyond their role in biodiversity support, and should therefore command intrinsic value among a matrix of more economically productive land uses. The role of larger herbivores has been significantly overlooked in our understanding of freshwater ecosystem function (Bakker et al., 2016; Moss, 2015); the reintroduction of such species may yet prove to be the missing ingredient in successful and sustainable long-term restoration of wetland landscapes.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2017.06.173.

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