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Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams

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SUMMARY

1. Small-scale discontinuities, formed by accumulations of wood, are recognised as a key feature of functionally intact forested streams because they promote organic matter retention, increase habitat complexity and provide flow refugia. Re-establishing such features in physically degraded streams is therefore a common priority for restoration schemes. Ecosystem engineering by beavers in the form of dam building might offer a natural mechanism for restoring degraded streams. Despite an increase in beaver reintroductions globally, the ecosystem engineering concept has rarely been applied to restoring biodiversity and ecosystem function, especially within degraded freshwater systems.

2. By comparing multiple beaver-modified and unmodified sites on headwater streams draining 13 ha of pastureland in eastern Scotland, U.K., we investigated if hydromorphological changes caused by reintroduced beavers (*Castor fiber*) translate into desirable biological responses when there is a long history of physical degradation and contraction of the regional species pool due to agricultural land use.

3. Beaver modified in-stream habitat by constructing 10 dams, thus creating a series of interconnected dam pools. Organic matter retention and aquatic plant biomass increased (7 and 20 fold higher respectively) in beaver ponds relative to unmodified channels, consistent with the lower fluctuation in stream stage observed below a series of dams. Growing season concentrations of extractable P and NO₃ were on average 49% and 43% lower respectively below a series of dams than above, although colour and suspended solids concentrations increased.

4. Macroinvertebrate samples from beaver-modified habitats were less taxon rich (alpha diversity on average 27% lower) than those from unmodified stream habitat. However, due to significant compositional differences between beaver versus unmodified habitats, a composite sample from all habitats indicated increased richness at the landscape scale; gamma diversity was 28% higher on average than in the absence of beaver-modified habitat. Feeding guild composition shifted from grazer/scrapper and filter feeder dominance in unmodified habitats to shredder and collector-gatherer dominance in beaver-created habitats.

5. Dam building by beaver in degraded environments can improve physical and biological diversity when viewed at a scale encompassing both modified and unmodified habitats. By restoring ecosystem processes locally, it may also offer wider scale benefits, including greater nutrient retention and flood attenuation. These benefits should be evaluated against evidence of any negative effects on land use or fisheries.

Keywords: *Castor fiber*, diversity, habitat heterogeneity, macroinvertebrates, restoration

Introduction

Small-scale discontinuities in streams caused by the accumulation of large wood (snags, logjams, woody deb-

ris dams) are recognised as an important natural component of functionally intact forested streams (Gurnell, Piegay & Swanson, 2002). Historically, these features have often been removed to improve drainage and flood

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conveyance. Their reinstatement is therefore often prioritised when restoring physically degraded streams (Poole, 2002). Beavers (*Castor fiber* and *Castor canadensis*) have experienced a substantial global population increase over the last century aided by protection and reintroduction programmes. Beaver have been advocated as a possible option for restoring ecologically degraded systems (Nolet & Rosell, 1998; Pollock *et al.*, 2014), reflecting their potential to create and re-establish natural discontinuities and unique habitats via dam building (Naiman & Rogers, 1997). Systems that are likely to benefit include forested stream channels from first to fourth order (Harthun, 1999; Burchsted *et al.*, 2010), arid and semi-arid environments (Gibson & Olden, 2014) and wetlands (Wright, Jones & Flecker, 2002; Elmeros, Madsen & Berthelsen, 2003; Sjöberg & Ball, 2011). However, reintroducing long-extinct species such as beavers to densely populated regions is also controversial; experience suggests that this can increase human–wildlife conflict and the need for intervention (Nolet & Rosell, 1998; Siemer *et al.*, 2013).

By building dams, beaver raise and stabilise water levels, thus maintaining a submerged lodge or burrow entrance. This reduces predation risk while increasing access to inundated wooded riparian zones (Rosell *et al.*, 2005). Beaver dams dissipate stream energy and slow flow, thereby altering hydraulic connectivity and discharge (Margolis, Raesly & Shumway, 2001a; Benke & Wallace, 2003). Ultimately, they transform sections of channel from erosional to depositional environments that act as a sink for plant propagules, nutrient-rich sediment and coarse organic matter (Anderson *et al.*, 2014). Where dam integrity is maintained, the ponded area will also support extensive aquatic vegetation (Rolauffs, Hering & Lohse, 2001). Over decadal time scales, dam disintegration and pond drainage follow abandonment of a beaver territory, allowing colonisation of exposed sediments by terrestrial plants, thus forming ‘beaver meadows’ (Naiman, Johnston & Kelley, 1988). However, in more dynamic situations, where cycles of occupation by beaver are short and breaching and rebuilding of dams is common, smaller dam ponds interconnected by sections of running water will occur (Gurnell, 1998). Beaver dams therefore directly or indirectly modify various physical, hydraulic and chemical processes in streams, creating a mosaic of habitats and food resources (Hood & Larson, 2014a; Smith & Mather, 2013). This increased habitat heterogeneity generally has positive effects on a diverse range of biota including aquatic plants (McMaster & McMaster, 2001), macroinvertebrates (Margolis *et al.*, 2001a), fish (Kemp *et al.*, 2011), amphibians

(Dalbeck, Luscher & Ohlhoff, 2007) and birds (Nummi & Holopainen, 2014).

Ponds formed by beaver are an additional and novel source of habitat heterogeneity that differ from other types of ponds and may support unique biological assemblages (Rolauffs *et al.*, 2001; Willby *et al.* 2016). Beaver ponds are characterised by higher lateral connectivity than the rivers they modify, with beaver-created channels enlarging the aquatic–terrestrial interface (Hood & Larson, 2014b), and are intermittently disturbed through foraging, caching of woody material, maintenance of dams and fluctuating water levels. The associated physical structures, i.e. dams, lodges, food caches (submerged wood with higher surface areas than conventional large wood inputs) and channels, further increase habitat complexity (Clifford, Wiley & Casey, 1993; France, 1997; Hood & Larson, 2014a). The habitat-altering effects of beaver dams in natural, mostly forested environments have long been recognised (e.g. Sprules, 1941) and the resulting physicochemical changes in such streams are well studied (see reviews by Gurnell, 1998 and Rosell *et al.*, 2005). Various authors have used macroinvertebrates as indicators of the effects of this habitat engineering (e.g. Clifford *et al.*, 1993; France, 1997; Benke & Wallace, 2003; Anderson & Rosemond, 2007), reflecting ease of sampling and sensitivity of invertebrates to the changes in sediment and water velocity that accompany damming (Nummi, 1989). However, one particular question that is integral to the thinking behind the reintroduction of beavers globally, but has not been addressed in previous studies, is whether the ecosystem engineer concept (Jones, Lawton & Shachak, 1994) extends to restoring biodiversity and ecosystem function within degraded freshwater systems, especially in regions where beaver have long been absent. Streams and artificial habitats such as drainage ditches are common in anthropogenic landscapes, but mostly lack physical and biological diversity due to historical straightening, removal of blockages and encroachment by surrounding land use into the riparian zone. Flood attenuation, nutrient storage and support for biodiversity are therefore heavily compromised. Using beaver to restore habitat heterogeneity to anthropogenic landscapes without the need for physical habitat engineering by humans therefore offers multiple potential benefits. However, it will fall short of expectations if the transformation of physical habitat by beaver through ecosystem engineering is not matched biologically (Byers *et al.*, 2006; Palmer, Hondula & Koch, 2014). This concern applies where beaver have been recently reintroduced (e.g. Belgium, Bosnia and Herzegovina, Croatia,

Denmark and Serbia; Halley, Rosell & Saveljev, 2012), but especially so where beaver have not yet been fully reintroduced (e.g. Britain) and where the potential merits of ecosystem engineering versus possible impacts on land use and fisheries are strongly contested.

Our study focused on the implications of beaver reintroduction for physicochemical processes and biodiversity in small agricultural streams, an extremely common but neglected habitat within the native range of Eurasian and North American beavers. We particularly assessed the associated changes in richness, abundance, composition and feeding function of aquatic macroinvertebrates. We evaluated (i) how the presence of beaver-modified habitats affects local and landscape-scale species richness and species accumulation rates; (ii) if species turnover increases between habitats when beaver-created habitats occur in the landscape; and (iii) whether the composition of invertebrate functional feeding groups in beaver-created and unmodified habitats is consistent with differences in their physicochemical properties.

Methods

Site and habitats

The study took place on a 13 ha site within a private estate of 525 ha near Blairgowrie, in eastern Scotland (56°37'32.81"N, 3°13'36.72"W). Blairgowrie receives approximately 820 mm of rain annually, and has a mean annual temperature of 8.4 °C (Meteorological Office UK, 2013). The study site, which is situated at an elevation of 200 m, is drained by a small spring-fed stream (the Burnished Burn), 0.5–2 m wide and 0.1–0.3 m deep, that runs for ~2 km through agricultural land used mostly for livestock grazing. The mean discharge of this stream at its outflow from the study site was 0.025 m³ s⁻¹ in 2010–11 (Fiona McLean unpublished data). This stream and its minor tributaries were straightened and realigned prior to 1860. A mature conifer plantation (*Picea* spp. and *Larix* spp.) forms the southern edge of the catchment and a small block of deciduous woodland (*Betula pubescens*, *Salix* spp., *Alnus glutinosa* and *A. incana*) replanted in 1990 encloses the source. In 2002, a pair of adult Eurasian beaver, *Castor fiber*, was introduced to this stream by the landowner to assess the value of beavers for wetland creation. Breeding first occurred in 2005, and 3–6 animals have been present annually thereafter. Beaver first dammed the upstream section of channel in 2003 and subsequently built eight more dams (four upstream and four downstream of this original dam) over the next 3 years. A tenth structure

was added in early summer 2011. The mean distance between dams was 53 ± 28 m (±SD, range = 20–600 m). The observed frequency of 5 dams km⁻¹ of channel is within the range 0.14–22 dams km⁻¹ reported from Russia and North America (Zavyalov, 2014).

Dam construction by beaver modified the surrounding habitat. Four discrete habitats were defined *a priori* for the purposes of sampling; (i) immediately upstream (0–3 m) of a dam (habitat US), (ii) the dam pond 5–10 m upstream from the dam (habitat VG), (iii) immediately downstream (0–3 m) of a dam (habitat DS) and (iv) unmodified sections of channel outwith the influence (>50 m) of the nearest dam on depth and flow (habitat UM) (Fig. 1). As unmodified sections of stream were not always present between successive beaver impoundments, samples from unmodified habitats were also collected from undammed tributary streams that were similar in terms of width, velocity, substrata and riparian characteristics. The mean hydrological distance of unmodified tributaries from any beaver activity was 317 ± 198 m (±SD, range = 100–650 m). Lentic conditions occurred in habitat US (mean water velocity = 0.2 cm s⁻¹, range = 0–3 cm s⁻¹), with high volumes of organic matter accumulating. This habitat was moderately disturbed due to beavers regularly maintaining dams with mud, rocks and cut branches, and in some cases, excavating burrows; submerged vegetation was therefore sparse. However, the dam structure itself often supported ruderal terrestrial plants, such as *Urtica dioica* and *Rumex obtusifolius*. Habitat VG was characterised by shallow (0.5–0.8 m deep), very slow moving waters (mean velocity = 0.1 cm s⁻¹, range = 0–1 cm s⁻¹) and extensive aquatic vegetation, the most abundant plant species being *Potamogeton natans*, *Callitriche stagnalis*, *Glyceria maxima*, *G. fluitans*, *Rorippa nasturtium-aquaticum*, *Myosotis scorpioides* and *Elodea canadensis*. Habitat DS was characterised by water flowing over and through the dam (mean velocity = 2.1 cm s⁻¹, range = 0–30 cm s⁻¹). Habitat UM was considered indicative of the conditions prior to dam construction (confirmed by visual assessments and archive photographs); water velocity ranged from 0 to 69 cm s⁻¹ (mean = 15.8 cm s⁻¹), the stream bed comprised a mixture of sand and coarse gravel, and there was a sparse coverage of the moss *Fontinalis antipyretica*.

Physicochemical measurements

Paired water samples (0.75 L) for the period 23 June 2010 to 13 May 2011 were obtained using ISCO 3700 automatic water samplers placed upstream and down-

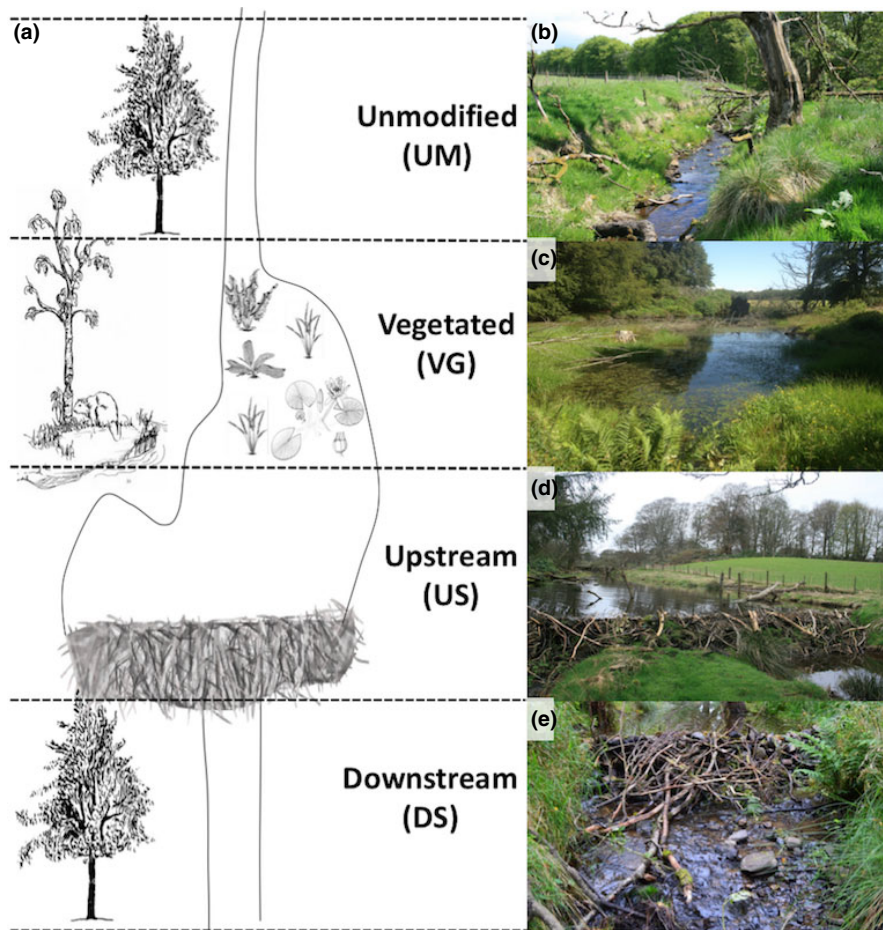


Fig. 1 A schematic diagram of the habitat types sampled in this study (a), in addition to photographs representative of these habitats; (b) a stream unmodified by beavers, (c) vegetated pond upstream of a beaver dam, (d) immediately upstream of a dam and (e) immediately downstream of a dam (all photos © N. Willby).

stream of a 500 m section of channel containing a series of four beaver dams. An integrated automatic stage (water level) recorder measured stage at each of these locations at 15 min intervals. Water samples were collected on a 12, 24 or 72 h cycle. Sampling was not flow proportionised, but was most frequent during periods when heavy rainfall was forecast and was reduced in the spring. No samples could be obtained during a prolonged period of sub-zero temperatures from 1 December 2010 to 1 March 2011. A total of 133 paired samples was collected and analysed for total suspended solids (TSS), colour, extractable P, nitrate, chloride and sulphate using standard techniques. TSS was determined from the weight of residue retained by pre-dried 1.2 μm glass microfibre filter papers. Colour was measured on a Thermo Spectronic Hellios Epsilon spectrophotometer as absorbance at 440 nm to provide an indication of dissolved organic carbon (DOC) (Pace & Cole, 2002). Extractable P was determined using the molybdenum blue method (Murphy & Riley, 1962). Concentrations of major anions were determined using a DIONEX, DX-120 Ion Chromatograph.

Samples of stream substrata (upper 5 cm) were collected in summer 2013 at randomly located positions in the four described habitat types: upstream and downstream of each of the 10 dams, and in unmodified habitats and vegetated habitats where present (total $n = 39$). Material was collected using a 10-cm diameter bottomless bucket and subsequently rinsed through sieves of mesh size 21.4 mm, 16 mm, 11.2 mm, 5.6 mm, 2 mm, 1 mm, 500 μm , 250 μm and 125 μm . Sieved material was dried at 80 $^{\circ}\text{C}$ for 24 h with the weight of the different size fractions being used to calculate substratum diversity and evenness. Dried samples were then aggregated to form coarse (1–21.4 mm) and fine (125–500 μm) fractions. The percentage of organic matter in each fraction was determined based on loss on ignition by burning 10 g of material in a pre-dried crucible at 550 $^{\circ}\text{C}$ for 24 h. Aquatic plant biomass per habitat was estimated by removing above-ground vegetation within replicate ($n = 7$) 20 cm \times 20 cm quadrants placed randomly within each habitat. Samples were dried at 60 $^{\circ}\text{C}$ for 24 h and weighed. Replicate measures ($\times 5$) of water depth were made randomly within all sampling locations.

Macroinvertebrate sampling

Macroinvertebrates were sampled in spring ($n = 35$), summer ($n = 37$) and autumn ($n = 37$) 2011 within the four described habitat types. Differences in sample numbers between seasons reflect the construction of a dam between spring and summer sampling periods and the lack of vegetated habitat at three sites. All dam systems present on the site were sampled, including the nine dams constructed between 2002 and 2006, plus a further dam formed in summer 2011. Semiquantitative samples were collected for 1 min using a D-framed kick net (mesh size 500 μm), over a fixed area of 2 m^2 , which encompassed the characteristic features of each habitat type. The net was swept through the water column, vegetation and any accumulated organic material to collect benthic, water surface and plant-associated organisms. When the stream bed was compacted, material was loosened by kicking and caught in a net placed immediately downstream. To minimise disturbance, only a single sample could be collected from each replicate example of each habitat on a given date. Samples were preserved using 70% denatured methylated spirit, sorted in the lab and identified to the highest practicable taxonomic resolution (see Table S1).

Treatment of data

Water-quality data were subdivided into growing season (May–September) and winter (October–April) periods. Variables were compared within seasons between habitats using a paired t -test with bootstrapping. Sediment organic matter content, Shannon's diversity Index (H'), Shannon's equitability (E_H) and aquatic plant biomass did not meet requirements for parametric analyses and therefore differences between habitats were analysed using Kruskal–Wallis tests with *post hoc* multiple comparisons. The absence of a satisfactory rating curve for the upstream monitoring station prevented stage being converted to discharge so the comparison of regime above and below the series of dams was limited to simple hydrological indicators such as time to peak stage and coefficient of variation in stage. Centralised stage (stage/median stage over the length of record) was used to compare the data from upstream and downstream stations while paired t -tests were used to evaluate differences in time to peak stage between stations.

Macroinvertebrate species richness was expressed as the number of taxon per sample or as H' , with species evenness represented by E_H . Differences in species richness with respect to habitat, season and dam age were analysed using a generalised linear model with a Poisson error distribution and log-link function. Quasi-Poisson

distributions were used to correct for overdispersion, as indicated in the results by a t value associated with each P -value, rather than the Z value given from a conventional Poisson distribution. To control for potential spatial pseudoreplication caused by unequal independence of replicates (due to beaver dams being distributed over the same stream system), the distance to furthest upstream sample was included as a term in these models. General linear models with *post hoc* multiple comparisons using Tukey's Honestly Significant Differences (HSD) were used to assess differences in macroinvertebrate H' and E_H between habitats within seasons, or within habitats between seasons. Macroinvertebrate H' and E_H were normalised prior to statistical analyses using a $\log_{10}(x + 1)$ transformation. To compare the accumulation rates of species per habitat type, accumulation curves were generated using individual-based rarefaction (Colwell, Mao & Chang, 2004), as abundance varied strongly between samples and species richness is highly sensitive to the number of individuals present. Species richness was estimated using the abundance-based estimator of Chao (1987).

Species abundance data were log-transformed before being converted to a pairwise, sample-by-sample dissimilarity matrix, using a Bray–Curtis dissimilarity Index (BCI). Species composition and turnover per habitat and season were then compared using non-metric multidimensional scaling (NMDS). A permutational multivariate analysis of variance was used to test the effects of habitat, distance to closest upstream sample and season on composition, based on the BCI dissimilarity matrix. Species characteristic of particular habitats were identified using the Indicator Value method (Dufrêne & Legendre, 1997).

All taxa were assigned to functional feeding guilds (FFG) using Schmidt-Kloiber & Hering (2015) (<http://www.freshwaterecology.info>). As feeding often spanned multiple guilds, the total number of individuals per species per sample were distributed across the reported guilds based on a 10-point assignment system (Moog, 1995). Since trait data did not meet assumptions of parametric tests, a Kruskal–Wallis one-way analysis of variance with *post hoc* multiple comparison tests was used to assess differences in FFG composition between habitats within seasons, and within habitats between seasons.

Species rarity was measured using U.K. mainland distribution data from the National Biodiversity Network (NBN, 2014). A rarity score was derived from the reciprocal of the log number of hectads in which each species was recorded. The sample rarity score comprised the abundance weighted mean species rarity score, where abundance equated to the log number of individuals of

each species recorded. Therefore, high sample rarity scores represent a greater than average abundance of rare species. These data did not meet assumptions of parametric tests; therefore, a Kruskal–Wallis one-way analysis of variance with *post hoc* multiple comparison tests was used to assess species rarity scores between habitats.

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

Results

Physicochemical characteristics

Differences in water chemistry above and below the series of dams were most pronounced during the growing season. Downstream reductions in summer concentrations of P and N (Table 1) were especially marked (49% and 43% respectively), while colour was on average twice as high downstream of monitoring stations. Suspended solids were higher downstream of monitoring stations throughout the year (by an average of 5.8 fold). Vegetated and upstream habitats were both deeper and had a higher per-

centage of coarse and fine substrate organic matter content (total organic matter content seven fold higher) than downstream and especially unmodified habitats (Table 2). Higher velocity downstream and unmodified habitats had the greatest substratum diversity, with unmodified samples being the most uneven. Vegetated habitats had a significantly greater aquatic plant biomass (~20 times higher) than unmodified habitats. Up- and downstream habitats had zero plant biomass.

Paired recording of stage from November 2010 to May 2011 above and below a 500 m section of channel containing a series of four dams captured nine peak run-off events (Fig. 2). The time to peak stage downstream of the dams during these events (34.6 ± 7.7 hours; mean \pm SE) was longer than at the upstream position (29.4 ± 5.6 hours; mean \pm SE), but not significantly so ($P = 0.17$). As a consequence of peak stage attenuation, the variation in stage was substantially lower below the dams compared to above them (coefficient of variation in stage = 0.22 and 0.62 respectively).

Macroinvertebrate richness and abundance

In total, 109 invertebrate samples were taken across three seasons with 156 taxa recorded from the 84,520

	Summer ($n = 61$)		Winter ($n = 72$)	
	Upstream	Downstream	Upstream	Downstream
Total suspended solids (mg L^{-1})	15.11 ± 2.71	$85.68 \pm 17.86^*$	11.77 ± 2.86	$43.29 \pm 5.06^{**}$
Colour @ 440 nm	0.07 ± 0.01	$0.14 \pm 0.01^{***}$	0.05 ± 0.00	0.06 ± 0.00
Extractable P ($\mu\text{g L}^{-1}$)	43.09 ± 4.53	$22.13 \pm 1.48^{**}$	23.10 ± 2.44	18.31 ± 2.06
Nitrate (mg L^{-1})	5.50 ± 0.39	$3.12 \pm 0.12^{**}$	5.05 ± 0.21	5.02 ± 0.24
Chloride (mg L^{-1})	6.92 ± 0.27	$5.57 \pm 0.06^{**}$	5.93 ± 0.24	5.98 ± 0.30
Sulphate (mg L^{-1})	3.13 ± 0.32	$3.58 \pm 0.16^*$	5.79 ± 0.19	5.63 ± 0.21

Asterisks indicate significant differences obtained from paired t-tests with bootstrapping ($P < 0.001$ ***, < 0.01 **, < 0.05 *).

Table 1 Summary of mean water chemistry by season and habitat (mean \pm SE) from upstream and downstream of a section of a channel containing four beaver dams.

Table 2 Physical characteristics and sediment structure and diversity per habitat, as mean \pm SE (min-max).

	VG	US	DS	UM	
Water depth (cm)	47.8 ± 3.7^a (12–78)	54.0 ± 3.9^a (15–100)	13.2 ± 2.2^b (1–49)	6.5 ± 0.5^b (2–14)	***
Coarse (>1 mm) organic matter content (%)	25.4 ± 3.6^a (11.3–45.6)	24.0 ± 4.4^a (8.5–51.6)	7.5 ± 3.9^b (1.0–41.2)	3.0 ± 0.7^b (1.3–6.2)	***
Fine (<1 mm) organic matter content (%)	18.5 ± 2.5^a (5.7–29.5)	18.1 ± 3.0^a (7.9–36.7)	8.2 ± 4.9^b (0.0–50.4)	3.1 ± 0.6^b (1.2–5.4)	***
Particle size diversity (H')	1.24 ± 0.05^a	1.35 ± 0.05^{ad}	1.70 ± 0.04^{bc}	1.52 ± 0.03^{cd}	***
Particle size equitability (E_H)	0.88 ± 0.02^a	0.87 ± 0.03^a	0.80 ± 0.03^{ac}	0.65 ± 0.02^{bc}	***
Plant biomass (DW g m^{-2})	554.9 ± 60.4^a (329.0–835.8)	0	0	27.84 ± 18.5^b (0–117.9)	**

Abbreviations; VG – vegetated, US – upstream, DS – downstream and UM – unmodified. Asterisks indicate significant differences obtained from Kruskal–Wallis tests ($P < 0.001$ ***, < 0.01 **, < 0.05 *). Numbers sharing the same superscript are not significantly different ($P > 0.05$).

individuals collected (Table 3). Vegetated (43.0%) and upstream (21.2%) habitats contributed most individuals to the total abundance, followed by unmodified (18.9%) and downstream habitats (16.9%). Unmodified habitats had significantly greater mean species richness per sample compared to downstream, upstream and vegetated habitats respectively (DS; $t_{104} = -3.58$, $P < 0.001$, US; $t_{104} = -5.06$, $P < 0.001$, VG; $Z_{104} = -2.00$, $P = 0.048$). Of the beaver-modified habitats, vegetated habitats had the greatest mean species richness (Table 3).

Distance to the furthest upstream sample did not significantly affect mean species richness ($t_{108} = 0.66$, $P = 0.512$), indicating that habitat effects were local and unchanged by upstream dams. Beaver-created habitats associated with the recently constructed dam (<1 year old) generally had a lower mean richness (VG = 13, US = 12, DS = 16) than habitats from older dams (4–8 years old, $n = 9$,

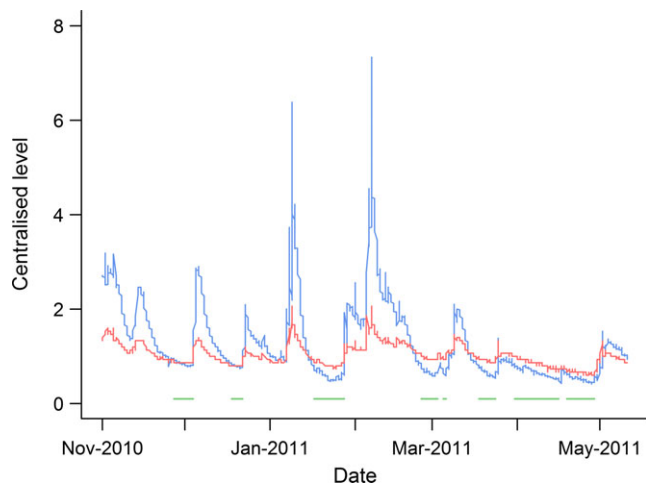


Fig. 2 Short-term variation in centralised stage upstream (blue line) and downstream (red line) of a section of channel containing four beaver dams. Periods of dry weather flow are shown in green.

Table 3 Summary of macroinvertebrate data by habitat (mean \pm SE).

	VG ($n = 21$)	US ($n = 29$)	DS ($n = 29$)	UM ($n = 30$)	Aggregate ($n = 109$)
Mean sample richness (range)	18.2 \pm 1.3 ^a (6–27)	14.3 \pm 0.9 ^b (8–27)	16.3 \pm 1.0 ^{ab} (5–33)	21.9 \pm 1.0 ^c (11–32)	17.7 \pm 0.6 (5–32)
Total richness	86	80	97	90	156
Abundance-based species estimator	98	106	112	106	167
Mean species rarity	0.35 ^a	0.36 ^a	0.36 ^a	0.38 ^b	*** 0.36
Mean individuals per sample (range)	1741.9 \pm 404.5 ^a (274–7344)	620.6 \pm 86.5 ^b (153–2156)	496.2 \pm 68.4 ^b (47–1226)	536.2 \pm 77.8 ^b (153–1840)	*** 780.3 \pm 95.9 (47–7344)
Total individuals	36,579	17,997	14,390	16,085	85,051
Shannon's diversity (H')	4.9 \pm 0.4 ^a	5.3 \pm 0.3 ^a	5.8 \pm 0.3 ^a	7.9 \pm 0.4 ^b	*** 5.6 \pm 0.2
Shannon's equitability (E_H)	0.27 \pm 0.02 ^a	0.36 \pm 0.02 ^b	0.36 \pm 0.02 ^b	0.36 \pm 0.02 ^b	** 0.33 \pm 0.01

Abbreviations for habitat codes are; VG – vegetation, US – upstream, DS – downstream and UM – unmodified, with sample sizes shown in brackets. Asterisks indicate significant differences obtained from Kruskal-Wallis tests ($P < 0.001$ ***, < 0.01 **, < 0.05 *). Numbers sharing the same superscript are not significantly different ($P > 0.05$).

VG = 19, US = 14, DS = 16), but these differences were not significant (VG; $t_{20} = -1.25$, $P = 0.228$, US; $Z_{28} = -0.88$, $P = 0.378$, DS; $Z_{28} = -0.29$, $P = 0.769$).

The greatest diversity (H') occurred in unmodified and to a lesser extent downstream habitats (Table 3). Significant seasonality in diversity within habitats occurred only within upstream sites, where spring samples had a greater mean diversity than summer or autumn ($F_{2,26} = 6.33$, $P = 0.006$; Table S2). Community evenness (E_H) was similar across upstream, downstream and unmodified habitats, but was markedly lower in vegetated habitats. Within-habitats, diversity in samples from the vegetated habitat was consistently least even, especially in the summer. The range of rarity scores was narrow (0.35–0.38), thus indicating similar levels of ubiquity of taxa in all habitats.

At the lowest rarefied number of individuals per habitat (effectively a measure of alpha diversity corrected for sampling effort), unmodified sites were more species rich than any beaver-modified habitats by an average of 11 species (range: 5–16 species) (Fig. 3). Of the beaver-influenced habitats, upstream and vegetated habitats had the lowest taxon accumulation rates. Downstream habitats displayed most seasonal variation in accumulation rate, with summer being notably less taxon rich than spring or autumn, although in comparison to other beaver-modified habitats, downstream areas still had the highest accumulation rates regardless of season (Fig. S1). In all habitat types, the individual-based taxon accumulation curve rarely reached a plateau, implying that further sampling would yield more species, perhaps related to habitat heterogeneity within individual habitats. However, observed richness averaged 87.1 \pm 1.6% of computed richness, based on the 12 habitat \times season combinations, indicating that sampling of the fauna was largely and

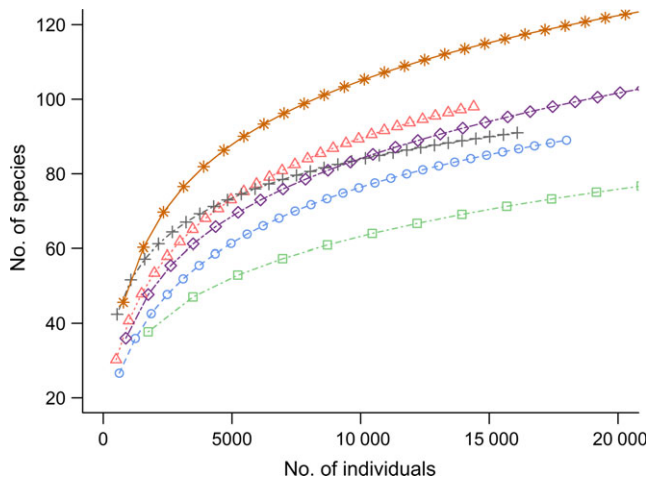


Fig. 3 Species accumulation curves based on number of sampled individuals per habitat; vegetated (green open squares), upstream (blue open circles), downstream (red open triangles), unmodified (black crosses), beaver-modified habitats combined (purple diamonds) and all habitats combined (orange stars). 95% confidence intervals are not shown for clarity but ranged from ± 1.8 to ± 2.7 species.

similarly effective. Unmodified habitats contained the highest proportion of unique species (38.6%), followed by vegetated (22.8%), upstream (21.0%) and downstream (14.0%) habitats. Most notably, due to a combination of variable accumulation rates, plus large differences in richness and abundance between habitats and the presence of unique taxa in each habitat, a composite sample from the four habitats resulted in greater landscape-scale richness of macroinvertebrates (mean = 28%) than for a similar sized sample of any beaver-influenced or non-influenced habitats considered independently (Fig. 3). For example, a random sample of 10 000 individuals from a landscape including both beaver modified and unmodified habitats would be expected to support 105 ± 4 species compared to 84 ± 2 species in a landscape containing no beaver-modified habitats.

Species composition

The most frequently occurring taxa were Chironomidae (present in 98% of samples), *Asellus aquaticus* (Asellidae: 90%), Oligochaeta (81%) and *Crangonyx pseudogracilis* (Crangonyctidae: 71%), with *A. aquaticus* (27.6%), *C. pseudogracilis* (19.3%) and Chironomidae (14.2%) contributing most individuals, all organisms typical of organically enriched conditions. The fauna of unmodified sites was compositionally distinct from beaver-influenced habitats (Fig. 4a). There was considerable overlap in species composition between different beaver-generated habitats that largely reflected their relative proxim-

ity: for example, macroinvertebrates of vegetated habitats were most similar to upstream habitats. The composition of upstream and downstream habitats also overlapped considerably as well as sharing part of their composition with unmodified sites. A mean BCI across all habitats of 0.61 ± 0.002 (\pm SE) (range: 0.15–1.00) indicated that, on average, ~39% of the overall taxon assemblage was shared between samples. Both the season sampled ($F = 3.9$, $R^2 = 0.06$, $P = 0.001$) and distance to the closest upstream sample ($F = 2.7$, $R^2 = 0.02$, $P = 0.007$; Fig. S2) had significant effects on species composition, but these were of secondary importance compared to habitat ($F = 11.8$, $R^2 = 0.25$, $P = 0.001$), with clear grouping of samples by habitat type (Fig. 4a).

Indicator taxa were mostly associated with unmodified and vegetated habitats, reflecting the strong contrast between lotic and lentic habitat (Fig. 4b). Characteristically, limnophilic species within the Dytiscidae, Heteroptera and Gastropoda (e.g. *Radix balthica*: Lymnaeidae) were associated with vegetated habitats, together with larval insects noted for their tolerance of anoxia (e.g. *Cloeon dipterum*: Baetidae). By contrast, rheophilic taxa, such as members of the Leuctridae, Baetidae (*Baetis rhodani*), Heptageniidae (*Rithrogena semicolorata*) and Elmidae, and the free-living caddis (e.g. *Rhyacophila dorsalis*), were associated with unmodified habitats.

Functional feeding group composition

The percentage of individuals within each functional feeding group varied across habitats (all tests; $\chi^2_3 > 9.5$, $P < 0.023$; Fig. 5). Filter feeders were most characteristic of unmodified habitats, while shredders, and to a lesser extent collector-gatherers, dominated beaver-modified habitats. Variations in predator abundance were low between all habitats. Significant seasonal differences in feeding group abundance did occur within habitats (Table S3), but were of minor importance compared to the differences between habitats.

Discussion

Changes in habitat and physicochemistry due to dam building

Small, straightened and unnaturally uniform streams are ubiquitous in anthropogenically modified landscapes. A lack of variation in depth, substratum and velocity, and poor lateral connectivity may have catchment-wide implications, including reduced biodiversity, low nutrient retention and poor flood attenuation. At our study

Fig. 4 Non-metric multidimensional scaling ordination (NMDS) of macroinvertebrate composition (a) based on a Bray–Curtis dissimilarity matrix per habitat; vegetated (green, open squares), upstream (blue, open circles), downstream (red, open triangles) and unmodified (black, crosses). All stress values were <0.12. Indicator species significantly associated each habitat ($P < 0.05$) are shown in plot (b).

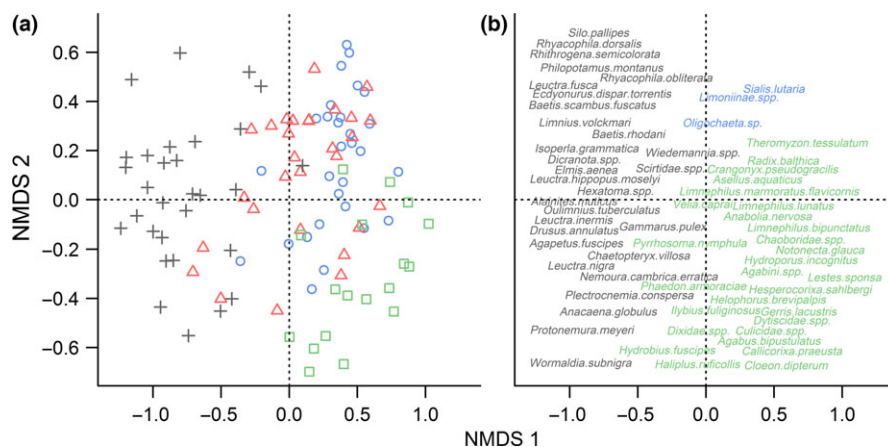
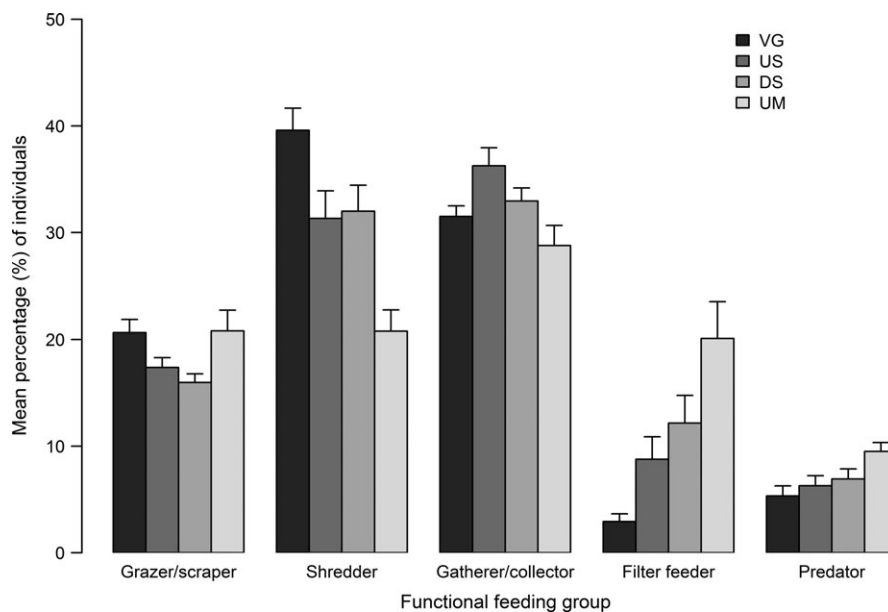


Fig. 5 The mean percentage of individuals in each functional feeding group per habitat. Error bars indicate standard error. VG, vegetation; US, upstream; DS, downstream; UM, unmodified.



site, the reintroduction of beavers initiated several years of habitat engineering that served to re-establish physical heterogeneity by creating a network of ponds, woody debris caches and aquatic plant-rich habitats, interspersed with running water.

The attenuation of peak flow is a common phenomenon in beaver-influenced streams, especially where dams occur at high density (Rosell *et al.*, 2005; Nyssen, Pontzele & Billi, 2011), and is consistent with our observations of reduced variation in stage below a series of dams. The accumulation of fine sediment and organic matter behind beaver dams is closely linked to the reduction in downstream transport and the increased input of felled or dead wood to the channel (Gurnell, 1998). Reported changes in stream or groundwater chemistry below beaver impoundments range from decreases (Correll, Jordan & Weller, 2000; Margolis, Castro & Raesly, 2001b) to increases (Klotz, 1998; Fuller & Peckarsky, 2011) in different fractions of N

and P, and are typically related to increased hyporheic exchange due to longer channel residence times (Lautz, Siegel & Bauer, 2006). The reductions in N and P in our study are more substantial than often reported, but were only significant in the summer, consistent with reports by Margolis *et al.* (2001b) and Klotz (2010). This suggests that biological processes, such as denitrification, or assimilation by macrophytes, are mainly responsible for the observed reductions. Nutrient storage by macrophytes in impounded agricultural streams may be promoted by the lower tree shading and higher fertility than in forested streams. The 20% reduction in summer chloride concentrations that we observed below the series of dams suggests that groundwater dilution might have also played a part in the lowered nutrient concentrations, though the reduction in chloride was much smaller than that observed for P and N (49% and 43% respectively). Whether such groundwater inputs reflect the influence of dams is unknown, but

would be consistent with reports of increased sub-surface flows or baseflow associated with beaver dams (Gurnell, 1998).

It is clear that habitat engineering by beaver could promote key regulating ecosystem services in agricultural streams, such as fine sediment trapping, nutrient assimilation and flow attenuation. In such streams, these processes will normally be compromised due to channel realignment and the removal of natural features that aid retention, such as woody debris dams. However, positive effects of beaver dams on ecosystem processes at a local scale are likely to be transient, since dams are dynamic on annual to decadal time scales and may also breach during high flows (Butler & Malanson, 2005). Stability of dams in agricultural landscapes might be lower due to more variable run-off, loss of volume due to increased sediment loading or, in some cases, deliberate removal. In this study, suspended solids and dissolved organic carbon (inferred from colour) both increased downstream. The increased suspended solids probably reflect bankside burrowing, the use of poorly consolidated materials in dam construction and exposure of steep sparsely vegetated banks or accumulated fine sediment under low flows. Turbidity is normally reported to decrease below beaver impoundments, although there are exceptions (Fracz & Chow-Fraser, 2013). The observed rise in colour is most likely a consequence of the decomposition of retained wood and litter inputs, plus inundation of herbaceous vegetation and organic-rich soils, and will be favoured by longer residence time and higher temperatures during the summer. Similar rises in DOC associated with beaver activity are often reported from non-agricultural landscapes (e.g. Cirimo & Driscoll, 1993; Margolis *et al.*, 2001b).

Macroinvertebrate response to habitat engineering

Invertebrate richness varied seasonally between- and within-habitats, but in general, unmodified habitats had highest species richness. However, the response of macroinvertebrates to habitat engineering by beaver is not consistent across the literature. In South America, where *Castor canadensis* is invasive, beaver ponds also had lower invertebrate richness than unmodified sites (Anderson & Rosemond, 2007), while in North America and Northern Europe, richness either did not differ (McDowell & Naiman, 1986; Redin & Sjöberg, 2013) or was reduced relative to unmodified sites (Smith *et al.*, 1991). Differences in scale of focus (i.e. patch versus landscape) and analytical approach (e.g. taxonomic resolution or correction for sampling effort) are likely expla-

nations for the variation in reported effects. As the number of invertebrates commonly varies strongly between samples, and richness generally reflects this differential sampling effort, invertebrate richness should strictly be estimated using individual-based rather than sample-based rarefaction.

In our study, habitat-specific accumulation curves confirmed that the vegetated and upstream habitats associated with beaver ponds accumulated species at a lower rate than downstream and unmodified habitats. This may reflect homogenisation of habitat due to retention of organic-rich sediment. Disturbance by beaver during foraging or dam maintenance could also favour habitat generalists, such as Chironomidae and *A. aquaticus* that consistently dominated vegetated samples, although Hood & Larson (2014b) suggest that active maintenance of aquatic habitat by beaver increases local niche diversity. Viewed at the landscape scale (i.e. across all habitats), invertebrate richness increased by an estimated 28% in the presence of beaver. This finding reflects sufficient turnover in species between habitats to promote coexistence at the larger scale (Harthun, 1999; Anderson & Rosemond, 2007). The benefits to biodiversity of beaver-engineered patches within a landscape have been observed in multiple groups including amphibians (Cunningham, Calhoun & Glanz, 2007), fish (Schlosser & Kallemeyn, 2000) and terrestrial plants (Wright *et al.*, 2002), although it is only in the latter case that the scale of this benefit has also been fully quantified (estimated to be a 33% increase in plant richness). The characteristics of the landscape in which effects occur should also be taken into account; in landscapes already rich in lentic habitats, the effects of beaver-created habitat on richness may be less significant, while if beaver-created habitats fully dominate the landscape, there may be a negative effect on richness due to loss of lotic habitat (Wright *et al.*, 2002). However, such concerns are probably redundant in landscapes heavily exploited by humans, as it is highly unlikely that beaver-modified habitats would dominate. Therefore, any contribution to habitat heterogeneity will be beneficial.

Changes in physical habitat structure and hydrology generated by beaver dams were related to differences in macroinvertebrate composition. Species of well-aerated flowing water and low rates of siltation, such as the caddisfly *Silo pallipes* (Goeridae), were replaced by others such as the baetid mayfly *C. dipterum* (Ephemeroptera) more typical of still waters. Species replacement in beaver-impounded areas is commonly reported (Margolis *et al.*, 2001a), but the identities of the major colonists vary and cannot be generalised at a coarse taxonomic

resolution. In our study, the generalist amphipod crustacean *Gammarus pulex* (Gammaridae) was present in low numbers across all habitats compared to the non-native *C. pseudogracilis*, which prefers littoral habitats with soft sediments (Mayer, Maas & Waloszek, 2012), and hence was more frequent and abundant in beaver-influenced sites. One possibility is that distribution patterns were influenced by interspecific competition and that increased habitat diversity favours coexistence through partitioning.

All habitats contained some unique taxa that were not simply a subset of generalists from unmodified habitats, a pattern reinforced by the similar rarity scores in all habitats. However, overlaps in composition were common, principally between upstream and downstream habitats, reflecting the broad ecological tolerance of the commoner fauna of degraded streams, plus downstream drift maintained by water flow over, around and through dams. Flow below dams created hydrologically similar conditions to unmodified sites, and therefore downstream sites were biologically and physically intermediate between the more extreme unmodified and vegetated habitats. Position of dams within a catchment has previously been reported to affect invertebrate richness and abundance, as sites situated lower down the catchment may receive greater invertebrate and organic drift (Redin & Sjöberg, 2013), or benefit from trapping of sediment or agricultural pollutants upstream (Clifford *et al.*, 1993). The number of individual macroinvertebrates was generally highest in summer in beaver-modified habitats in this and other studies (McDowell & Naiman, 1986; Smith *et al.*, 1991), reflecting the greater relative importance of non-insect taxa and the concentrating effects of low flows (McDowell & Naiman, 1986). It should be noted that as samples were taken from habitats within the same stream system the possible effect of invertebrate drift may violate statistical independence of samples, especially for the most downstream dams. However, when distance to furthest upstream sample was included in richness and composition models, it was either not significant or had a low explanatory power. Furthermore, in the NMDS analysis, no samples in close hydrological proximity were clustered together, reflecting underlying differences in species composition and confirming the importance of local habitat conditions relative to downstream drift.

Despite a long history of alteration of the drainage network and a comparative scarcity of mature ponds in the region to furnish suitable colonists, habitat engineering by beavers evidently had profound effects on macroinvertebrate assemblages in a short period of time.

Artificially created ponds typically reach colonisation saturation within 3–4 years (Williams, Whitfield & Biggs, 2008); so, the beaver ponds in our study most likely contained a mature macroinvertebrate assemblage as all but one were a minimum of 4 years old at the time of sampling. Even the one dam constructed during 2011 did not have significantly lower faunal richness, implying that colonisation was rapid. It is highly likely that the proximity of beaver ponds of different ages and their hydrological connectedness aids colonisation of newly engineered ponds.

Changes in community composition were reflected in shifts in functional feeding group structure. Unmodified sites were most often characterised, in this and other studies, by an abundance of filter feeders, grazer/scrapers and scarcity of shredders (McDowell & Naiman, 1986; Margolis *et al.*, 2001a). By contrast, downstream, upstream and vegetated habitats were dominated by shredders and gatherer/collectors, which presumably profit from entrapment of particulate organic matter, plant tissue and detritus (Naiman *et al.*, 1988; Simanonok *et al.*, 2011). Accumulation and processing of organic matter and its potential downstream drift may benefit filter feeders both upstream (Nummi, 1989; Rolauffs *et al.*, 2001), and downstream (Margolis *et al.*, 2001a; Redin & Sjöberg, 2013). Emerging aquatic insects also act as conduits of material, energy and nutrients to terrestrial ecosystems with the potential to alter the dynamics of terrestrial trophic interactions (Knight *et al.*, 2005). Changes imposed by habitat engineering may therefore have wider ecological significance. Higher organisms such as bats and salmonid fish may benefit from the increased density of aerial or aquatic invertebrates (Nummi *et al.*, 2011; Kemp *et al.*, 2011), while the seasonal differences in macroinvertebrate abundance between habitats may reduce fluctuations in prey availability at coarser spatial scales.

Role of habitat engineering by beavers in the restoration of agricultural streams

Thousands of kilometres of straightened and homogenised agricultural streams overlap the native range of Eurasian and North American beavers. The potential for improving poorly retentive streams such as these through the re-establishment of small-scale natural discontinuities has been a driving force behind the reintroduction of beaver to many parts of their range (Pollock *et al.*, 2014). We illustrate that the discontinuities created by beaver through dam building are hotspots of habitat heterogeneity that promote aspects of ecosystem

processes such as retention of water, nutrients and organic matter (Törnblom *et al.*, 2011), as well as enhancing aquatic biodiversity. Admittedly, in the absence of pre-damming data on stage regime, chemistry and macroinvertebrates, the differences between habitats cannot be attributed unequivocally to beaver dams, but there is no other simple explanation for such large differences on this scale and the habitats that we studied only existed as a product of dam building by beaver.

At the landscape scale, we found that invertebrate richness, abundance and diversity were positively affected by this habitat engineering. These biological changes occurred despite the low connectivity with suitable sources of colonists within this agricultural landscape, which may have limited their dispersal. Since the vast majority of stream restoration projects rarely demonstrate a biodiversity recovery post-hydrogeomorphic adjustment (Palmer *et al.*, 2014), habitat engineering via beaver reintroductions may be especially valuable because of the apparently predictable and consistent response of a wide range of aquatic biota. Beaver modifications are local features that affect habitat heterogeneity at a coarser scale; whether such benefits remain meaningful at the catchment scale is still unclear. Nevertheless, our findings demonstrate positive ecological effects of engineering by beaver within degraded freshwater systems, arising from the construction of natural features that may prove difficult to replicate by conventional methods of habitat creation. This suggests that beaver could contribute more widely in the future to the restoration of freshwater habitats provided that suitable strategies can be adopted to support coexistence with humans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of macroinvertebrate species.

Table S2. Summary of macroinvertebrate data by habitat and season (mean ± SE).

Table S3. Summary of the percentage of individuals in each functional feeding group per habitat and season.

Figure S1. Species accumulation curves based on number of sampled individuals for spring, summer and autumn, per habitat and all habitats combined.

Figure S2. Non-metric multidimensional scaling ordination of macroinvertebrate composition based on a Bray–Curtis dissimilarity matrix for the distance to closest upstream sample and per season.

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