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Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the responses of contrasting biota

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3 **Rewilding wetlands: beaver as agents of within-habitat heterogeneity and the**
4 **responses of contrasting biota.**
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33 **Abstract**
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36 Ecosystem engineers can increase biodiversity by creating novel habitat supporting species
37 that would otherwise be absent. Their more routine activities further influence the biota
38 occupying engineered habitats. Beavers are well-known for transforming ecosystems
39 through dam building and are therefore increasingly being utilised for habitat restoration,
40 adaptation to climate extremes, and in long term rewilding. Abandoned beaver ponds
41 develop into meadows or forested wetlands that differ fundamentally from other terrestrial
42 habitats and thus increase landscape diversity. Active beaver ponds, by contrast, are
43 superficially similar to other non-engineered shallow wetlands, but ongoing use and
44 maintenance might affect how beaver ponds contribute to aquatic biodiversity. We explored
45 the 'within-habitat' effect of an ecosystem engineer by comparing active beaver ponds (BP)
46 in southern Sweden with coexisting other wetlands (OW), using sedentary (plants) and
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3 mobile (water beetles) organisms as indicators. BP differed predictably from OW in
4 environmental characteristics and were more heterogeneous. BP supported more plant
5 species at plot (+15%) and site (+33%) scales, and plant beta diversity, based on turnover
6 between plots, was 17% higher than in other wetlands (OW), contributing to a significantly
7 larger species pool in BP (+17%). Beetles were not differentiated between BP and OW
8 based on diversity measures but were 26% more abundant in BP. Independent of habitat
9 creation beaver are thus significant agents of within-habitat heterogeneity that differentiates
10 beaver ponds from other standing water habitat; as an integral component of the rewilding of
11 wetlands re-establishing beaver should benefit aquatic biodiversity across multiple scales.
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21 **KEYWORDS:** Beaver, wetland, aquatic plants, beetle, richness, diversity, heterogeneity
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27 **Introduction**

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29 Ecosystem engineers alter the supply of resources to other organisms and probably
30 influence all ecosystems in some way (Jones et al., 1997). Ecosystem engineers generally
31 have positive effects on biodiversity (Romero et al., 2015), via a variety of mechanisms
32 including the creation of novel habitat, modification of existing habitat, reduction in patch size
33 or increase in patch turnover. However, increased habitat heterogeneity is a unifying theme.
34 Heterogeneity itself is a cornerstone of the maintenance of biodiversity but restoring
35 heterogeneity at biologically relevant scales through direct human intervention is
36 challenging; re-establishing populations of the larger key ecosystem engineering species, a
37 common element of trophic rewilding, might therefore prove effective in achieving a step
38 change in the restoration of biodiversity. However, to justify this rationale the mechanisms by
39 which such ecosystem engineers affect biodiversity and the scale at which these
40 mechanisms operate require better understanding.
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54 Freshwaters are crucial for the conservation of global biodiversity and functioning of
55 ecosystems, as well as contributing ecosystem services essential to society (Vigerstol and
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3 Aukema, 2011). Despite this, most freshwater habitats have been impacted by multiple
4 anthropogenic stressors for many centuries and are losing biodiversity at unprecedented
5 rates and faster than terrestrial habitats (Dudgeon et al., 2006). Various 'hard engineering'
6 options are available to restore freshwater habitats, ranging from river meandering and
7 excavating new clean water ponds, to diversion of external nutrient loading and sediment
8 removal to reduce internal loading. However, softer lower cost, 'biotic' options that exploit
9 the distribution or behaviour of organisms or trophic interactions, can also be effective,
10 ranging from use of donor seedbanks, biomanipulation of fish stocks in lakes, to the
11 reintroduction of keystone species (Nienhuis et al., 2002).
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21 The Eurasian beaver (*Castor fiber*) has been widely reintroduced throughout its native range
22 in recent decades. Initial motivations for reintroduction were to reverse a severe decline
23 caused mainly by hunting, which had reduced *Castor fiber* to a few small and highly
24 fragmented populations (Halley & Rosell, 2002). Since the status of the species has been
25 secured, emphasis has shifted to exploiting the ecosystem engineering activities of beaver;
26 the use of beavers (*C. fiber* and *C. canadensis*) to restore rivers and increase landscape
27 heterogeneity (Burchsted et al., 2010; Pollock et al., 2014), or adapt to floods and droughts
28 (Hood & Bayley, 2008; Gibson & Olden, 2014) is gaining traction. Beaver are also
29 increasingly featuring in long-term rewilding projects where targets are broadly unscripted
30 (Law et al., 2017), but empirical evidence of effects is often lacking. In this article we explore
31 how reintroduction of beavers might benefit freshwater biodiversity in impacted landscapes.
32 We use a cross-sectional comparison of active beaver ponds and other wetlands in an area
33 of Sweden where beaver have long been established. We also discuss if the observed
34 spatial differences mirror the temporal changes observed in Scotland following beaver
35 reintroduction after a prolonged (400 year) absence.
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51 Beaver dam streams to raise and stabilise water levels, thus maintaining a submerged lodge
52 entrance and increasing access to resources, whilst reducing exposure to terrestrial
53 predators (Hartman, 1996). Existing aquatic habitats such as lakes and lowland rivers,
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3 where abundant, are also commonly used by Eurasian beaver, sometimes with minimal
4 hydrological alteration. Damming converts land into aquatic habitat (beaver ponds) with
5 largely predictable effects on nutrient cycling and decomposition dynamics that are
6 expressed via water chemistry and downstream transport (Naiman et al., 1988). The
7 recovery of northern hemisphere beaver populations from near extinction in the early 1900s
8 to ~30 million animals has been associated with the creation of an estimated 9500-42000
9 km² of shallow aquatic habitat (Whitfield et al., 2015). The successional changes in beaver
10 ponds following abandonment are well described (McMaster and McMaster, 2001) and can
11 yield novel habitats such as beaver meadows that further enhance landscape diversity
12 (Wright et al., 2002). In wetland-poor environments beaver ponds may represent a novel
13 habitat in their own right. The combination of novel engineered and non-engineered habitats,
14 including the coexistence of engineered sites covering successional states from newly-
15 formed to long-abandoned, enhances landscape diversity for many groups of organisms e.g.
16 aquatic plants (McMaster & McMaster, 2001), other herbaceous plants (Wright et al., 2002),
17 invertebrates (Rolauuffs et al., 2001), fish (Kemp et al., 2011), amphibians (Dalbeck et al.,
18 2007), bats (Nummi et al., 2011), and waterfowl (Nummi & Holopainen, 2014).

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35 However, alongside these classical 'between-habitat' effects it is increasingly recognised
36 that ecosystem engineers can exert important effects at finer spatial scales – nested within
37 habitats – that may also influence biodiversity at coarser scales. These effects can also
38 apply through both non-engineering (e.g. consumptive) and engineering (e.g. burrowing)
39 pathways (Prugh & Brashares, 2012). In the case of beaver, herbivory alone (i.e. in the
40 absence of dam building) has major effects on wetland vegetation richness and biomass
41 (Law et al., 2014; Parker et al., 2007). Dam maintenance and its effect on water level regime
42 (Gurnell, 1998), together with inputs of felled or windblown deadwood (France, 1997) and
43 canals dug to transport felled material (Hood & Larson, 2013), should further differentiate
44 active beaver ponds from other wetlands in the wider landscape. A simple test of the
45 importance of these within-habitat effects would be to compare active beaver ponds with
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3 nearby superficially similar other wetlands to identify how and at what scale these habitats
4 differ. In the absence of strong differences the effects of beaver might in theory be recreated
5 by conventional approaches, such as pond creation, or restoring existing water bodies (e.g.
6 Biggs et al. 2005; Thiere et al. 2009). Beaver bring their own specific management
7 challenges (e.g. damage to forestry, flooding of agricultural land, threats to infrastructure
8 integrity) and pose important dilemmas (e.g. benefits for aquatic biodiversity, flood
9 attenuation, storage of nutrients and sediment (Law et al., 2016; Puttock et al., 2018)
10 versus the potential impact of increased global methane emissions (Whitfield et al., 2015)). It
11 is therefore pertinent to ask if we actually need ecosystem engineers such as beaver to
12 achieve 'beaver-like' biodiversity benefits and, what specifically, beavers offer to the
13 rewilding of wetlands.
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25 Few studies question how ecosystem engineering by beaver affects disparate biota in
26 parallel, or in comparison to superficially similar wetlands formed by independent processes.
27 Scales finer than the water body are also commonly ignored. Plants (submerged, floating-
28 leaved and emergent taxa) and water beetles found in wetlands are taxonomically diverse,
29 easily sampled, indicative of particular environmental conditions and differ in their dispersal
30 ability, making them ideal subjects for a comparative study of biodiversity in beaver ponds
31 and other wetlands at different spatial scales. Here we test the following hypotheses: (i)
32 beaver ponds contain greater wetland plant and water beetle richness at contrasting spatial
33 scales (plot or sample versus site) than other wetlands in the landscape, (ii) spatial turnover
34 in biota is systematically higher within individual beaver ponds than other wetlands,
35 reflecting increased habitat heterogeneity and active use, making active beaver ponds
36 unique in the hydroscape.
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53 **Materials and methods**

54 *Field sites*

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3 The study was conducted in July 2012 within a 100 x 100 km area between Örebro and
4 Skinnskatteberg, in central southern, Sweden (59° 30' N, 15° 10' W, elevation range: 28-156
5 m). Within this area, wetlands that were created by beaver, i.e. beaver ponds (henceforth
6 BP; Fig. 1a), were identified by the presence of well-maintained beaver dams that
7 impounded an area of shallow, standing water. Given the regional topography all of the BP
8 studied were valley wetlands as opposed to small cascade dam systems. The minimum age
9 of BP sampled was estimated at 5 years based on age and extent of standing dead wood
10 and aerial imagery from 2006-2010 (Google Earth 7.1.2.2041). All BP supported active
11 beaver colonies as indicated by freshly grazed herbaceous plants or coppiced trees, canal
12 creation, dam maintenance and lodge construction. Other (i.e. non-beaver) wetlands
13 (henceforth OW; Fig. 1b) were permanent, shallow, standing freshwaters (i.e. ponds or non-
14 eroding lake margins and associated minerotrophic wetlands), formed naturally by river
15 migration or during the last glacial retreat, enlarged in one case through artificial
16 impoundment. Their hydrological regime was uninfluenced by beaver dams, although most
17 sites showed evidence of occasional use by beaver. OW were located in close proximity (< 5
18 km) to sampled BP, but were not paired with specific sites. A total of 10 BP (1.3 ± 0.5 ha, 0.6
19 – 2.1 ha; mean ± SD, range) and 10 OW (0.9 ± 0.4 ha, 0.3 – 1.7 ha) were sampled. All sites
20 were situated in areas dominated by managed forestry or low intensity agriculture.

39 *Methods*

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42 To compare wetlands of varying size we applied a fixed sampling effort per site, with
43 samples distributed over an area of <1.5ha at all sites. For plants, 25 plots of 2 x 2 m were
44 located a minimum of 10 m apart but otherwise randomly in each of the 20 wetlands (n =
45 500). Wetland plants (i.e. all submerged, floating-leaved, emergent and marginal plants,
46 including tree saplings and bryophytes) were identified to the highest feasible taxonomic
47 level. Nomenclature followed Karlsson & Agestam (2013). Species cover was estimated
48 visually and assigned a score on a scale of 1-5 (1 = < 2%; 2 = 3 - 10%; 3 = 11 - 25%; 4 = 26
49 - 50%; 5 = > 51%). Water beetles were sampled in shallow water (< 0.75 m deep) and
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3 associated vegetation using a D-framed net (1 mm mesh) swept continuously through the
4 water column, over the bed and through aquatic vegetation within an area of 2 x 2 m for
5 approximately 1 minute. Five sweep samples were taken in each of the 20 wetlands (n =
6 100). Beetles were sorted and counted in the field. Specimens of adults and larvae were
7 preserved in 80% methylated spirit and later identified by light microscopy to the highest
8 taxonomic level feasible. We considered only true water beetles i.e. those “at least partly
9 submerged for most of the time in their adult stage” (Jäch & Balke, 2007). Beetle
10 nomenclature followed Nilsson (2014).
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19 For each sample (plot or sweep) the mean plant height and water depth were determined
20 from six replicate measurements. The extent of leaf litter, open water, woody debris, bare
21 ground and grazing was scored visually on a 1-5 scale. Water conductivity was measured
22 using a multi-range conductivity meter (Hanna instruments HI 9033) calibrated to 25 °C.
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28 *Treatment of data and statistical analyses*

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31 Alpha diversity was assessed as numbers of species per sample (plot for plants, sweep for
32 beetles), each sample being equivalent to 2 x 2 m. To estimate beta diversity we calculated
33 the mean Bray-Curtis dissimilarity index (BCI) between all pairwise combinations of plot-
34 level plant composition data or sweep-level beetle data from a site. This provided a measure
35 of within-site heterogeneity. We used two measures of gamma diversity; (i) the species pool
36 per site, derived from an aggregation of the plots or sweeps, and (ii) the estimated overall
37 species pool per wetland type derived from species accumulation curves. A sample-based
38 species accumulation curve was computed for vegetation based on a maximum sample size
39 of 250 plots per wetland type (25 plots in each of 10 sites) without replacement. An
40 individual-based rarefaction curve (Colwell et al., 2004) was used for beetles due to the
41 pronounced variation in number of individuals per sample. Both curves were extrapolated to
42 observe the effects of doubling plot number or abundance. Expected species richness was
43 calculated using Chao’s species estimator based on a species abundance matrix (Chao,
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3 1987). Finally, we compared beetle abundance between wetlands based on individuals per
4 sample, or per site (based on aggregating 5 samples).
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7 The effects of wetland type (i.e. BP vs OW) and specific environmental variables on sample
8 or site level plant richness, beetle richness and beetle density were tested using generalised
9 linear mixed-effect models with a log-link Poisson error distribution (R library lme4 (Bates et
10 al., 2012). Plant alpha diversity, maximum plant coverage per plot (%) and plant height were
11 additionally included in the beetle model. Site was included in all sample level models as a
12 random effect. Continuous environmental variables were standardised to zero mean and unit
13 standard. Since no environmental variables were found to be collinear based on checking
14 using the corvif function in the R library AED (Zuur, 2010) all were retained in the models.
15 Beta diversity values (BCI) were not normally distributed and failed to meet parametric
16 requirements after transformation so non-parametric Kruskal-Wallis tests were used to test
17 the effect of wetland type.
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30 All statistical analyses and graphics were generated using R Studio version 2.15.0 (R
31 Development Core Team, 2013) with the additional packages vegan (Oksanen et al., 2012),
32 fossil (Vavrek, 2011, plyr (Wickham, 2011), reshape2 (Wickham, 2007) and iNEXT (Hsieh et
33 al., 2016). All model outputs are given in Supplementary Material, Table 1.
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41 **Results**

42 *Environmental conditions*

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47 The typical conditions prevailing in BP and OW are illustrated in Fig. 1. The plot level
48 environmental data collected during vegetation sampling is summarised in Fig. 1c via a PCA
49 the first two axes of which captured 42% of the observed variation. The conditions found in
50 OW are essentially a subset of those recorded in BP, with BP demonstrating greater overall
51 variation in the range of local conditions present across a common number of wetland sites
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3 (10 per wetland type) and samples (25 per wetland). BP were characterised by more woody
4 debris, bare ground and open water, while OW were characterised by taller, more extensive
5 vegetation and associated litter, and deeper water.
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9 [Figure 1]
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11 *Alpha diversity*

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15 BP were more plant species-rich (+15%) at the plot scale in comparison to OW (Fig. 2a),
16 although this difference was marginal ($p = 0.06$). BP also had a higher richness of beetles
17 per sample (+16%) than OW (Fig. 2d) but this difference was not significant ($p = 0.19$).
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21 A generalised linear mixed effects model revealed that three variables, water depth, extent
22 of litter and bare ground all had highly significant ($p < 0.001$) negative effects on plot level
23 plant species richness (Supplementary Information; Fig. 1). Having accounted for the
24 variation explained by these variables the term wetland type was the only remaining
25 significant variable ($p = 0.015$), with richness being higher in plots in BP. This indicates that
26 there is direct residual effect of wetland type on plant richness that is not captured via the
27 measured environmental variables.
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36 Based on the same modelling approach none of the measured environmental variables
37 (including plant height, cover and richness) could explain a significant amount of variation in
38 the sample level beetle richness (range of p values = 0.11 - 0.65; Supplementary
39 Information; Fig. 1). The effect of wetland type was marginal ($p = 0.07$).
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45 [Figure 2]
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47 *Beta diversity*

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50 Within BP, vegetation plots were significantly more dissimilar (+17%; $p = 0.013$) from each
51 other than in OW, indicating higher within-site beta diversity (Fig. 2b). However turnover in
52 beetle composition between samples did not differ between wetland types ($p = 0.5$) (Fig. 2e).
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Gamma diversity

Site level richness for plants was significantly higher (+33%; $p < 0.001$) in BP than OW (Fig. 2c), consistent with the marginally higher alpha diversity and significantly higher plant beta diversity in BP. By contrast there was no significant difference ($p = 0.21$) in site level richness of beetles between BP and OW (Fig. 2f; $p = 0.25$). Wetland area had no effect on site scale plant ($F_{1,18} = 0.66$, $p = 0.42$) or beetle ($F_{1,18} = 0.01$, $p = 0.96$) species richness.

[Figure 3]

For plants the estimated total species pool in BP (128 species) was 17% higher than in OW (109 species) for the same sampling effort. Species accumulation curves for both wetland types (Fig. 3a) illustrate the higher rate of plant species accumulation in BP and the larger overall species pool (based on non-overlapping 95% confidence intervals). Rarefaction indicated that for an equivalent level of sampling effort (i.e. the same number of individuals) the number of beetle species was marginally higher (+10%) in BP but not significantly so (Fig. 3b). Although accumulation curves were not fully asymptotic, the total number of plant species recorded was 98% of the Chao estimator value confirming that sampling was satisfactory. For water beetles it was evident that greater un-sampled richness exists within both wetland types (87% of expected value).

Beetle abundance

The number of individuals per sample was higher in BP than OW (+26%; $p = 0.034$). Wetland type was the only variable that significantly explained variation in sample beetle density despite inclusion of a range of sample-specific environmental variables as predictors. At the site level BP contained higher numbers of beetles, though at this level the effect was marginal ($p = 0.086$).

Discussion

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3 The creation of wetlands by beaver through the damming of streams is unique amongst
4 global fauna and has the potential to create, modify, restore and rewild habitat (Naiman,
5 1988; Pollock et al., 2014; Law et al., 2017) and thus benefit freshwater biodiversity. Our
6 study reveals some more nuanced effects, namely that our focal biota respond differently to
7 wetland creation by beaver and that marked differences exist between active BP and
8 superficially similar OW that coexist in the same landscape.
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11 For plants, alpha diversity was marginally higher in BP than OW but turnover between
12 patches (beta diversity) was much higher in BP and consequently both site richness and the
13 overall plant species pool was larger in BP than OW. In BP, fluctuations in water level can
14 be rapid due to changes in dam height or integrity, and, due to limited storage capacity and
15 a shallow bank profile, small changes in depth can expose extensive marginal habitat
16 (Pollock et al., 1998; Gurnell, 1998). This increases the area of bare ground and favours
17 recruitment of annuals which may be excluded from deeper water or continuous tall
18 vegetation. Smaller scale disturbances that are unique to BP also enhance habitat
19 complexity, e.g. canal building and felled or wind-blown trees, plus lodges and cached
20 material contributing to woody debris accumulations (France, 1997). Together these
21 characteristics render high internal habitat heterogeneity a defining feature of BP that
22 differentiates them from OW and probably promotes coexistence through reduced
23 interspecific competition (as indicated by reduced plant height and litter in BP). The
24 importance of wetland type in explaining patterns of local richness over and above the effect
25 of variables, such as water depth and litter extent, testifies to the added direct effects of
26 beaver, such as selective plant foraging and herbivory (Law et al., 2014; Parker et al., 2007),
27 on wetland vegetation. This suite of direct and indirect effects imposes an ongoing dynamic
28 unique to BP that promotes plant species diversity at a range of spatial scales. Aside from
29 being ecosystem engineers (*sensu* Jones et al., 1997) beaver can therefore justifiably also
30 be regarded as agents of within-habitat heterogeneity. Wetlands used, but not created by
31 beavers, might be expected to show similar but less pronounced differences from OW
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3 (neither used or created by beavers), with herbivory alone then being the main source of
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5 differences.

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7 Beaver ponds supported a higher abundance of beetles, but none of the diversity measures
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9 differed between BP and OW. The response of beetles was also uncoupled from that of
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11 vegetation (i.e. there was no link between beetle richness or abundance and vegetation-
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13 based predictors). These findings suggest that for beetles the diversity of microhabitats is
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15 either similar across wetland types (even if the habitats themselves differ), the regional
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17 species pool lacks the specialists that might exploit additional novel microhabitats in BP, or
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19 the mobility of beetles within and between wetlands blurs any relationships between
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21 richness and environment. However, given the higher densities of beetles in samples from
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23 BP the overall quality of habitat is evidently superior. Since beaver will not affect beetles
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25 directly several factors might contribute to this improved habitat quality. These include: (i)
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27 increased availability of vegetated shallow edge habitats and canal building (Hood & Larson,
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29 2013), which have been shown to enhance beetle abundance (Bloechl et al., 2010); (ii)
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31 increased availability of invertebrate prey (Law et al., 2016) and nutrients derived from
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33 decomposition of former terrestrial vegetation; and (iii) reduced exposure to fish predation
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35 compared to other wetlands of a similar age due to a combination of reduced fish access or
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37 habitat suitability (Fairchild et al., 2000), or higher water colour in BP due to elevated
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39 dissolved organic carbon (Correll et al., 2000), and (iv) high volumes of submerged felled or
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41 windblown deadwood acting as a dietary resource or refugia (France, 1997; Thompson et
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43 al., 2016). The relevance of these factors might be pond age-dependent (e.g. sparsely-
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45 vegetated young ponds are preferentially colonised by dytiscids (Fairchild et al., 2000)) but
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47 we focussed intentionally on mature BP to provide a balanced comparison with OW
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49 established in the landscape, rather than introduce age as a confounding variable.
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52 *Implications*
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3 Beaver ponds are a natural component of northern hemisphere landscapes and have
4 increased greatly in extent following recovery of beaver populations over the past century,
5 albeit probably short of their historic extent (Whitfield et al., 2015). Beaver ponds are now
6 commonly managed to maintain drainage, restrict forestry losses or to protect the integrity of
7 transport infrastructure (Törnblom, et al., 2011). Conversely, beaver are increasingly being
8 reintroduced for their value as creators of wetland habitat, to restore incised stream
9 ecosystems (Pollock et al. 2014), or where adaptation to hydrological extremes is required
10 due to depleted wetland resources (Hood & Bayley, 2008). Can spatial differences in
11 biodiversity in wetlands associated with forested landscapes, such as Sweden, where
12 beaver already occur naturally at high densities (Hartman, 2011), offer a useful guide to the
13 temporal changes in wetland biodiversity that occur when beaver are reintroduced to other,
14 more intensively agricultural countries?
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27 Isolation has weak effects on the wetland biota of BP under natural conditions (Wright et al.,
28 2004) but in human-impacted landscapes greater inter-wetland distances might limit
29 dispersal. The absence of a diverse and highly connected regional species pool might also
30 constrain colonisation and local heterogeneity. However, long-term monitoring of the
31 ecological effects of habitat engineering by beaver in Scotland, to which they have recently
32 been reintroduced (Gaywood, 2015), reveals that responses closely emulate the differences
33 between BP and OW we observed in Sweden. Thus, Law et al. (2014) found that after 9
34 years exposure to beaver foraging alpha diversity of plants in a swamp more than doubled
35 and gamma diversity of plants in swamp and quaking bog habitat tripled. Spatial turnover in
36 composition between plots also increased significantly, rising by 20% in swamp and by five
37 fold in quaking bog habitats. In a separate study of an agriculturally degraded fen to which
38 beaver were reintroduced Law et al. (2017) found that after 12 years plant alpha diversity
39 had increased on average by 46%, whilst gamma diversity increased by 148%.

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53 Heterogeneity, measured by dissimilarity of plot composition, increased by 71%. The strong
54 similarity in findings with the present spatial study suggests that it is reasonable to
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3 extrapolate the patterns reported here to situations where beaver are reintroduced after
4 prolonged absence.
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10 **Conclusions**

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12 Ecosystem engineers create unique habitats and thus benefit wider biodiversity at multiple
13 spatial scales. This study illustrates that use or maintenance of engineered habitats by
14 beaver also enhances landscape scale diversity by creating lentic habitat that is distinctively
15 heterogeneous in terms of habitat and vegetation, rather than being novel *per se*. Thus,
16 benefits of ecosystem engineering also accrue during the phase of active pond creation and
17 maintenance by beaver, (and probably also to a lesser extent when beaver colonise pre-
18 existing water bodies), not solely as a consequence of the genuinely novel habitats (e.g.
19 Wright et al., 2002) that follow beaver pond abandonment. Beaver are textbook ecosystem
20 engineers and much-studied, but, like other large aquatic herbivores (Bakker et al., 2015;
21 Moss, 2016), their importance as agents of finer scale heterogeneity within-habitats is
22 largely overlooked. As one of very few large(ish) herbivorous mammals strictly associated
23 with freshwater beaver represent an integral component of both trophic rewilding and the
24 improved ecological status of freshwaters; in those parts of their native range from which
25 they have long been absent population expansion and reintroduction is gradually reinstating
26 their influence. Provided they can be accommodated beaver may yet prove most valuable in
27 landscapes artificially deficient in wetlands where the processes that would naturally drive
28 heterogeneity have long been lost or tamed. It is tempting to assume that any natural
29 process or feature can be replicated through human intervention. However, while anyone
30 can make a pond there is only one way to make a beaver pond.
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Statements

Competing interests

The authors declare that they have no conflicts of interest in presenting this work for publication

Author contributions

1
2
3 NW developed the project methodology and obtained principle funding. Primary data collection was
4 carried out by NW and AL. FE and OL provided information on beaver activity and distribution for
5 central Sweden and advised on choice of sites using database collated by OL. Identification of beetle
6 specimens was carried out by AL with the assistance of GF. Data analyses were undertaken by AL
7 with input from NW. Manuscript was written by NW with input from AL and additional comments from
8 GF and FE.
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12

13 14 *Research ethics*

15
16 The research was undertaken in compliance with the research ethics requirements of the University of
17 Stirling
18
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20 21 *Data access*

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23 All data referred to in this article and code used in analyses are deposited in DataSTORRE – the
24 University of Stirling research data repository <https://datastorre.stir.ac.uk/handle/11667/39>
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Figure captions

Figure 1: Examples of a beaver pond (A) and other wetland (B) within the study area.

Principal Components Analysis (PCA) of plot level environmental data collected in beaver ponds (blue) and other wetlands (red). Ellipses cover 95% of the variation in scores for each wetland type on the PCA axes shown (C).

Figure 2: Boxplots comparing beaver ponds (blue) and other wetlands (red) in terms of (A) alpha diversity of plants (richness per plot); (B) beta diversity of plants, (Bray Curtis dissimilarity); (C); gamma diversity of plants (richness per site); (D) alpha diversity of beetles (richness per sweep); (E) beta diversity of beetles; (F) gamma diversity of beetles. Boxes show median and enclose interquartile range, whiskers show 10th and 90th percentiles. Dots show individual data points. ^{*} p <0.01; ^{*} p <0.05; ^{***} p <0.001.

Figure 3: Species accumulation curves for beaver ponds (blue, dashed lines), other wetlands (red, dotted lines) for (A) plants (sample-based accumulation at plot scale) and (B) beetles (individual-based rarefaction at sweep scale). In both cases lines are extrapolated to estimate the effect of doubling sampling effort. Shaded polygons indicate 95% confidence intervals.

Figure 1 – parts a, b and c (*full, single column figure space*)

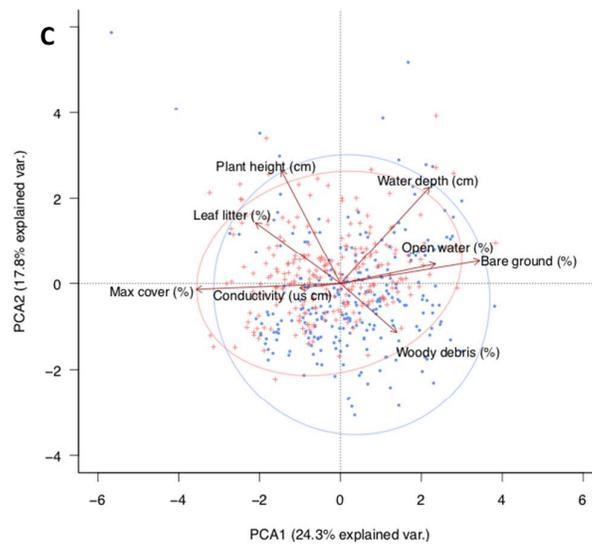
Figure 2 – parts a-f (*half page figure*)

Figure 3 – parts a,b (*single half column figure*)

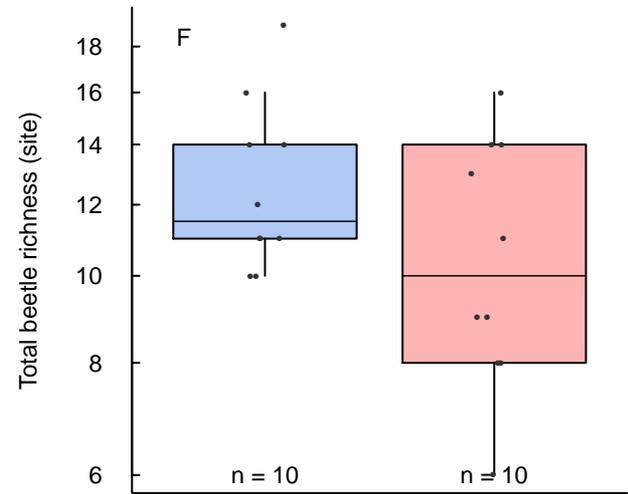
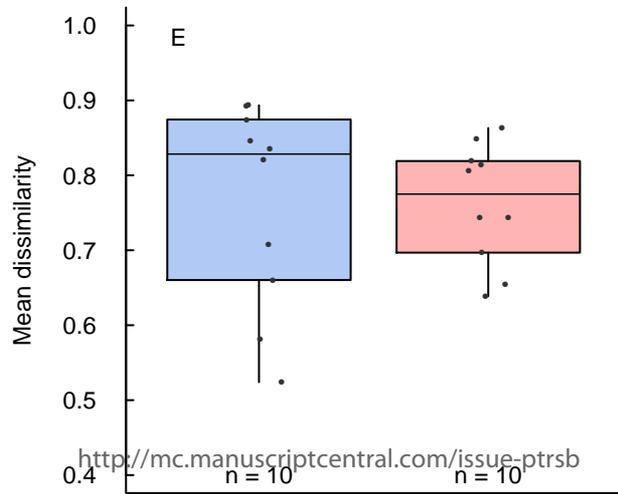
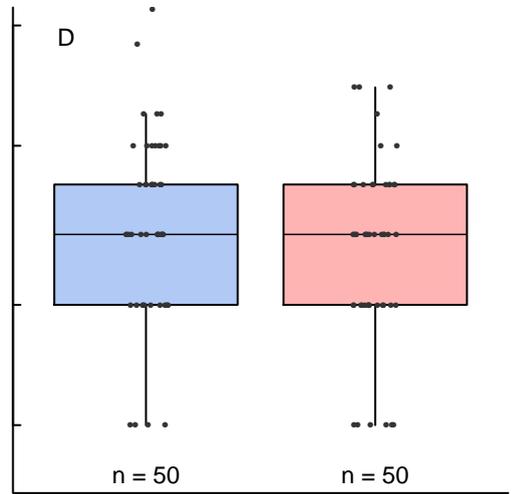
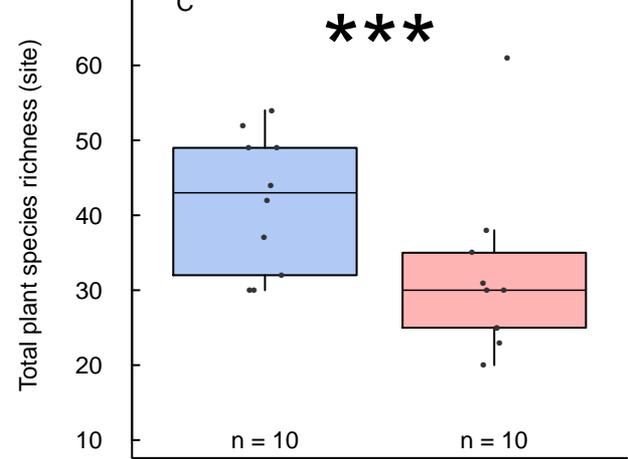
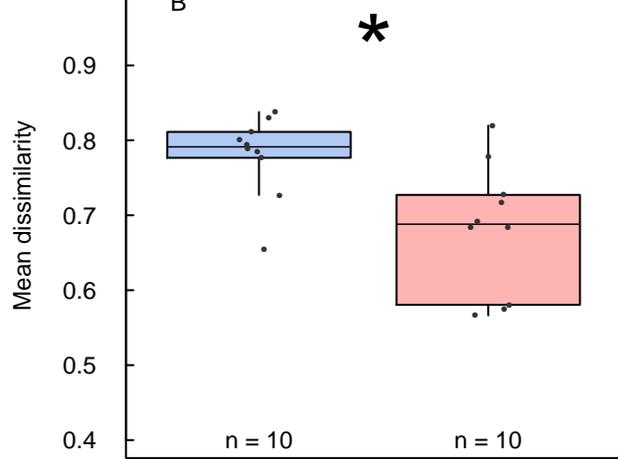
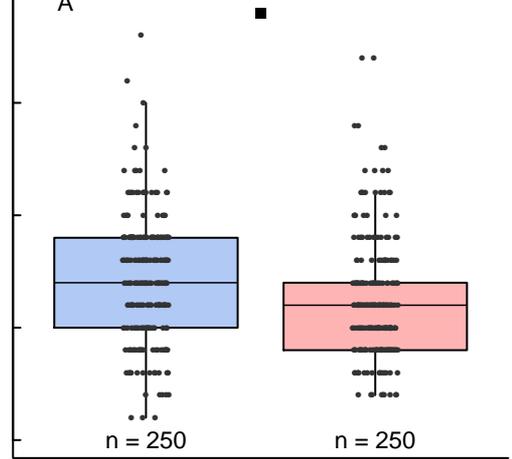
Supplementary Material

Table 1: Model choice, effect sizes and their significance for response variables illustrated in Figure 2.

Figure 1: Outputs from generalised linear mixed effects models showing effect sizes and their significance for predicting plot or sample level alpha diversity. A: Plants. B: Beetles.



Plant species richness (plot)
Beetle species richness (sample)



Beaver Other Wetland

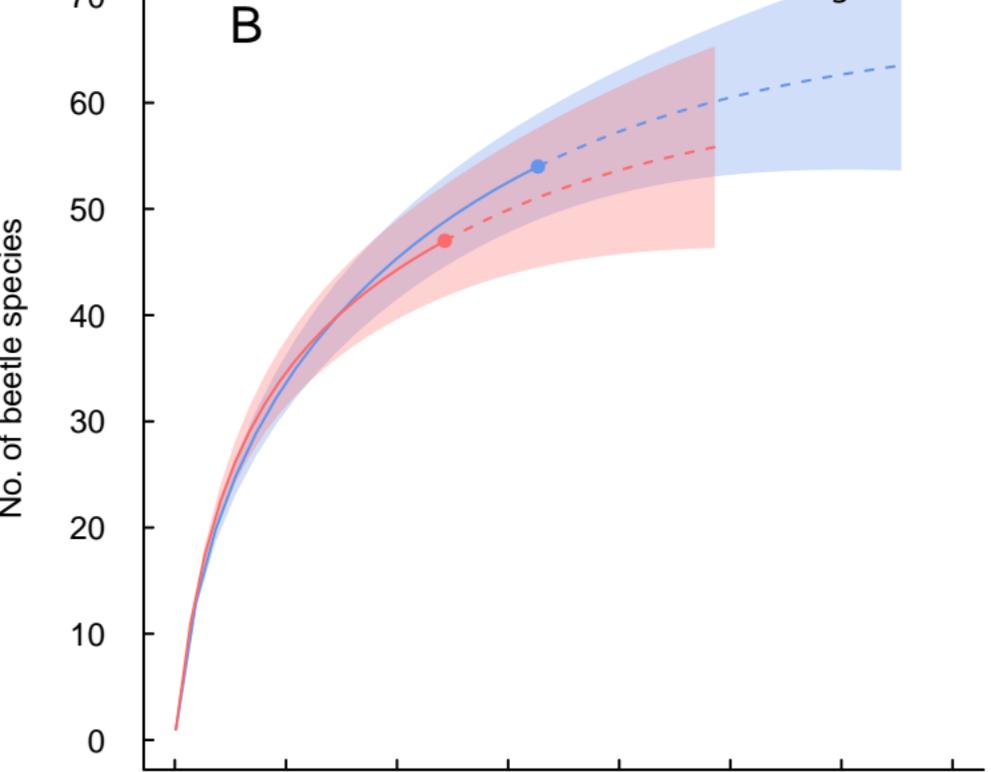
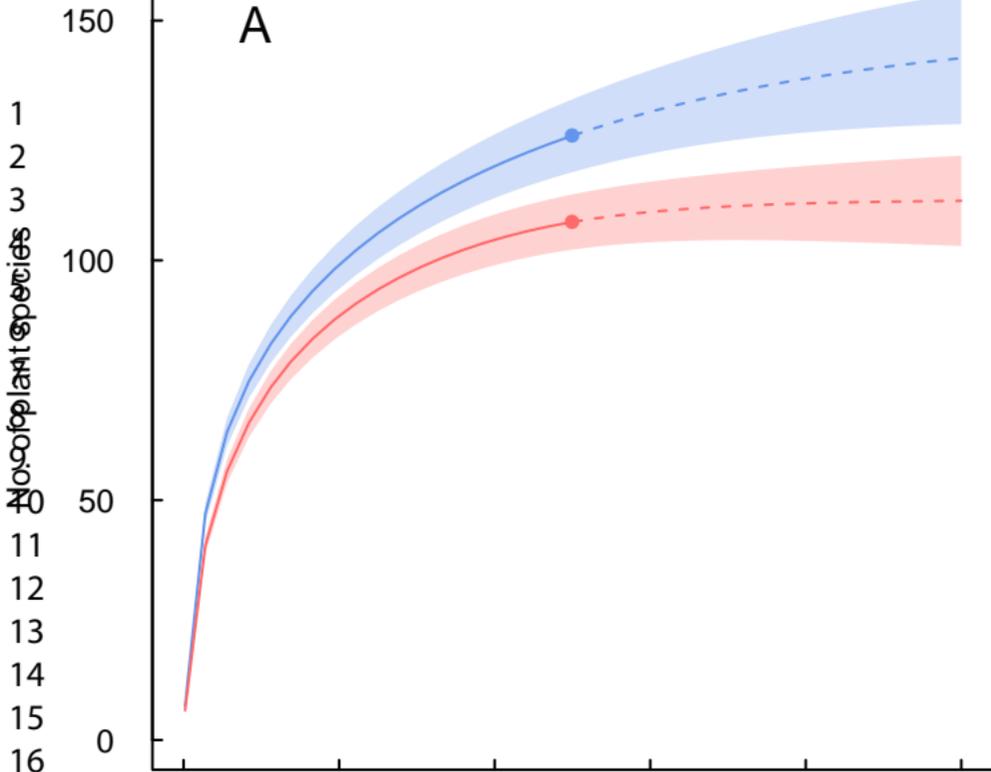
Beaver Other Wetland

Beaver Other Wetland

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No. of samples

No. of individuals