Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands

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SUMMARY

1. Habitat fragmentation and wetland loss due to anthropogenic causes are usually attributed to physical modifications of the environment; however, the loss of key species can compound these impacts and further reduce the connectivity of aquatic ecosystems.

2. Ecosystem engineers can play a critical role in modifying aquatic systems by altering the bed of ponds and streams, increasing water coverage and influencing biogeochemical processes within and adjacent to freshwater habitats. However, there is a paucity of research on how these organisms enhance connectivity among aquatic habitats, especially in otherwise isolated wetland systems.

3. In this study, we collected field data at natural and agriculturally impacted sites to quantify physical alterations to otherwise isolated, morainal wetlands modified by beavers, and to determine how these modifications might enhance connectivity. For finer-scale analysis, we collected and modelled bathymetric data for 16 wetlands, eight of which were occupied by beavers and eight abandoned by beavers.

4. We demonstrated that beavers actively increase the volume-to-surface area ratio of wetlands by almost 50% and that their digging of foraging channels increases average wetland perimeters by over 575%. Some channels were 200–300 m long, which enhanced the interface between the riparian zone and upland forests. A coarse estimate of soil displacement due to the digging of channels by beavers exceeded 22 300 m^3 within the total 13 km^2 natural area. Additional measures of wetland depth, basin complexity and basin circularity revealed other dramatic differences between wetlands with beavers and those without in both natural and agricultural landscapes.

5. Exclusion or removal of beavers could limit ecosystem processes and resilience, especially in areas with otherwise isolated aquatic habitats and limited connectivity. Conversely, reintroduction of such an ecosystem engineer into areas targeted for restoration could result in significant increase in habitat heterogeneity and connectivity.

Keywords: beaver channels, *Castor canadensis*, ecosystem engineer, isolated wetlands, landscape connectivity

Introduction

Anthropogenic landscape fragmentation decreases structural connectivity at a range of ecological scales; however, the concept of fragmentation is often strictly associated with human activities such as deforestation or agricultural expansion into wetland habitats. Indeed, wetland draining, infilling and similar perturbations have resulted in an estimated loss of approximately 50% of the world's wetlands, although country-specific losses often greatly exceed that amount (Mitsch & Gosselink, 2007). The loss of these aquatic habitats disrupts connectivity essential for the movement of wetland-dependent species, such as amphibians, across the landscape (Shalk & Luhring, 2010; Anderson, 2013). Loss of key wildlife and plant species can also disrupt wetland connectivity and ecological processes, particularly if these species alter landscapes in dynamic ways (i.e. ecosystem engineers). However, the effect of loss of such species on landscape-level processes has received limited attention in the literature.

In both Eurasia and North America, beavers (*Castor fiber* and *C. canadensis*, respectively) were lost throughout much of their former range by the end of the 19th

century (Nolet & Rosell, 1998; Hood & Bayley, 2008a) and their recovery provides some indication of the role of key species in landscape-level processes. As ecosystem engineers (Jones, Lawton & Shachak, 1994), their loss had dramatic effects on open-water coverage and fluvial morphology (Johnston & Naiman, 1987; Hood & Bayley, 2008a), although these effects have diminished because both species have recovered to stable population densities in much of their former range (Nolet & Rosell, 1998). Other ecosystem engineers in aquatic systems, such as the common hippo (*Hippo amphibious*), face current threats that in turn will reduce the hippo's influence on stream ecosystems and the species they support (McCarthy *et al.*, 1998; Moore, 2006). Loss of these species ultimately changes their former habitats, with compounding ecological effects.

There has been a continuing debate about the appropriate application of the term 'ecosystem engineer', in part to avoid broad overgeneralisations (Jones *et al.*, 1994; Power *et al.*, 1996; Wright & Jones, 2006). Ecosystem engineers modify their physical environment directly or indirectly either through construction by the engineer of physical structures ('autogenic engineers') or by transforming matter from one state to another via mechanical means ('allogenic engineers'; Jones *et al.*, 1994). In aquatic systems, plants are often associated with the former category, while most animals such as beavers, hippos and alligators fall within the latter category (Jones *et al.*, 1994; McCarthy *et al.*, 1998). Although some assert that to a certain extent all species might be considered ecosystem engineers, the fact that some species have greater influence on ecosystems than others is widely acknowledged (Jones, Lawton & Shachak, 1997; Power, 1997a,b; Reichman & Seabloom, 2002; Berke, 2010).

One of the most ubiquitous ecosystem engineers in aquatic systems in both North America and Eurasia is the beaver (Ives, 1942; Johnston & Naiman, 1987; Nolet & Rosell, 1998; Hood & Bayley, 2008a; Wright, 2009). Ecosystem engineering by beavers affects the connectivity of aquatic habitats. For example, the digging of channels away from the pond edge by North American beavers (*Castor canadensis*) creates structural connectivity by physically connecting one landscape feature such as a beaver pond to another adjacent wetland or upland habitat (Hood & Bayley, 2008a). Those same channels could facilitate the movement and foraging of other organisms [e.g. amphibians migrating between the pond and adjacent forest (Anderson, 2013), foraging by invertebrates (Hood & Larson, 2014)].

Various studies have advocated that spatial and temporal scales are important in assessing the true impacts of engineered landscapes on both biotic and abiotic processes (Berkenbusch & Rowden, 2003; Pringle, 2008; Wright, 2009). Typically, analyses of specific ecosystem engineers in aquatic systems have linked the influence of an engineer to the particular physical feature that it engineers. For example, crayfish (*Orconectes limosus*) extensively modify the bed of streams and rivers (Statzner, Peltret & Tomanova, 2003), while Pacific salmon (*Oncorhynchus* spp.) maintain habitat complexity when digging their redds (Moore, 2006; Rüegg *et al.*, 2012). As the perspective expands beyond the individual feature, a network of engineered habitats often emerges. One beaver pond can lead to another, which may connect to another and so on. Indeed, if we use the perspective of metapopulation analysis (Levins, 1969), we can imagine connected populations of engineers across landscapes at varying spatial and temporal scales. The 'artefacts' (Jones *et al.*, 1994) of engineering, those physical structures created by these populations, can influence ecological systems for 10s if not 100s of years (Ruedemann & Schoonmaker, 1938; Ives, 1942; Johnston & Naiman, 1987), especially if sites are reoccupied over time. Just as our ability to understand ecosystem engineering begins at the level of the individual feature, our ability to model the effects of these differences must begin by quantifying ecosystem modification at varying spatial and temporal scales.

Although most references to beavers as ecosystem engineers refer almost exclusively to their dam-building and/or tree-cutting activities (Jones *et al.*, 1994; Cuddington, Wilson & Hastings, 2009; Wright, 2009; Berke, 2010), not all beavers build dams. In areas where dam building is limited or non-existent, beavers still have a disproportionate influence on ecosystem form and processes (Hood & Bayley, 2008a; Bromley & Hood, 2013). Although various models have been developed to estimate the ecological effect of ecosystem engineering (Wright & Jones, 2004; Byers *et al.*, 2006; Gilad *et al.*, 2007; Cuddington *et al.*, 2009), studies that quantify the impact and scale of engineering on ecological landscapes (e.g. tonnage of soil moved or volume of water impounded) are less common (Johnston & Naiman, 1987; Reichman & Seabloom, 2002).

By quantifying the physical changes wrought by beavers in a non-riverine boreal moraine landscape, we aimed to test the spatial and temporal influences of an ecosystem engineer from the single wetland to landscape scale. In addition, we used these findings to link ecosystem engineering to the establishment and maintenance of landscape connectivity. Specifically, we tested the hypotheses that (i) the volume of water retained

would be higher in wetlands occupied by beavers, (ii) wetlands occupied by beavers would have more complex basin morphometry than those abandoned by beavers or that had lacked beavers for a long time, (iii) morphometric complexity would increase connectivity among otherwise isolated wetlands modified by beavers, and (iv) beavers would increase habitat heterogeneity in wetlands through their excavation of soil.

Methods

Study area

Miquelon Lake Provincial Park (MLPP, approximately 13 km^2) is located within the dry mixed-wood boreal forest at the southern extent of the Cooking Lake Moraine (CLM) in east-central Alberta, Canada. The terrain is a mixture of morainal hills and shallow kettle depressions, many of which are associated with naturally isolated wetlands (often <2 m deep). No rivers are present and, where streams do exist, they are often intermittent (Hood & Bayley, 2008*a*). Orthic Gray Luvisols are the dominant soil type (Mitchell, 1990), which allows for good drainage but poor crop production. Trembling aspen (*Populus tremuloides*) is the dominant tree species, with pockets of white spruce (*Picea glauca*), white birch (*Betula papyrifera*) and balsam poplar (*Populus balsamifera*) (Hood & Bayley, 2008b). The park has a continental climate, which is characterised by warm summers and cold winters (mean *annual temperature*, 3.0°C; SD = 1.3°C). Mean annual precipitation is 457 mm (Environment Canada, http://www.weather.gc.ca), although record-breaking droughts occurred in 2002 and from July 2008 to autumn 2009 (Hood & Bayley, 2008a; Hood & Larson, 2014).

Wetlands are common throughout the Cooking Lake Moraine and are often connected by channels excavated by resident beavers. During drought or anthropogenic drainage of ponds, extensive channel excavation by beavers is also visible on the bottom of active and recently abandoned wetlands (Fig. 1). Beaver has thus 'engineered' habitat at both the local and landscape scale. Due to hunting and trapping, beavers were locally extinct in the Cooking Lake Moraine by the mid- to late 1800s and were only reintroduced into Elk Island National Park at the northern extent of the moraine in 1941 (Hood & Bayley, 2008a). Since then, beavers have re-established throughout the moraine, but no evidence of beaver occupancy (lodges, channels) can be seen on aerial photographs from Miquelon Lake Provincial Park taken in 1949. Reoccupation of the park probably occurred after this date. Therefore, this landscape represents a recently recolonised and modified system.

During an initial survey of 71 wetlands in the park, Bromley & Hood (2013) found that all wetlands had evidence of either current or historic use by beavers. To determine occupancy, all beaver lodges in the park were surveyed on foot from January to March 2008 and were classified as 'active' (if a winter food cache was present in front of the lodge) or 'inactive' (if neither a food cache nor a frost vent was present) (Bromley & Hood, 2013). All lodge locations were mapped using a hand-held Garmin 60 Cx Geographic Positional System (GPS, ±3 m accuracy) and then transferred into a geographic information system (GIS, ArcMap 10.2 by ESRI™, Redlands, California). Density of active lodges in the park in 2008 was four active lodges per km^2 (Bromley & Hood, 2013).

Local scale field mapping and bathymetry

To quantify effects of ecosystem engineering by beaver at the local (wetland) scale, we conducted bathymetric surveys in MLPP in May and June 2008, on eight wetlands with active beaver lodges and eight wetlands that had been abandoned by beavers. Water level is generally highest in May and June during the ice-free season and remains relatively stable prior to the increased evapotranspiration period in July and August. Prior to lodge
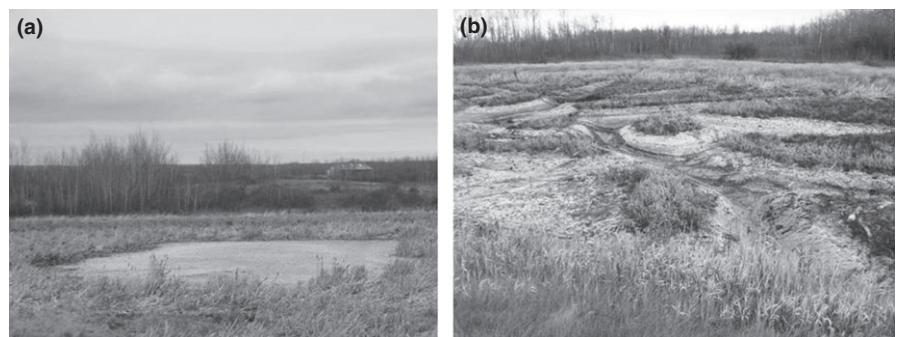
Fig. 1 Bed complexity of a wetland lacking beavers for many years and one recently abandoned during the drought in August 2008. The two wetlands were approximately 500 m apart, one on nearby agricultural lands (a) and the other within Miquelon Lake Provincial Park (b).

surveys in 2008 (Bromley & Hood, 2013), no census of beaver populations had taken place in the park; thus, it was not possible to determine the exact length of time that the wetlands had been occupied or abandoned by beavers. However, using 'artefacts' (Jones *et al.*, 1994) such as lodge condition and the appearance of cut trees, we felt confident that no resident beavers had been in our inactive wetlands for at least 2 years or more. Beavers were commonly seen in the active wetlands during our study, and fresh mud and scent mounds confirmed the presence of beavers in a particular wetland.

To obtain bathymetric data, we systematically measured depths by boat along a 10-m × 10-m grid across the entire surface of the wetland and on foot in all associated channels. We recorded each survey point with a hand-held GPS and then measured depths to 1-cm accuracy with a folding ruler. For deeper areas in the wetland (>2 m), we used a hand-held sonar, which was routinely calibrated with ruler measurements. These values then allowed us to determine differences in mean basin depth for active and inactive wetlands. Channel depth for all wetlands and a subset of channel widths were also measured. In small bays and areas that were difficult to reach by boat, additional depth measurements were taken on foot. Bathymetric data were then transferred to GIS for modelling and analysis. Wetland perimeters were also mapped with the GPS while circumnavigating the wetted edge of the waterbodies. These GPS track points were then used to aid on-screen digitising of pond perimeters through the use of a 2007 black and white orthophoto (0.25 m pixel size).

Using the ordinary kriging function in ArcGIS Spatial Analyst (ArcMap 10.2 by ESRITM, Redlands California), we interpolated the bathymetry points gathered in the field to create a raster. We then created an analysis mask for the newly created raster with the wetland perimeter shapefile set as the analysis boundary. From the resulting raster, we created contour intervals. The final output allowed us to visualise the bottom of each wetland at comparable depth intervals (Fig. 2). To calculate the two-dimensional area of the pond surface and three-dimensional surface area of the pond bottom and water surface, as well as the volume of water in each wetland, we used the ArcGIS 3D Analyst functional surface volume calculation. The reference plane was set to zero and the reference surface to 'below' to accommodate the negative values for wetland depths below the water surface. With output from the volume calculations, we were able
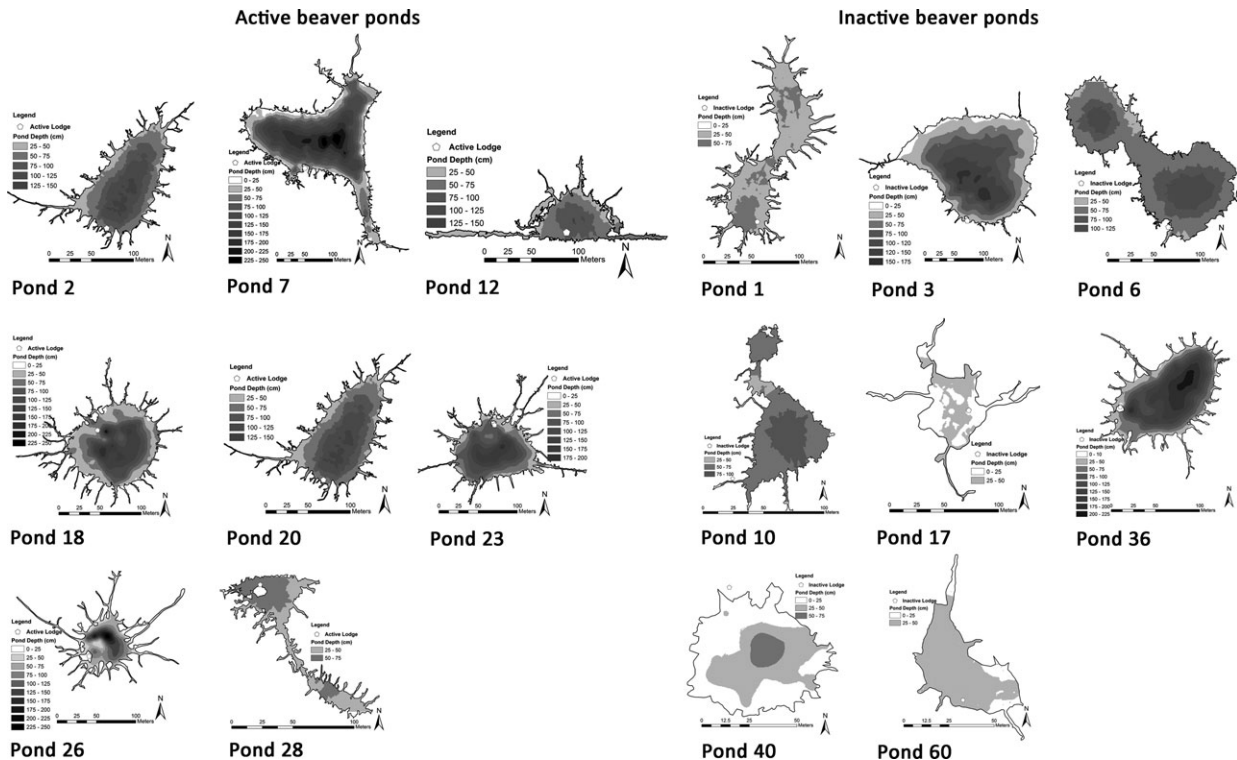

Fig. 2 Bathymetric comparisons of eight active and eight inactive beaver wetlands in Miquelon Lake Provincial Park, Alberta, Canada, in May and June 2008.

to create a standardised wetland volume by dividing each wetland volume by its 2D surface area (volume m^3/2D surface area m^2). We also developed a basin complexity index (BCI) by dividing the 3D surface area of the wetland bottom by the 2D area at water surface (BCI = 3D surface area m^2/2D surface area m^2, where values closer to 1 indicated that the surface and wetland bottom were more similar and less 'complex'). This measure helped us assess the degree to which beavers modified the bottom of the wetland, a local scale effect.

Landscape scale wetland metrics

To assess landscape scale habitat modifications by beaver, we digitised the entire wetted perimeter of 26 active wetlands and 24 abandoned wetlands in MLPP using the 2007 orthophoto, including all channels connected to the wetted wetland edge. We then digitised the wetted perimeter of the main basin of each wetland without including any channels to allow for comparisons of perimeters, wetland areas and basin circularity calculations of the wetlands with and without beaver channels. Previous studies indicated that the main basin of the active wetland would probably be larger than if the same wetland completely lacked beavers (Johnston & Naiman, 1987; Hood & Bayley, 2008a), so we used these perimeter data to examine how beaver changed perimeter lengths through digging of channels at the landscape scale. We maintained the map scale between 1:115 and 1:250 while digitising to allow for comparable perimeter measurements, thereby addressing the dependence of fractal behaviour on scale (Bárdossy & Schmidt, 2002).

To compare the shape of wetlands that had lacked beavers in the long term with those occupied recently, we used aerial photographs from 1949 to digitise the perimeters of the same 50 wetlands (prior to re-establishment of beavers in MLPP) and then used the 2007 orthophoto to digitise an additional 25 wetlands on adjacent agricultural lands. The agricultural wetlands had no obvious sign of beaver activity (lodges, channels, dams). To assess shoreline complexity for all wetlands (i.e. 1949, agricultural wetlands from the 2007 orthophoto and 50 active and inactive wetlands in 2008), we used Miller's (1953) basin circularity (*c*) shape index ($c = 4\pi A/P^2$) to determine how closely shape of the basin was to a perfect circle, where A = pond area and P = pond perimeter. A value of one (1) indicates a circular shape, while a smaller value represents a more complex shoreline.

Finally, to assess the spatial distribution of beaver channels and estimate soil displacement, we used the 2007 orthophoto to identify and digitise all beaver channels within the park, where beaver activity was not constrained by adjacent land use. Obvious channels, whether wetted or dry, were delineated along their entire length based on signs of excavation and vegetation differences. In most cases, channels in the orthophoto contained water, but for this analysis, we digitised the length of the entire channel to aid in our quantification of ecosystem engineering. We then calculated their lengths using the GIS and identified whether they were connected to another channel. From the series of historic aerial photos dating back to 1949, we identified any channels that were not beaver created/modified channels and then excluded them from the analysis. From channel lengths obtained from the orthophoto and the average width and depth measurements obtained from field measurements, we were able to determine a rough estimate of soil displacement and total channel length resulting from channel excavation by beavers. We acknowledge this method provides only a coarse estimate of the amount of soil displacement and, for this analysis, we followed the assumptions that (i) channels are straight-sided and flat-bottomed and do not generally taper near the end, and (ii) mean depth and width for the digitised channels matched those measured in the field.

Statistical analyses

From the field data and GIS analyses, we assessed bathymetric differences and other wetland metrics relative to wetlands with ('active') and without ('inactive') beavers (STATISTICA, 10; StatSoft Inc., 2011). Using wetland type (active versus inactive) as a grouping variable, we calculated a series of independent *t*-tests to compare: (i) depth of water (cm) in the main body of wetlands, (ii) depths of water (cm) in channels, (iii) standardised water volumes in the wetlands and (iv) basin complexity indices. To analyse the difference in perimeter lengths for active and inactive wetlands (with and without channels included in the perimeter lengths), we used a repeated measures ANOVA, where wetland type and the presence or absence of channels were categorical factors and perimeter length was the response variable. Lastly, we analysed basin circularity data with a one-way ANOVA, with pond type as the factor (i.e. 1949 inactive, 2007 agricultural inactive, 2008 MLPP active and 2008 MLPP inactive) and the log-transformed basin circularity as the response variable.

For all analyses, we tested the data for normality using the Kolmogorov–Smirnov test and tested homoge-

neity of variances using the Brown and Forsythe test (Brown & Forsythe, 1974). Non-normal data were transformed as noted above and residuals were examined for significant differences. Results were considered significant at $\alpha = 0.05$.

Results

Local scale bathymetry

Water in the main body of the wetland was consistently deeper in wetlands with beavers than those without ($t_{665} = 3.271$, $P = 0.001$, $\bar{x}_{\text{with beavers}} = 0.65$ m, SD = 0.43 m, $\bar{x}_{\text{without beavers}} = 0.56$ m, SD = 0.32 m), and the difference in water depths in channels was even more pronounced ($t_{161} = 6.66$, $P < 0.001$, $\bar{x}_{\text{with beavers}} = 0.43$ m, SD = 0.16 m, $\bar{x}_{\text{without beavers}} = 0.19$ m, SD = 0.08 m). Maximum water depth was 2.25 m for active ponds and 1.42 m for inactive ponds, while 25 channel depths were shallower at 0.77 m and 0.19 m, respectively.

Active ponds had consistently higher standardised volumes ($\text{m}^3 \text{ m}^{-2}$) than inactive ponds ($t_{13} = 2.20$, $P = 0.046$, $\bar{x}_{\text{with beavers}} = 0.75$ m, SD = 0.183 m, $\bar{x}_{\text{without beavers}} = 0.51$ m, SD = 0.224 m). Active beaver wetlands also had more complex bottoms than inactive wetlands (Fig. 2), as indicated by the larger basin complexity indices (BCI; $t_{13} = 3.11$, $P = 0.008$). For these statistical analyses, we removed one inactive wetland (Pond 36) that we realised in subsequent years was regularly reoccupied by beavers from an adjacent pond. All but two active wetlands (Ponds 20 and 28) had the most complex wetland bottoms, while all but one inactive wetland (Pond 36, BCI = 5.6) had the least complex wetland bottoms.

Landscape wetland metrics

Pond perimeters (with channels included) for wetlands with beavers ('active') were, on average, 42.7% longer than the perimeters of wetlands currently lacking beaver ('inactive'). Active wetlands also had wetted areas that were 59.9% larger than inactive wetlands (Table 1). When all 50 wetlands were analysed together, beaver channels increased overall perimeter relative to basin perimeter by 578% on average, due to an additional 46 182 m of wetted shoreline. Wetlands without beavers had a greater per cent increase in pond perimeter lengths when channels were added to the basin perimeter than wetlands with beavers, despite having smaller pond areas and perimeters in general (Table 1). Even when ponds were no longer occupied by beavers, the perimeters of the ponds remained significantly longer

Table 1 Perimeter and area metrics for 16 wetlands in Miquelon Lake Provincial Park, Alberta, Canada, eight of which had active beaver colonies (active) and eight of which were abandoned by beavers (inactive). The entire perimeter of a wetland including adjoining beaver channels was digitised from a 2007 black and white orthophoto (0.25 m pixel size). The perimeters of the main basin of the same wetlands (excluding channels) were then digitised for comparison. The standard deviation (SD) is in brackets.

Wetland Status	Min. Perimeter	Max. Perimeter	Mean Perimeter	Min % increase of wetland perimeter due to channels	Max % increase of wetland perimeter due to channels	Mean % increase of wetland perimeter due to channels	Min. area	Max. area	Mean Area	Min % increase of wetland area due to channels	Max % increase of wetland area due to channels	Mean % increase of wetland area due to channels
Active n = 8	864 m	6752 m	2527 m (1286 m)	102%	4177%	541.5%	2476 m²	73 504 m²	17 704 m² (21 224 m²)	1.7%	577%	59.2%
Inactive n = 8	197 m	4526 m	1449 m (969 m)	22%	2928%	616.7%	334 m²	30 068 m²	7091 m² (7997 m²)	0.4%	985%	121.6%

than the main basin perimeters when channels were included in the perimeter measurements ($F_{1,48}$ = 12.06, P = 0.001, Fig. 3).

Both active and inactive wetlands in the park had lower basin circularity indices and, therefore, more complex shorelines ($\bar{x}_{\text{MLPP Active}}$ = 0.03, SD = 0.02, $\bar{x}_{\text{MLPP Inactive}}$ = 0.06, SD = 0.10) than the same wetlands in 1949, prior to recolonisation by beavers ($\bar{x}_{1949 \text{ Inactive}}$ = 0.50, SD = 0.22). The 25 unoccupied wetlands on agricultural lands in 2007 ($\bar{x}_{\text{Agricultural Inactive}}$ = 0.50, ds = 0.23; $F_{3,117}$ = 130.3, P < 0.0001) had almost identical basin circularity indices as those in the park in 1949 (prior to the recolonisation of beavers) and had less complex shoreline development than ponds in the park in 2007 (Fig. 4).

As determined from the 2007 orthophoto, over 1700 beaver created/modified channels were present in MLPP (approximately 13 km^2) with a total length of 39 848 m (approximately 40 km). Mean channel length was 23.4 m (SD = 31.6 m) with minimum and maximum lengths of 1.1 m and 506.7 m., respectively. The maximum length was formed by beavers connecting three wetlands. Once the middle wetland dried up, the beavers maintained a channel through the old basin to maintain access to the third wetland. This channel only appeared on aerial photographs after beavers recolonised the park (post 1949). The subset of channel widths and depths from field measurements resulted in a mean channel width of 1.4 m (SD = 0.96 m, n = 823 widths)

Fig. 4 Comparisons of log-transformed basin circularity indices for wetlands lacking beavers in 1949 in Miquelon Lake Provincial Park, Alberta, Canada, those same wetlands in 2007 when beavers had recolonised the park, and agricultural wetlands (Ag.) in 2007 on agricultural lands adjacent to the park. 'I' and 'A' denote inactive and active ponds, respectively. Vertical bars indicate 95% confidence intervals.

and a mean channel depth of 0.4 m (SD = 0.20 m, n = 823 depths). Using these metrics, a rough estimate of soil displacement resulting from beaver channel excavations away from the wetland edge was 22 315 m^3 of soil for the entire park. This value does not include the soil that beavers would have excavated during lodge or dam construction or any additional channelling excavations along the bottom of the wetlands.

Discussion

Loss and degradation of aquatic habitats pose ongoing threats to global biodiversity and ecological health (Mitsch & Gosselink, 2007). Additional anthropogenic pressures on species whose engineering activities facilitate or drive ecosystem processes compound the issue of habitat loss in these complex systems. For example, the magnitude of habitat modification by beavers in non-riverine systems demonstrates the multifaceted influence that an ecosystem engineer can have from the local (e.g. wetland) to landscape level (Johnston & Naiman, 1987; Westbrook, Cooper & Baker, 2006; Wright, 2009). The increase of wetted perimeter of morainal wetlands by more than 575% on average demonstrates the important role one species can play in patch dynamics, spatial connectivity and habitat creation. Complex configuration of these perimeters (Fig. 5) also increases within-pond habitat heterogeneity by increasing shoreline complexity, cover for waterfowl
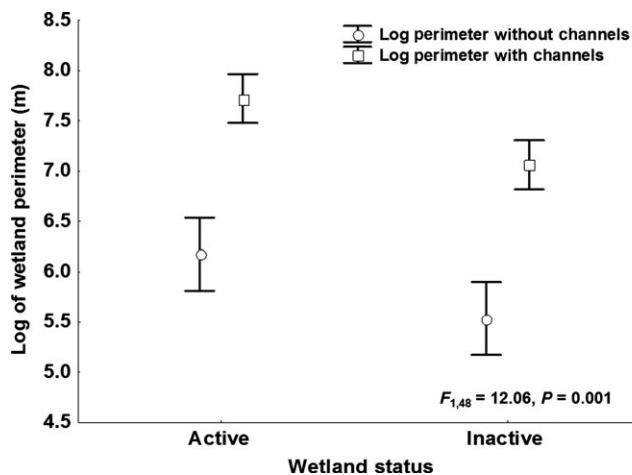

Fig. 3 Comparison of log-transformed perimeter lengths of wetlands with beavers (active) and wetlands lacking beavers (inactive) in Miquelon Lake Provincial Park, Alberta, Canada. A wetland's perimeter was measured with its associated beaver channels, and then, only the main body of the wetland without beaver channels was measured as a comparison. Vertical bars indicate 95% confidence intervals.
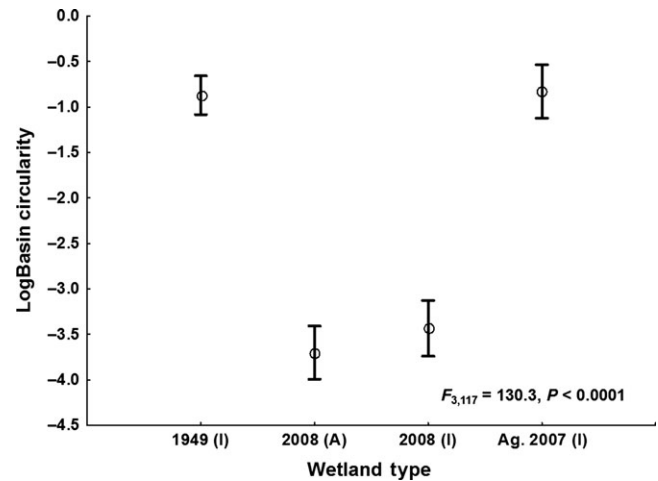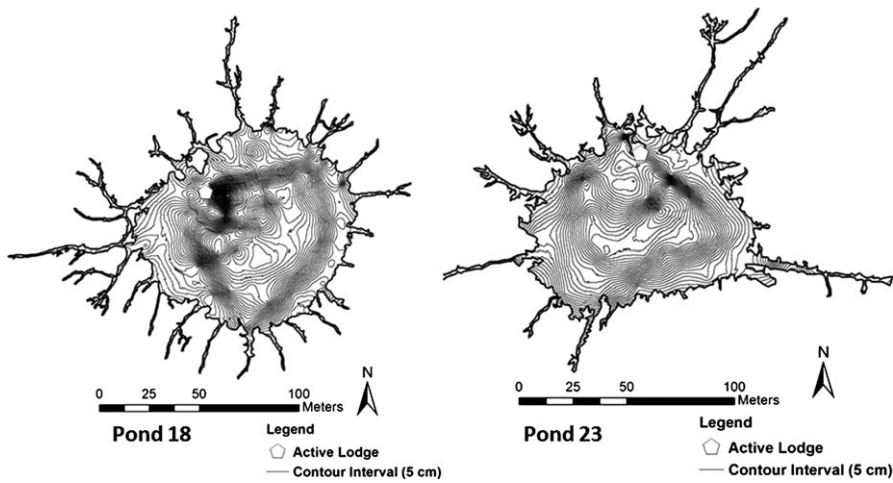
Fig. 5 Bathymetric maps of Ponds 18 and 23 in Miquelon Lake Provincial Park, Alberta, Canada. The field data for the maps were gathered in May and June 2008.

(Nummi & Holopainen, 2014) and potential dispersal corridors for other species to upland and adjacent aquatic habitats (Anderson, 2013).

We also highlighted the effects of ecosystem engineering by beavers beyond dam building and the resulting impoundment of water. Creation and/or modification of channels by beavers appears to direct and maintain water in these otherwise isolated wetlands (Hood & Bayley, 2008a), which might prove especially important in areas predicted to experience increased drought due to climate change (Schindler & Donahue, 2006). During the 2008/2009 drought, we observed that channels and within-wetland excavations focussed water into beaver-modified wetlands (especially immediately in front of the lodge; Fig. 5). These modifications helped to maintain some water in these wetlands while many other ponds dried completely. This drying trend was especially apparent on adjacent agricultural lands, where beaver-modified wetlands were few.

Modification of wetland substratum can have temporal effects as well. Although an average 10-cm difference in water depth in our wetlands might seem slight, in many ecosystems where shallow wetlands are dominant, this difference in water depth could be critical for the overwinter survival of species that forage under the ice for several months of the year (Smith & Peterson, 1991; Ferrell *et al.*, 2010). During the drought of 2002 in east-central Alberta, some beaver ponds in Elk Island National Park, in the northern part of the CLM, froze to the bottom, resulting in overwintering mortality of approximately 10% of the beaver colonies (Hood & Bayley, 2008a). The combination of excavation by beavers of deep holes at lodge entrances and disturbance of the water by beavers when accessing food caches prevented complete freezing in many ponds. Other aquatic organisms (e.g. some amphibians, mammals and invertebrates) would also benefit from access to water under the ice throughout the winter.

Habitat modification by ecosystem engineers in aquatic systems not only affects abiotic factors, such as soil displacement and water storage (Johnston & Naiman, 1987; Jones *et al.*, 1994; Westbrook, Cooper & Baker, 2006; Hood & Bayley, 2008a), but also substantially alters the type, amount and configuration of habitat for other species (Anderson, 2013; Hood & Larson, 2014). Anderson (2013) determined that wood frogs (*Lithobates sylvaticus*) preferentially use beaver channels to disperse from their natal ponds to upland habitats, following metamorphosis. Beaver channels can also act as preferred habitats for some predaceous aquatic invertebrates (Hood & Larson, 2014). Similarly, channels created by common hippos through their movements between aquatic and terrestrial feeding grounds maintain unobstructed corridors in new and existing stream channels (Naiman & Rodgers, 1997; McCarthy *et al.*, 1998).

Despite the apparent importance of channel excavation by beavers (Hood & Larson, 2014), or those created by common hippos (Naiman & Rodgers, 1997; McCarthy *et al.*, 1998), these novel habitats have received little attention in aquatic ecology. By digging channels, beavers extend their territories, provide aquatic access to and from upland foraging areas and reduce predation risk. However, the capacity of channelled wetlands to withstand even extreme drought (Hood & Bayley, 2008a) demonstrates a less obvious, but equally important, role of these channels in the distribution of water and expansion of aquatic habitats. With a density of over 3000 m of channel km^2 in our study, digging of channels within such morainal landscapes is one of the

primary mechanisms by which beavers modify their environment. Beavers do build dams in these areas, but these activities are often limited and focus primarily on plugging culverts and blocking the flow of small intermittent streams. Such effects of channel construction, both physically and chemically through soil displacement, are probably in other similar landscapes, but are as yet undocumented in the literature.

As demonstrated by the difference in bottom complexity indices for wetlands occupied by beavers and abandoned wetlands, beavers also extensively excavated channels in the bed of their wetlands, which also would influence bioturbation and wetland form and function. These extensive excavations probably have effects on microhabitat development, as does nest digging by freshwater fish and migratory Pacific salmon (Gottesfeld *et al.*, 2004; Moore, 2006).

Bioturbation by ecosystem engineers in aquatic systems is often linked to nest digging, foraging and movement within the waterbody (Moore, 2006). Soil disturbance by ecosystem engineers and associated local habitat effects are well documented (Hansell, 1993; Jones *et al.*, 1994; Reichman & Seabloom, 2002; Pringle, 2008). In southwest Alaska, at high population density, spawning sockeye salmon (*O. nerka*) could displace the entire streambed, which exceeds the effects of many flood events (Gottesfeld *et al.*, 2004; Moore, 2006). Much of the research on soil displacement by ecosystem engineers focusses on lotic habitats where high-energy flood events are common and the engineered habitats are occasionally 'reset'. In isolated lentic habitats, the legacy of artefacts of ecosystem engineers might be more enduring, with important implications for local habitat and landscape-level connectivity.

Soil is a fundamental feature of any habitat and, as such, soil displacement and the resulting bioturbation in aquatic habitats can have important influences on biotic communities and habitat configurations (Statzner *et al.*, 2003). Burrowing and tunnelling can also alter hydrological processes, soil chemistry, seed dispersal and habitat availability for other taxa (Meadows & Meadows, 1991; Hansell, 1993; Jones *et al.*, 1994). An estimate of soil displacement in our study due to channelling by beavers was about 1717 m^3 of soil km^2. Excavation and associated bioturbation also influence water and particle fluxes at the sediment–water interface, which can then affect solute exchange and nutrient cycling (Mermillod-Blondin, 2011). Additional research could assess how these chemical changes might create large-scale, indirect effects, even in previously disturbed landscapes and aquatic systems.

Reflecting a global trend in wetland degradation (Junk *et al.*, 2013), agricultural expansion has resulted in loss of 70% of wetlands in Canada's Prairie Provinces (Schindler & Donahue, 2006). Remaining wetlands on agricultural lands can be dramatically altered to increase agricultural production. Agricultural wetlands identified on our 2007 orthophoto had the same average basin circularity index as MLPP wetlands in the 1949 aerial photographs, which had been devoid of beavers for almost a century (Hood & Bayley, 2008a). This lack of complexity has important implications for habitat heterogeneity for other species. Visual and morphometric comparisons of these wetlands to those modified by beavers are striking. Such differences provide a cautionary tale about potential landscape-level effects of removing an ecosystem engineer. Conversely, in North America and Eurasia, where beavers are reintroduced to aid ecological restoration (Nolet & Rosell, 1998), the return of a species that can alter ecosystems so dramatically demands a better understanding of associated biotic and abiotic changes that could occur.

High shoreline complexity is one of the most important factors for enhancing biodiversity in wetlands (Hansson *et al.*, 2005). In our study, the influence of beavers on shoreline and basin complexity at the local (wetland-specific) scale was easily observed; however, this complexity was also readily apparent at the landscape scale. Beaver channels were used not only to link a wetland with its adjacent upland habitats; they also joined one wetland with another over 10s or in many cases 100s of metres. Those wetlands would similarly be joined through the same process over increasingly larger scales. Many of these beaver-modified wetlands (active ones in particular) had an outward appearance resembling neurons with dendritic extensions into the 'tissue' of the surrounding landscape (Figs 2 & 5). Similarly, such channels expanded connections and access to additional habitat at a broad scale.

Ecological network analysis might offer an opportunity to examine further the role that ecological engineering plays at various spatial and temporal scales. Well-connected ecological pathways result in more efficient energy flows (Proulx, Promislow & Phillips, 2005; Fath *et al.*, 2007). Reconfiguration of wetlands by ecosystem engineers and the ecological networks they create through channel construction play an important role in landscape connectivity. Although ecological network theory mainly examines trophic networks (Proulx *et al.*, 2005; Fath *et al.*, 2007), ecological engineering can build on key concepts of ecological network analysis to model connectivity across landscapes. Using beavers as an

example, the lodge could be a 'node', channels and wetland shorelines could be 'edges', which could then provide a base from which to model pathways, nodes clusters, keystone wetlands and various other measures of connectivity and ecological function [see Proulx *et al.* (2005) for specific definitions for ecological networks].

The degree to which an organism can alter its environment, thereby influencing landscape-level biotic and abiotic processes, can be difficult and time-consuming to quantify. The interplay of a number of ecosystem engineers within the same aquatic system adds an increased level of complexity. We demonstrated the dramatic effects of just one ecosystem engineer, the beaver, can have within boreal moraine wetlands. However, beavers often share aquatic habitats with other 'structural ecosystem engineers' (Berke, 2010), such as chironomids, freshwater fish and various species of aquatic and riparian plants. From a soil perspective alone, the cumulative influences on various ecological processes are probably large.

Acknowledgments

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