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REVIEW

Beavers affect carbon biogeochemistry: both short-term and long-term processes are involved

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ABSTRACT

1. With the recent population increase of beavers (*Castor* spp.), a considerable amount of new riparian habitat has been created in the Holarctic. We evaluated how beaver-induced floods affect carbon (C) dynamics in the beaver ponds, and in the water-atmosphere and riparian zone interface.
2. Beaver disturbance affects soil organic C storage by decreasing or increasing it, resulting in a redistribution of C. Upon flooding, the concentration of dissolved organic carbon (DOC) increases in the water. This C can be released into the atmosphere, it can settle down to the bottom sediments, it can be sequestered by vegetation, or it can be transported downstream. The carbon dioxide (CO₂) emissions vary between 0.14–11.2 g CO₂ m⁻² d⁻¹, averaging 4.9 CO₂ g m⁻² d⁻¹. The CH₄ emissions vary too, from 27 mg m⁻² d⁻¹ to 919 mg m⁻² d⁻¹, averaging 222 mg CH₄ m⁻² d⁻¹. Globally, C emission from beaver ponds in the form of CH₄ and CO₂ may be 3.33–4.62 Tg (teragram, 10¹² g) yr⁻¹.
3. The yearly short-term sedimentation rates in beaver ponds vary between 0.4–47 cm yr⁻¹, and individual ponds contain 9–6355 m³ of sediment. The approximate global estimate for yearly C sedimentation is 3.8 Tg C; beaver ponds globally contain 380 Tg sedimented C. After being formed, beaver pond deposits can remain for millennia.

4. Both C sequestration and CO₂ and methane (CH₄) emissions in ponds of various ages should be taken into account when considering the net effect of beavers on the C dynamics. With present estimates, beaver ponds globally range from a sink (−0.47 Tg yr^{−1}) to a source (0.82 Tg yr^{−1}) of C. More research is needed with continuous flux measurements and from ponds of different ages. Likewise, there is a need for more studies in Eurasia to understand the effect of beaver on C biogeochemistry.

Keywords: Carbon dioxide, carbon sequestration, methane, organic matter, sedimentation

Running head: Beaver biogeochemistry

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49 **INTRODUCTION**

50 There is growing evidence showing that large vertebrates can have considerable effects on
51 the biogeochemical processes in ecosystems (Sjögersten et al. 2008, Wilmers & Schmitz
52 2016, Sobral et al. 2017). Herbivores often act by grazing or browsing on vegetation
53 biomass, thereby affecting net primary production and plant species composition,
54 influencing nutrient cycling with their faeces and ultimately affecting soil microbial biomass
55 (Köster et al. 2015, Bakker et al. 2016). Herbivore grazing may also alter physical soil
56 properties such as moisture and temperature (van der Wal & Brooker 2004, Gornall et al.
57 2009).

58 Ecosystem engineers are organisms that physically change the environment by their
59 activities (Jones et al. 1994, Wright & Jones 2006). Numerous case studies illustrate the
60 ways in which engineering organisms modify environments by digging, burrowing or
61 damming. They can have pronounced effects at both large and small spatial scales, and can
62 influence a variety of environments such as various soil and sediment types and water
63 bodies. By affecting the physical characteristics within patches or ecosystems, the
64 engineering organism can change their microbial communities and their functioning.
65 Ecological engineers can thus substantially modify microbial processes such as
66 denitrification, nitrification and mineralization (see reviews by Gutierrez & Jones 2006,
67 Hastings et al. 2007).

68 Beavers (Eurasian beaver *Castor fiber*, American beaver *Castor canadensis*) are important
69 ecosystem engineers in the Northern Hemisphere, capable of modifying the landscape and
70 ecosystems of their riparian habitat (Johnston 2017). The American beaver is also an alien
71 species in South America (Anderson et al. 2009) and in some parts of Europe (Parker et al.
72 2012). Beavers mainly act by building dams and drastically changing hydrology, thereby
73 creating and maintaining water-logged flooded habitats (Baker & Hill 2003). Both abiotic
74 and biotic conditions in riparian areas are changed by damming. A water-level rise may
75 considerably widen wetland areas and also change the physical, chemical and biological
76 conditions in the riparian zone. Both beaver species are assumed to have equivalent effects
77 on the environment (Danilov & Fyodorov 2015), but the American beaver appears to
78 reproduce slightly faster (Parker et al. 2012).

79 Beavers influence the morphology and hydrology of a drainage network, creating a shifting
80 mosaic of patches at various phases of succession in a wet-dry continuum. The occupation
81 time of a beaver colony at a certain site varies from three years to many decades (Johnston
82 & Naiman 1990a, Hyvönen & Nummi 2008). Beavers typically dam first-order to fourth-
83 order streams, and small lakes or peatlands; in streams the dam frequency is 2.5 km^{-1}
84 (Naiman et al. 1988, Nummi & Hahtola 2008, Johnston 2017). Beavers also excavate canals
85 to create deeper-water access to riparian foraging areas; canal excavation can increase
86 average wetland perimeters by 575 % (Hood & Larson 2015). As a result, beavers can have
87 strong long-term impacts on landscape features, particularly because their dams may

endure for much longer than the animals actually inhabit a site. At the landscape level, the magnitude of effects caused by beavers depends on landscape geomorphology, habitat productivity, the size of the beaver population, and the patch dynamics that the animals create (Johnston 2001, Jones et al. 1997, Wright et al. 2003, 2004).

Both the Eurasian and American beaver were on the verge of extinction in the early 1900s due to overexploitation. At that time, only approximately 1000 beavers in small isolated populations survived in Europe; the original population was estimated to be 10 million animals (Halley et al. 2012, Vehkaoja 2016). In North America, most of the American beaver populations at middle and southern latitudes had vanished by 1900 (Baker & Hill 2003). Both species have thereafter shown remarkable recovery. In North America, beavers had returned to most of their original range by the 1950s (Jenkins & Busher 1979), and their present population is estimated to be 30 million (Whitfield et al. 2015). This is still a low number, though, compared to the pre-overhunt situation: 60–400 million beavers roamed in North America before the arrival of Europeans (Seton 1929). The increase in the Eurasian beaver population is more recent, and the species is recolonising or has recolonised, during the last decades, many parts of its original range. The population amounts to at least one million animals and is increasing (Halley et al. 2012).

Mainly by creating impoundments in waterways, beavers have exerted a huge impact on wetland habitats: Hey and Philippi (1995) estimated that before the arrival of Europeans, beavers accounted for over 200000 km² of ponds in the upper Mississippi and Missouri River basins. The extensive loss of upstream beaver wetlands has led to drastically changed hydrological and biogeochemical regimes of riverine systems. In Chesapeake Bay in the east coast of the USA, the loss of upstream beaver wetlands is considered to be one of the reasons behind the eutrophication of the Bay induced by excess supply of nitrogen (Brush 2009). It is obvious that many wetland attributes were changed by beaver removal before modern research, and, therefore, much of our understanding on wetlands is derived from sites lacking this influential ecosystem engineer which normally would be present (Naiman et al. 1988, Nummi & Kuuluvainen 2013).

Due to the recent and ongoing population increase and the beavers' substantial ecological role, there is an emerging need to understand their biogeochemical impact on the boreal landscape. Carbon (C) dynamics, i.e. emissions of greenhouse gases (GHG) methane (CH₄) and carbon dioxide (CO₂), and C sequestration (in sediments and vegetation) are important ecological processes that beavers influence. Beavers thus have the power to affect global climate change. The strength of this power is not known, however, although beavers' ability to mitigate climate-induced extreme weather events has been recognised (Hood & Bayley 2008). Impacts of beavers may have elements of both pulse and press disturbance (Grosse et al. 2011). Pulses are one-time or episodic short-term events that are often extreme in nature and affect a system very rapidly. In the case of the beaver, these include GHG emissions and leaching of C to the water from the flooded shores. Presses occur at the

decadal to century-scale; in beaver ponds and meadows, C sedimentation and storage in plants and soil is such a press disturbance (Johnston 2017). At the landscape level, the net effect of beaver ponds on the C budget is poorly understood. C in small water bodies such as beaver ponds can be released into the atmosphere as GHGs (Bubier et al. 1993, Huotari et al. 2013), it can be transmitted downstream (Naiman 1982, Cirimo & Driscoll 1993), it can settle down to the bottom sediments (Einola et al. 2011, Wohl 2013), or it can be stored in beaver meadow vegetation and soil, creating long-term C storage (Johnston 2014, 2017).

We evaluated how beavers affect the short-term and long-term C cycling processes and assessed the importance of beavers at the landscape and global level, by using existing published information. Our main literature searches were performed in Web of Science and Google Scholar by coupling beaver AND biogeochemistry, beaver AND methane, beaver AND carbon dioxide, and further by using the reference lists of the articles found. These methods rendered us with 13 studies (21 ponds, Table 1) concerning CH₄ in 11 scientific journals, one report and one MSc thesis, while four studies (seven ponds) were focused on CO₂ (Table 2); two of the studies (six ponds) had measured both emissions. Traditional literature searches were used for other aspects.

CARBON AT THE AQUATIC-TERRESTRIAL INTERFACE

The CO₂ emitted from soils mainly originates from the decomposition of soil organic matter (SOM), but respiration of roots and their associated microorganisms is another important source of soil CO₂ (Högberg & Read 2006, Kuzyakov 2006). SOM quantity as well as its quality mainly determine how much CO₂ is emitted from the soil (Karhu et al. 2010, Hamdi et al. 2013). Soils in the areas originally inhabited by beavers, especially in the boreal zone, constitute a vast C reservoir, which beaver-induced hydrological changes can affect (Hengl et al. 2014). Flooding caused by beavers increases the amount of water in soil, often rendering it hypoxic or even anoxic and thus restricting the decomposition of SOM, which may lead to increasing soil C stocks. The soil C stocks in the boreal zone have accumulated over a long time, as the cold and moist climate has resulted in the slow decomposition of SOM (Schuur et al. 2015). In the high-latitude soils of North America the soil organic C content averages 33 kg m⁻² in unfrozen and perennially frozen mineral soils, and 108 kg m⁻² in unfrozen and perennially frozen peatland soils (Grosse et al. 2011); in Finland the mire ecosystems contain 72 kg C m⁻² (mean; Kauppi et al. 1997).

A large amount of C has accumulated in wetlands due to anoxic conditions which slow down the decomposition of organic matter (OM) by microbes. The prevailing anoxia and large supply of OM favour CH₄ production by anaerobic microbes, and wetlands are a globally important source of GHGs, generally accounting for 20–30% of global CH₄ emissions (Bartlett & Harriss 1993, Mitch et al. 2013). Annually, wetlands emit ca. 115 Tg (teragram,

10¹² g) of CH₄, ca. 20 Tg of which originates from boreal wetlands. Flooded areas constructed by beavers are one important, but less well-known component of C dynamics. Alongside the population growth of beavers, so far ca. 25000 km² of new aquatic pond habitat and 550000 km of riparian habitat have been created in boreal and temperate zones (Whitfield et al. 2015).

Fluxes of elements, such as C, are spatially and temporally variable, as are their biogeochemical cycling rates. Enhanced fluxes and reaction rates at the zone where terrestrial and aquatic ecosystems meet have been recognised already for some time (Huttunen et al. 2003, Juutinen et al. 2003a). These biogeochemical hot-spots (McClain et al. 2003) may occur in permanently water-covered littoral zones, and especially in recently flooded riparian zones, where both standing and decaying vegetation is abundant (Juutinen et al. 2003b, Kankaala et al. 2003, Larmola et al. 2004). Through the aquatic-terrestrial interphase, beaver ponds receive a substantial amount of dissolved organic carbon (DOC) and dissolved inorganic carbon, together with nutrients, in drainage and runoff water from the surrounding catchment (Vehkaoja et al. 2015; see Rasilo et al. 2015) and also from the decaying vegetation in the flooded area (Nummi 1989, Naiman et al. 1994).

SHORT-TERM CARBON EMISSIONS FROM BEAVER PONDS

Many studies have shown that beaver ponds are hot-spots of GHG emissions (Table 1). The estimated total annual gaseous C flux of 210 g C m⁻² yr⁻¹ from a beaver pond has been contrasted to the aerial C sink provided by forests (-5 g C m⁻² yr⁻¹; Roulet et al. 1997). These estimates of CH₄ and CO₂ emissions were based on laboratory incubations of beaver pond soils (Updegraff et al. 1995, Scanlon & Moore 2000), along with gas flux measurements using chambers (Naiman et al. 1991, Bubier et al. 1993, Lazar et al. 2014) and flux gradient techniques (Roulet et al. 1997). Beaver ponds show considerable variation in their fluxes, and the variability appears to have both temporal and spatial components (Moosavi & Crill 1997, Dove et al. 1999, Weyhenmeyer 1999). However, there is not a single study of beaver pond GHG emissions from Eurasia and there is only one study based on the continuous flux gradient technique (Roulet et al. 1997). So far, there are no emission studies from beaver ponds based on continuous micrometeorological eddy covariance measurements, which are already common-place in wetland studies and are becoming more common in aquatic research (Laurila et al. 2012, Vesala et al. 2012). These gaps certainly affect our knowledge on temporal as well as spatial variation in beaver ponds.

In general, gas emission studies in beaver ponds have been strongly focussed on CH₄ fluxes. Emissions can be considerable, and may, in certain regions, account for over 30% of the CH₄ emissions (Roulet et al. 1992). The estimate for beaver pond CH₄ emissions is not accurate because it arises from complex interactions among fermentative, methanogenic and methanotrophic processes that vary nonlinearly with oxygen, temperature and C content,

all of which also vary temporally and spatially (Moosavi & Crill 1997, Grant & Roulet 2002). However, with the range of estimated present population size, beaver-created wetlands are estimated to account for 0.18–0.80 Tg of CH₄ emissions per year (Whitfield et al. 2015).

The CH₄ emissions from various beaver ponds vary strongly, ranging from 27 mg CH₄ m⁻² d⁻¹ (Ford & Naiman 1988) to 919 mg CH₄ m⁻² d⁻¹ (Bubier et al. 1993; Table 1). The mean for all 21 ponds included in this review is 222 mg CH₄ m⁻² d⁻¹ (Fig. 1). This figure (27.8 kg CH₄ m⁻² year⁻¹, open water period 125 d) is almost one third higher than the figure (20 kg CH₄ m⁻² year⁻¹) used for global beaver pond emissions in Whitfield et al. (2015). Large variation occurs both between beaver ponds in various regions and between ponds within the same area (Table 1). We tested whether latitude (°N), annual precipitation, annual mean temperature and mean temperature in the growing season have an effect on CH₄ emissions; generalised linear models were performed in R. Latitude was the only factor affecting CH₄ emissions. The higher the latitude, the greater the CH₄ emissions (value = 19.958, standard error = 9.473, t-value = 2.107, P = 0.049).

Temporal variation is found on a daily, seasonal and annual level, as well as in ponds of various ages. In the more northerly areas, measurements normally took place during one open water season from May to September-October; in a more southerly location (Lazar et al. 2014), samples were taken during a period lasting from autumn to the next summer. Typically, sampling was not done with high frequency and samples were taken weekly or even at longer intervals (e.g. Roulet et al. 1992, Yavitt et al. 1992, Bubier et al. 1993, Moosavi & Crill 1997).

Only a few studies provide the age of the impoundments. In one case, a new pond had a higher CH₄ flux (ca. 400 mg CH₄ m⁻² d⁻¹) than the older ones (30–130 mg CH₄ m⁻² d⁻¹; Lazar et al. 2014), whereas in another study, the fluxes in a pond older than 30 years were similar to those in a three-year-old pond, i.e. 138 and 162 mg CH₄ m⁻² d⁻¹, respectively (Yavitt et al. 1992).

During the summer, water level and sediment temperature along with wind speed have been shown to affect the CH₄ emissions from beaver ponds, with episodic release of CH₄ bubbles (ebullition) in particular following trends in sediment temperature (Moosavi & Crill 1997, Roulet et al. 1997, Dove et al. 1999). Larger CH₄ effluxes occur when warming of the pond sediments generates episodic ebullition through heat flux (Grant & Roulet 2002). In small lakes, ebullition does not occur until a threshold temperature is reached, and this temperature is linked to the point where sediment pore water becomes saturated with CH₄ (Wik et al. 2014). In shallow waters such as beaver ponds, the threshold is controlled by temperature-driven changes in gas solubility and production rates of CH₄ (Martens et al. 1998). The effects of beavers on water temperature have been studied quite extensively with varying results, but with the common conclusion that beaver damming increases water

temperature (Majerova et al. 2015); at higher temperature gas solubility decreases. The daily variation in CH₄ ebullition is also related to changes in atmospheric pressure, and bubble fluxes tend to be higher when the pressure is decreasing (Maeck et al. 2014). This all creates problems for the timing of sampling, and highlights the importance of high frequency measurements in beaver ponds.

Contradictory findings in the CH₄ fluxes have been observed when considering the summer water level decrease, as the fluxes can either increase (Weyhenmeyer 1999) or decrease (Bubier et al. 1993) as a consequence of water level drawdown. In the short term, fluxes of CH₄ as well as CO₂ can be highest during the day (Roulet et al. 1997). Occasionally, not much diurnal variability has been observed in the beaver pond itself, but some has been recorded in the flooded mire bordering the pond (Moosavi & Crill 1997), probably as a result of diurnal variation in soil surface temperature affecting soil CO₂ effluxes, as most of the CO₂ is produced in soil surface layers (Pumpanen et al. 2008). When aquatic macrophytes such as water lilies (Nymphaeaceae) and reeds (*Phragmites* spp.) are present in beaver ponds (Ray et al. 2001), the diurnal CH₄ flux pattern is believed to be present, as observed in lake littoral zones (Dacey & Klug 1979, Kki et al. 2001). However, flux measurements over 24 h cycles from beaver ponds in that successional state are yet to come.

Spatially, large variation in CH₄ fluxes occurs in various parts of the beaver pond complex. Dove et al. (1999) found that approximately twice as much CH₄ was emitted from the open section of the beaver pond (320 mg CH₄ m⁻² d⁻¹) than from a section vegetated with sedge *Carex* spp. (155 mg m⁻² d⁻¹); a similar pattern was found by Grant and Roulet (2002) by combining and modelling CH₄ efflux from chamber and flux tower measurements. Naiman et al. (1991) observed that the annual CH₄ flux from the submerged vegetation and open zones was ca. 30 times higher (63 mg C m⁻² d⁻¹) than that from the boreal forest and sedge meadow zone (1.98 mg C m⁻² d⁻¹). Moosavi and Crill (1997) found, again, that mean summer season flux of CH₄ was 153 mg CH₄ m⁻² d⁻¹ from the pond, but as high as 1144 mg CH₄ m⁻² d⁻¹ from the flooded mire bordering the pond. Higher CH₄ fluxes from the sedge meadow are due to sedges acting as conduits of CH₄ between the anoxic peat layers and the atmosphere (Noyce et al. 2014).

In addition to CH₄, CO₂ is a major GHG. Although the Global Warming Potential of CH₄ is 28-32 times higher over a 100-year time horizon, the magnitude of CO₂ emissions and their contribution to the climate on a global scale is much larger than that of CH₄ (Etminan al. 2016). CO₂ fluxes from beaver ponds have been measured in only a few studies, and fluxes have ranged from 0.14 g CO₂ m⁻² d⁻¹ (Naiman et al. 1986) to 11.2 g CO₂ m⁻² d⁻¹ (Yavitt & Fahey 1994), the mean being 4.9 g CO₂ m⁻² d⁻¹ (Table 2, Fig. 1). We tested if there were correlations between CO₂ and latitude (N), annual precipitation, annual mean temperature and mean temperature in the growing season. The mean annual temperature correlated positively with CO₂ emissions ($r_s = 0.869$, $t = 3.920$, $P = 0.011$). The other factors did not

have a significant correlation with CO₂, although the CO₂ fluxes tended to be higher in older ponds. Seasonal differences are large, but variation is not consistent. Lazar et al. (2014) found significantly higher CO₂ fluxes in autumn than in spring or summer, whereas Yavitt and Fahey (1994) recorded the highest fluxes at midsummer. By damming fast-flowing streams and creating stagnant ponds instead, beavers probably decrease gas transfer velocities in the landscape, since gas transfer velocities in streams are usually much higher than those in small lakes (Heiskanen et al. 2014). However, there are no spatial studies on the effects of beavers on gas transfer velocities.

Spatiotemporal variability has been found in growing-season net ecosystem CO₂ exchange in different parts of a beaver pond. While the mesic margin of a beaver pond switched from a net sink to a source of CO₂ (as well as most peatland locations did) during a dry summer, the wet beaver pond margin remained as a CO₂ sink (Bubier et al. 2003). In comparison, in a boreal lake, the upper flooded shoreline with highest plant biomass acted as a source of CO₂, whereas the lower flooded zone was a sink of CO₂; this difference could be related to the amount of OM and resulting ecosystem respiration (Larmola et al. 2003). In lakes, inter-annual differences in littoral net ecosystem productivity can be linked to water level changes as well as phenology of aquatic plants (Larmola et al. 2004), but there are no specific studies on annual variation in net ecosystem productivity in beaver ponds. Wegener et al. (2017) compared aquatic ecosystem metabolism in a beaver-influenced river segment to a non-affected one. Due to changes in hydrology, gross primary production and especially ecosystem respiration increased, rendering the system more heterotrophic.

The annual global emission of C in CH₄ and CO₂ can be estimated at 3.33–4.62 Tg. The range represents CH₄ estimates from Whitfield et al. (2015) and this review; the CO₂ emissions are assumed to be 27-times higher as found in this review.

DISSOLVED ORGANIC CARBON FLUXES

When beavers increase the water level of a pond or stream, a reversible increase of DOC may occur in the water. This is no surprise, as the soil-derived C flux is known to be the largest component of the C flux to inland waters, and is also potentially strongly affected by the riparian zone (Rasilo et al. 2015). Vehkaoja et al. (2015) found that a considerable increase in DOC occurred in the water of ponds upon flooding by beavers. After three years of inundation, the C concentration reverted to pre-flood levels. Furthermore, in that study DOC concentrations did not increase downstream along the lake chain (Vehkaoja et al. 2015). Similarly, Devito et al. (1989) and Koschorreck et al. (2016) found no net export of DOC from beaver ponds; nor did Naiman et al. (1986), but they noted that at the watershed level export does occur (Naiman 1982). Cirimo and Driscoll (1993), on the other hand, found a beaver pond to be a net annual source of DOC, whereas Correll et al. (2000) found a

beaver pond to reduce the annual discharge of total organic carbon. Wegener et al. (2017) reported that beaver activity created an environment where DOC was retained. Thus, there is no consistent conclusion on DOC export from beaver dams.

During the first impoundment years, DOC within beaver wetlands mainly originates from dying herbaceous vegetation and tree leaves (Hodkinson 1975, Nummi 1989). Such DOC is mostly composed of low-molecular-weight carbohydrates, which are easily available for microbial consumers. In contrast, C in the following impoundment years might mainly originate from flooded soils that were initially terrestrial (Rasilo et al. 2015). DOC originating from soils comprises biologically refractory high-molecular-weight humic and fulvic acids, which are mostly removed by photochemical reactions (Olefelt et al. 2013). At least in beaver wetlands that are open and exposed to sunlight and especially to ultraviolet radiation, this is one plausible alternative for the removal of DOC as CO₂ (Salonen & Vähätalo 1994, Vehkaoja et al. 2015). However, in humic water bodies such as beaver ponds, ultraviolet radiation attenuates quickly and thus the photochemical removal processes can only take place in the thin surface layer (Huovinen et al. 2003). Especially in older ponds, waterborne autochthonous DOM and particulate OM of inlet streams may be the main source of C (Hodkinson 1975). While studying quality and biodegradability of DOM, Catalán et al. (2017) found that beaver damming and later pond ageing have similar effects on DOM quality, but the stagnant pond systems, in comparison to stretches of streams, modify C sources and processing for a longer time.

LONG-TERM CARBON DYNAMICS IN BEAVER-AFFECTED PATCHES AND LANDSCAPES

Beaver damming alters sediment transport and storage patterns along riparian landscapes, and beaver activities translocate chemical elements from the upland forest vegetation to pond sediments. A considerable amount of C may be stored in submerged forest trees in the beaver ponds; in a study in North America the amount of C varied between 1993 and 9206 g C m⁻² (Johnston 2017). Beaver-inundated forest patches have been found to contain a mean of 31 m³ of dead wood per hectare, but occasionally up to 280 m³ can be found (Thompson et al. 2016); the average represents 1491 g C m⁻² (Fig. 1). The difference found by Thompson et al. (2016) reflects the pattern that when beavers dam a creek usually the whole inundated area consists of forest, whereas when a pond is dammed the inundated area may partly consist of a former meadow or bog (authors' observations).

It takes a long time for woody tissue to decompose. Usually the decomposition requires a few decades or centuries, but in anaerobic conditions, beaver-felled or inundated trees may be preserved for thousands (or even hundreds of thousands) of years, and thus they become a long-term store of C (Garrison 1967, Aalto et al. 1989). Beavers also cut and transport wood to the water from un-flooded shores (Wohl & Scott 2017). Colonies remove

on average eight Mg (megagram = 10^6 g) of trees (four Mg of C, Liu & Westman 2009) per year from the browsing zone around their ponds. Beavers consume only a small fraction of this as food, but most is used for the dam; an average dam contains seven Mg of wood (Johnston & Naiman 1990b). Lodges and food caches also contain considerable amounts of wood but these have never been quantified. The area affected by beaver foraging and flooding may even constitute one quarter of the landscape (Johnston 2001). Beaver foraging thus also affects C storage, as has been shown for tropical herbivores (Sobral et al. 2017).

Naiman et al. (1986) noted that a beaver pond contains substantially more benthic OM per unit area than a shallower riffle: 7800 vs. 160 g DW m^{-2} . The standing stock of OM was 50-fold more in the pond than in the riffle; this increased to almost 350-fold when computed per linear meter of channel. Johnston (2014) found the density of C to be about twice as high in beaver meadow soils (15.1 kg m^{-2}) than in non-impounded forest soils (8.2 kg m^{-2}). The amount of sediment in beaver ponds reflects the size of the pond, and can vary greatly: individual ponds may contain 9–6355 m^3 of sediment (Table 4, Meentemeyer & Butler 1999, Butler 2012, Wohl & Scott 2017). However, few studies have used dating techniques to check whether beaver pond sediments were actually deposited during the lifetime of the beaver pond. Landscape-level sediment accumulation in beaver ponds has also been estimated, showing that beaver dams retained 3.2×10^6 m^3 of sediment in small-order streams in a 673- km^2 study area. This would have been enough to cover the bottom of the surface streams in the drainage with an additional 42 cm of sediment (Naiman et al. 1986).

As only part of the C in beaver ponds is exported downstream or returned to the atmosphere, the pond sediments accumulate substantial standing stocks of C (Hodgkinson 1975, Naiman et al. 1994, Levine & Meyer 2014). With 13 million beaver ponds globally (Pollock et al. 2003, Whitfield et al. 2015), 765 m^3 sediment per pond, and 38 kg C m^{-3} (Johnston 2017), there would be presently 378 Tg C sedimented in beaver ponds. Sedimentation is suggested to occur relatively rapidly in the early years after dam construction, after which sedimentation slows down (Butler & Malanson 1995). The yearly short-term sedimentation rate varies between 2 and 47 cm yr^{-1} (Pollock et al. 2007a, Giriat et al. 2016 and references therein). Clearly lower sedimentation rates (0.4 cm yr^{-1}) have been found in the decadal or centennial time scale (Devito & Dillon 1993, Polvi & Wohl 2012). With this decadal rate, and assuming 25000 km^2 of flowages (Whitfield et al. 2015) and 38 kg C m^{-3} , the yearly global C sedimentation would be 3.8 Tg. During a post-glacial period spanning 4300 years, aggradation rate was found to be ~ 0.05 cm yr^{-1} (Polvi & Wohl 2012). Lakes usually show much larger C evasion than accumulation: in boreal lakes smaller than 0.1 km^2 in size, evasion to accumulation ratio can be > 40 . If they are similar to small lakes, beaver ponds are very likely to be hot-spots of C processing (Kortelainen et al. 2006). However, none of the sedimentation studies in beaver ponds contains information on atmospheric C fluxes.

The persistence of beaver-induced sediments varies depending on hydrologic, geomorphic and environmental factors. Often, part of the fine sediment is quickly transported out of the former beaver pond after dam breaching (Levine & Meyer 2014, Wohl & Scott 2017), but considerable long-term sedimentation may still take place (Polvi & Wohl 2012, Wohl et al. 2012). Sometimes the breached dam also initiates a forced meander where sediments accumulate; the overbank sedimentation caused by beaver damming can often be more important than meandering (Levine & Meyer 2014). Breaching of the abandoned dam can result in at least partial erosion of the pond sediment, although establishment of rooted aquatic macrophytes and other wetland vegetation commonly limits evacuation of pond sediment (Wohl & Scott 2017). Beaver pond deposits can remain for thousands of years, as has been shown from late Holocene deposits dated with radiocarbon (Persico & Meyer 2009, Polvi & Wohl 2012, Persico & Meyer 2013) or ground penetrating radar (Kramer et al. 2012).

After the last glaciation, beavers also enhanced C storage by having a role in peatland formation (Gorham et al. 2007). Bog expansion caused by a rising water table could be catalysed by beaver damming in low-gradient landscapes. When there is an adequate supply of water but flow is inadequate to re-establish a stream, beaver patches may serve as nuclei for paludification, providing sites for the establishment of peat-forming sedges and bryophytes (Johnston 2001, Charman 2002).

Beaver impoundments indirectly accelerate OM accumulation by promoting growth of productive aquatic plants that generate thick litter layers and form peat tussocks. Sedge meadows have moderate primary productivity (Johnston 2001) and relatively slow decomposition rates (Chamie & Richardson 1978), which optimises OM accumulation (Johnston 2017). Beaver impoundments also promote the formation of floating peat mats. This growth form promotes the accumulation of OM, because plant productivity in the floating mat remains stable and high, while decomposition is slow due to anoxia below the mat (Johnston 2001).

Beaver pond sediments may accumulate more C than normal lake sediments, as ponds are not permanent water bodies. Beaver impoundments alternate between being flooded and drained as they are colonised and abandoned by beavers. After abandonment, beaver ponds may become beaver meadows, colonised by wetland grasses and sedges that can sequester C via photosynthesis (Johnston 2014). In mountainous headwater catchments, beaver meadows store the great majority of C along rivers. This C storage source cumulatively represents approximately 8% (relict) to 23% (active) of the estimated total landscape C storage (Wohl 2013). The estimated 23% of total landscape C storage within active beaver meadows agrees well with another estimate for total C storage in unconfined valley bottoms (25%), which included beaver meadows and old-growth forest with substantial downed wood (Wohl et al. 2012).

Beaver engineering results in significant landscape-scale C storage. Thus, restoration of beaver populations and beaver meadows is of critical importance in management strategies designed to enhance ecosystem services such as habitat provision and C sequestration (Pollock et al. 2007b, Wohl 2013). When beavers were removed, the C storage of wet beaver meadows were replaced by the alternative “steady state” of relatively dry grasslands (Wolf et al. 2007, Green & Westbrook 2009): dry grassland soils average 4–10 kg C m⁻² (Buringh 1984), as opposed to 30–40 kg C m⁻² found in relict beaver meadows and 115–140 kg C m⁻² (Fig. 1) in active beaver meadows (Wohl 2013). A considerable amount of habitat heterogeneity was also lost, since creek channel complexity increases downstream of beaver dams. The increased complexity forms a positive feedback for beaver-induced sedimentation. A multi-thread channel increases potential channel length for further damming, which, again, increases the potential area for beaver ponds and the volume of trapped sediment (Polvi & Wohl 2012).

CONCLUSIONS

While being a source of atmospheric GHGs, beaver ponds – similar to wetlands in general – also sequester C (Johnston 2014, Mitch et al. 2013). This feature of simultaneously acting as both a source and a sink for C turns a landscape of beaver ponds into a very complicated system. Beavers perturb ecosystems in a way that comprises elements of both press and pulse disturbance (Grosse et al. 2011). In addition, it is evident that beaver-induced C dynamics contain both processes that increase C release to the atmosphere and processes that reduce it.

The balance between C sequestration and GHG emissions is of crucial importance when the role of wetlands is considered from the viewpoint of e.g. habitat restoration (Mitch et al. 2013). Wetlands are generally held as neutral in terms of radiative forcing (Mitch et al. 2013), but the widely varying figures for beaver ponds show that, globally, the ponds range from a sink (–0.47 Tg year⁻¹) to a source (0.82 Tg year⁻¹) of C.

Uncertainty in these figures is caused, for example, by the great amount of spatial and temporal variation in GHG emissions in beaver pond habitats, and by the fact that the emissions have only rarely been measured continuously, and from ponds of various known ages. Finally, more research on beaver-C dynamics is definitely needed in Eurasia, since hardly anything is known about beaver ponds on Eurasian soils.

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Table 1. Emissions of methane (CH₄) from beaver ponds in Canada and the USA. GS = growing season. Numbers in brackets are the pond ages in years, if known.

Study	Location	Latitude (°N)	Annual mean temperature	Mean temperature in GS	Annual precipitation (mm)	CH ₄ (mg m ⁻² d ⁻¹)
Bubier et al. 1993	Ontario	49	+1°C	+14°C	780	919
Bubier et al. 1993	Ontario	49	+1°C	+14°C	780	136
Bubier et al. 1993	Ontario	49	+1°C	+14°C	780	365
Bubier et al. 1993	Ontario	49	+1°C	+14°C	780	147
Dove 1999	Manitoba	56	-4°C	+12°C	585	238
Ford and Naiman 1988	Quebec	50	+1°C	+17°C	1120	27
Lazar et al. 2014	Rhode Island	41	+10°C	+19°C	1270	30 (10)
Lazar et al. 2014	Rhode Island	41	+10°C	+19°C	1270	400 (4)
Lazar et al. 2014	Rhode Island	41	+10°C	+19°C	1270	130 (14)
Naiman et al. 1991	Minnesota	49.5	+1°C	+14°C	620	78
Moosavi & Crill 1997	Manitoba	56	-4°C	+12°C	585	649*
Roulet et al. 1992	Ontario	45	+4°C	+14°C	1102	30
Roulet et al. 1992	Ontario	45	+4°C	+14°C	1102	47
Roulet et al. 1992	Ontario	45	+4°C	+14°C	1102	91
Roulet et al. 1997	Manitoba	55	-3°C	+11°C	517	112
Vitt et al. 1990 ^α	Alberta	54	+4°C	+16°C	470	518
Weyhenmeyer	Ontario	45	+4°C	+15°C	1000	37
Windsor 1993 ^α †	Quebec	56	+1°C	+17°C	1120	685*
Yavitt et al. 1990	West Virginia	39	+8°C	+16°C	1333	162 (3)
Yavitt et al. 1990	West Virginia	39	+8°C	+16°C	1333	138 (30)
Yavitt et al. 1992	Adirondack (New York)	43	+12°C	+17°C	1100	150
Mean						222

^α ref. Moore 1994

† Temperatures from Ford & Naiman 1988

* mean for various pond sections

948 Table 2. Emissions of carbon dioxide (CO₂) from beaver ponds in Canada and USA. GS = growing
 949 season. Age of pond shown, if known.

Study	Area	Latitude (°N)	Annual mean temperature	Mean temperature in GS	Annual precipitation (mm)	Age of pond $\bar{x}$	CO ₂ (g m ⁻² d ⁻¹)
Lazar et al. 2014	Rhode Island	41	+10°C	+22°C	1270	4	4.0
Lazar et al. 2014	Rhode Island	41	+10°C	+22°C	1270	10	5.0
Lazar et al. 2014	Rhode Island	41	+10°C	+22°C	1270	14	7.0
Naiman et al. 1986	Quebec	50	+1°C	17,1°C	1120		0.51
Roulet et al. 1997	Manitoba	55	-3°C	+11°C	517		0.1
Yavitt & Fahey 1994	Adirondacks	43	+12°C	+17°C	1100	3	7.6
Yavitt & Fahey 1994	Adirondacks	43	+12°C	+17°C	1100	30	11.2
Mean							4.9

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969 Table 3. Sediment storage in beaver ponds. Modified from Wohl and Scott (2017), with addition of
 970 Pollock et al. (2007), Westbrook et al. (2011) and Levine and Meyer (2014). ? = not known.

Study	Sediment volume (m ³)		974
	Mean	Range	
Butler & Malanson 1995, USA	945	11-5084	978
Meentemeyer & Butler 1999, USA	111	9-267	8
Westbrook et al. 2009, USA	750	(one pond)	973
Butler 2012, USA	3069	876-6355	10
Levine & Meyer 2014, USA	92	48-182	974
Pollock et al. 2007a, USA	554	?	13
Green & Westbrook 2009, Canada	387	98-842	8
John & Klein 2004, Germany	223	33-516	975
Mean	765		
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Fig. 1. Carbon (C) dynamics in the beaver wetland. The figure shows the main states and amounts of carbon in beaver wetlands. C is emitted as methane (CH₄) and carbon dioxide (CO₂), while also being stored in deadwood and sediments. The amount of DOC (dissolved organic carbon) is high during the first three impoundment years. The value of sedimented C is obtained from Wohl 2013; methane and carbon dioxide from this paper; DOC from Vehkaoja et al. 2015; and C stored in deadwood is calculated using values from Liu and Westman 2009 (dry weight of conifers) and Thompson et al. 2016 (average deadwood amount at beaver sites).