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Article *in* Biogeochemistry · May 2015

DOI: 10.1007/s10533-015-0105-4

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Biogeochemistry (2015) 124:405–415
DOI 10.1007/s10533-015-0105-4

Spatiotemporal dynamics of boreal landscapes with ecosystem engineers: beavers influence the biogeochemistry of small lakes

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Received: 1 December 2014 / Accepted: 28 April 2015 / Published online: 17 May 2015

Abstract It has been suggested that beavers affect biogeochemical processes and the environment on a relatively large scale, thus acting as ecosystem engineers. In this long-term study we evaluated the effects of beavers on water chemistry in small boreal lakes of Southern Finland. We addressed the following three questions; does water chemistry differ between beaver and non-beaver lakes; does water chemistry differ between the flood years in comparison to the antecedent years; and does the flood impact downstream lakes? The results showed that beaver lakes had higher dissolved organic carbon (DOC) concentrations but lower dissolved oxygen (DO) concentrations than non-beaver lakes. DOC concentration increased during the first three beaver-impoundment years when compared to the pre-impoundment situation, and DO concentrations simultaneously decreased. Lake DOC concentrations furthermore declined back to initial levels after the impoundment had lasted for 4–6 years. The opposite occurred with DO. No clear effects caused by beaver impoundments were found in downstream lakes however. Beaver activity had no effect on N and P concentrations in lakes, but our results emphasize that the beaver affects the carbon cycling in the boreal zone. Further research is therefore needed to clarify its effect on the carbon balance at different spatial scales.

Keywords Beaver impoundment · Before–after setting · Biogeochemical hot spot · Boreal lakes · Carbon balance · Dissolved organic carbon · Nutrient pulse

Responsible Editor: Jennifer Leah Tank.

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Introduction

Apart from playing a role as assimilatory and dissimilatory compartments in ecosystems and their element cycling, organisms may also influence different chemical and microbial processes. One way of achieving this is physical ecosystem engineering, which affects the environment at both spatial and temporal scales. Ecosystem engineering is a widespread phenomenon, and includes processes such as digging, burrowing, and damming (Gutiérrez and Jones 2006; Wright and Jones 2006). Hastings et al. (2007) recently pointed out that although all organisms affect their physical environment, the influence of ecosystem engineers is much more profound and protracted than the impact organisms usually have on their environments. Ecosystem engineers may affect biogeochemical processes by changing physical and chemical conditions, and as a result the heterogeneity of the environment and the biota may be enhanced (Gutiérrez and Jones 2006).

Regarding biodiversity, the beaver (*Castor* sp.) can be considered an important ecosystem engineer capable of modifying wetlands in the Northern Hemisphere and ecosystems therein (Jones et al. 1994; Wright et al. 2002), mainly by building dams and thus creating and maintaining flooded habitats (Baker and Hill 2003). Damming changes both the abiotic and biotic conditions of a wetland or lake. A rise in water level may considerably increase wetland area and also change the physical, chemical, and biological conditions in the surrounding terrestrial catchment. Redox conditions will be changed in the soil as a result of the damming, and organic carbon and nutrients may be released and transported to the recipient lakes depending on soil type. If the soil is predominantly composed of inorganic minerals, the loading effect may differ from that in organic soils (Naiman et al. 1988). Trees and other dying terrestrial vegetation that finally fall into the water bring nutrients and energy to aquatic ecosystems (Collen and Gibson 2001; Nummi and Kuuluvainen 2013).

Beavers may also alter the morphology and hydrology of a drainage network, which creates a mosaic of temporally and spatially unevenly distributed patches (Naiman et al. 1994). As a result, in the long term beavers can influence landscape features, particularly because their dams may endure much longer than the animals actually inhabit a site.

Beavers (Eurasian beaver *Castor fiber* L. and American beaver *C. canadensis* Kuhl) were on the verge of extinction in the nineteenth century due to overexploitation, and only eight small isolated populations of the Eurasian beaver remained in the Eurasian continent (Halley and Rosell 2002). Both species have subsequently recovered remarkably. The recovery of the Eurasian beaver is more recent and the species has recently recolonized or is recolonizing many parts of its original range (Halley et al. 2012). We therefore need to understand the beavers' impact on the boreal landscape.

The boreal landscape contains huge pools of both terrestrial and aquatic carbon, which play an important role in the global carbon balance (Couture et al. 2012; Olefeldt et al. 2013; Moen et al. 2014). Large fractions of the boreal landscape are covered with lakes (Downing et al. 2006), making lakes probably more significant to the carbon balance of boreal areas than of any other region (Tranvik et al. 2009). Boreal forests and peatlands receive their carbon from the atmosphere (Apps et al. 1993; Weber and Flannigan 1997; Lavoie et al. 2005), while boreal lakes receive their carbon largely from terrestrial ecosystems (Sarvala et al. 1981; Arvola et al. 1990; Olefeldt et al. 2013). Most of their carbon is in the form of dissolved organic carbon (DOC), which is then mineralized and transformed (Tranvik et al. 2009; Kortelainen et al. 2013). A minor portion of the DOC accumulates in the lake sediments (von Wachenfeldt and Tranvik 2008; Einola et al. 2011).

Several studies have focused on how beavers change the biogeochemistry of boreal lotic waters, thus altering them into lentic waters (Naiman et al. 1994; Margolis et al. 2001; Hill and Duval 2009). According to our knowledge until currently none have emphasized the biogeochemistry of already existing boreal lentic waters. Our 35-year study is the first to demonstrate the effects of a beaver (*C. canadensis*) impoundment on water chemistry before and during impoundment in small boreal lakes. We address the following three questions: (1) Does water chemistry differ between beaver and non-beaver lakes? (2) Does water chemistry differ between the impoundment years in comparison to the antecedent years? (3) Do the possible effects of the impoundment reach the downstream higher order lakes?

Materials and methods

Study area

Our study area (66.50 km^2) is situated in the Evo forest area in Southern Finland (61°10′N, 25°05′S) (Fig. 1). The area belongs to the southern boreal vegetation zone (Ahti et al. 1968), and consists of approximately 100 small, humic headwater lakes with an average surface area of 4.3 ha (0.3–45.0 ha). A major number of the lakes are interrelated with brooks, and they thus form a network of lakes in the landscape (see Järvinen et al. 2002). The lakes in our study area are situated in the uppermost reaches of River Kokemäenjoki, the fifth largest river basin in Finland.

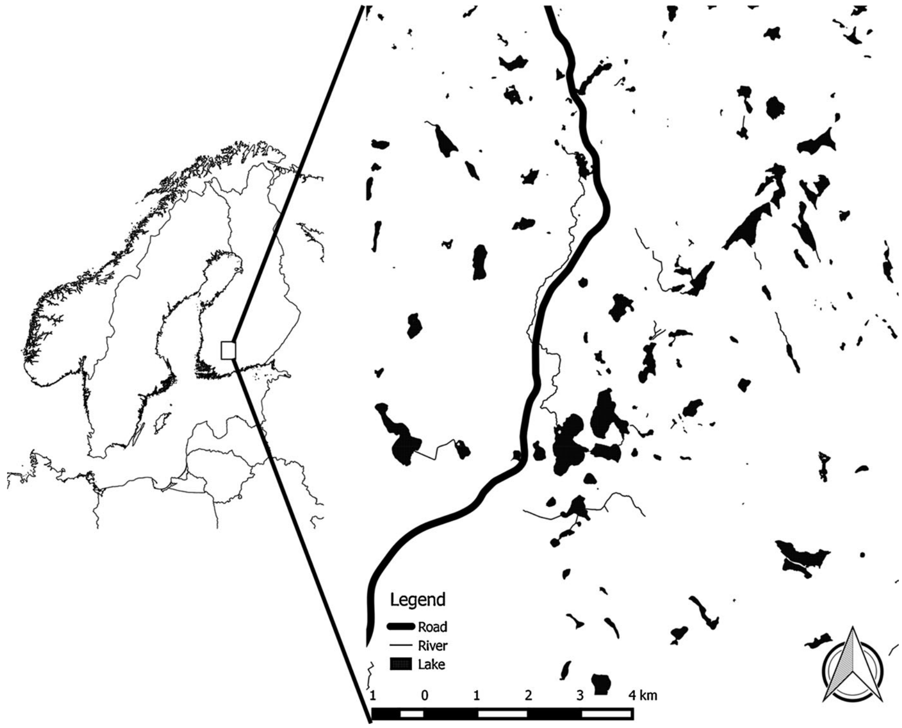

Fig. 1 Map of the study area. Our study area is situated in the Evo, Southern Finland (61°10′N, 25°05′S)

A typical study lake has one or more inflows and one outflow, and is considered to receive water mainly from surface runoff, although five of the lakes have no visible inflowing streams or outflow (Arvola et al. 2010). Four of these are considered groundwater lakes and one is a spring lake with several large springs at the bottom. Similar lake systems can be found from wide areas in western Eurasia (Fennoscandia and western Russia) and most parts of boreal Canada (Zoltai 1995; Lehrer and Döll 2004).

The topography of the area is relatively gentle and varies from 125 to 185 m above sea level (a.s.l.). The soils at Evo are low in nutrients, and consist primarily of glaciofluvial deposits. Glacial till is the dominant soil type. The average ice-cover period is over 5 months (from late November to early May) for the larger lakes in our study area and slightly longer for smaller lakes. The thermal growing season is 160–170 days (see Jylhä et al. 2014). Forestry has molded the development of Evo's forests, which are mainly coniferous with patches of deciduous trees. The most common tree species is Scots pine (*Pinus sylvestris* L.), which covers over half of the area's tree stands. There is no agricultural activity in our study area. Beaver lakes in our study area are most commonly formed by the damming of an existing lake (Nummi and Hahtola 2008). Currently the area's beaver population consists solely of American beavers, which were introduced to the area in 1950s (Parker et al. 2012). Beavers usually inhabit a site for 3 years (Hyvönen and Nummi 2008).

The study lakes were determined by a hydrologic position in the lake chain (lake category, a modification from the stream order system) (e.g. Strahler and Stahler 1983). Seepage lakes without visible inlets or outlets were classified as 0-lakes. The uppermost lakes in the chains were designated category number 1 and so on. The category number of the lower basins in branched chain systems is always determined according to the longest chain arm.

Data collection/sampling methods

We collected data from a total of 37 lakes (Table 7 in Appendix 1). All of these lakes exist in the absence of beavers. Beavers have dammed 15 of these (the damming took place at various points during 1978–2012), and 22 have never been dammed or flooded by beavers (1978–2012). Lakes were visually inspected for beavers every year since 1970. During 35 years the lakes were sampled twice a year for water chemistry variables: total phosphorus (TP), total nitrogen (TN), DOC, DO and pH were determined from the samples. The first sampling round was conducted in late March–early April (mostly during weeks 13–14). For data analysis we chose the spring DO concentration results of the lakes. All other chemistry results were taken from the autumn sampling round, which was carried out at the end of October–the first week of November (usually during week 44), when the lakes go through their autumnal turnover. On average the lakes freeze on November 18 ± 7.4 days (95 % CI) (see Jylhä et al. 2014).

The DO concentrations were measured at a depth of 1 m at the deepest point of each lake using YSI instruments (El-ke Sensor, MJ 2000, GWM-Engineering Oy, Kuopio, Finland). The autumn samples were taken from the uppermost 1 m water layer, kept dark and cold, and analysed in the laboratory of the Lammi Biological Station, University of Helsinki, according to standard methods (see Arvola et al. 1996, 2014).

The Finnish Meteorological Institute provided annual precipitation data, gathered from a meteorological station situating in the study area. To exclude the influence of annual precipitation changes on the water chemistry we transformed the data so as to correlate the limnological and annual precipitation data, and subsequently used the residuals received from the correlation.

DOC concentrations were not measured during 1994 and 1999–2012, so we therefore used water color as a proxy for DOC during these years. Both water color and DOC data were available from 1977 to 1998 (except 1994) for all the lakes, and the missing DOC concentrations were calculated according to Eq. (1) (see Jones and Arvola 1984):

$$y = 0.0305x + 4.1295 \quad (1)$$

where y = DOC and x = water color.

These calculations were performed before data transformation.

Data analysis

We first compared how DOC, pH, DO, TP, and TN differed between the two lake types, i.e. beaver and non-beaver lakes. Because almost all the beaver lakes belonged to the 1st or 2nd order lakes, we decided to make the comparison of these two lake types just between the lakes interlinked to these two lake orders. In addition, we compared the beaver-impoundment years of beaver lakes with non-beaver lakes of the 1st and 2nd order lakes to clarify the effect of beavers. Lake depth has previously been shown by Mulholland (2003) to affect DOC concentration. We therefore tested whether lake depth, area or the topography index of a lake had an effect on DOC in our study lakes. All lakes were included in this test. No effects were observed (Table 1). All of the analyses were performed with generalized linear mixed modeling (Bolker et al. 2009; Zuur et al. 2009) by using the glmer function in the lme4 library (Bates and Maechler 2009) in R 2.15.0 (R Development Core Team 2013). Equation (2) is as follows:

$$\text{Variable\_value}_{ij} = \alpha + \beta_i \times \text{Lake\_type/\_depth/\_area/\_topographyindex}_{ij} + a_i, \quad (2)$$

where $\text{Variable\_value}_{ij}$ is the value of DOC/…/TN of lake i in year j, where i = 1,…, 37, and j = 1977,…, 2012. α is the intercept, β is the coefficient of the lake type/depth/area/topography index and term a_i is a random effect indicating inter-lake variation. We used each study lake as a random variable to control the variation between the lakes. The lake types were used as a categorical parameter.

In the next analysis we wished to further investigate the temporal aspects of the beaver effect with an experiment-like before-after setting. We determined the five variables by comparing data from the beaver lakes before and during beaver occupation. During the 35 study years (1978–2012), 15 of the 37 lakes were dammed by beavers and provided valid before–after data. Some lakes were flooded by beaver's on several occasions, but only the first impoundment of the study period was taken into account in our analysis. We used a natural experiment-like setting where 'pre-beaver impoundment'- and 'during beaver impoundment'-situations were compared because beavers occupied new lakes in the landscape during the course of our study (Smith 2002; Roni et al. 2005). Beaver occupation was divided into two categories: the first 3 years of occupation, and the fourth to sixth years of occupation. The impoundment duration effect was also analyzed with generalized linear mixed modeling (see above) by using the glmer function in the lme4 library in R 2.15.0. The yearly value of variables in the impounded lakes was explained by the impoundment classification of lakes. We used the study lakes as a random variable to control the variation between the

Table 1 The link between DOC and lake depth, surface area and topography index

	Value	SE	DF	t-value	p value
Depth					
Intercept	0.7485	2.6304	1088	0.2845	0.7760
Depth	−0.0364	0.2920	35	−0.1246	0.9016
Area					
Intercept	1.0206	1.1667	1088	0.8748	0.3819
Area	−0.0818	0.0928	35	−0.8818	0.3839
Topography index					
Intercept	0.9738	2.4981	1088	0.3898	0.6968
Topography index	−0.0152	0.0659	35	−0.2303	0.8192

The value represents the coefficient of the lake depth, SE denotes standard error, DF the degrees of freedom, t-value the test value, and p value the statistical significance

lakes. The lake types were used as a categorical parameter. Equation (3) is as follows:

$$\text{Variable\_value}_{ij} = \alpha + \beta_i \times \text{Impoundment\_category}_{ij} + a_i, \quad (3)$$

where $\text{Variable\_value}_{ij}$ is the value of DOC/…/TN of lake i in year j, where i = 1,…, 37, and j = 1977,…, 2012. α is the intercept, β the coefficient of the impoundment category, and the term a_i a random effect indicating inter-lake variation.

We finally wished to analyze the influence of the beaver impoundment on downstream lakes not experiencing direct beaver influence. We compared the five variables in these non-beaver lakes in the same way as in the previous analyses: pre-impoundment, the first 3 years of beaver occupation, and the fourth to sixth beaver occupation years. We used the generalized linear mixed model similarly in this analysis as we did in the previous analyses. Equation (4) is as follows:

$$\text{Variable\_value}_{ij} = \alpha + \beta_i \times \text{Impoundment\_category}_{ij} + a_i, \quad (4)$$

where $\text{Variable\_value}_{ij}$ is the value of DOC/…/TN of lake i in year j, where i = 1,…, 37, and j = 1977,…, 2012. α is the intercept, β the coefficient of the impoundment category, and the term a_i a random effect indicating inter-lake variation.

Results

Nearly every beaver lake belonged to the 1st (6/15) or 2nd (7/15) lake order, and beavers never built a dam on a groundwater or spring lake. The water chemistry (DOC, TN, TP, pH and DO) of the beaver and non-beaver lakes belonging to 1st and 2nd lake order were initially somewhat the same (Tables 2, 3). The differences between them occurred when beavers arrived at the sites. This was seen when compared the DOC concentrations of beaver-impoundment years of the beaver lakes and non-beaver lakes. The beaver-impoundment years of beaver lakes had significantly higher DOC than the non-beaver lakes ($p = 0.0205$). The other four water chemistry variables were not different (Table 4).

DOC concentrations increased significantly in beaver lakes ($p = 0.0080$) during the first three beaver-impoundment years when compared to the pre-impoundment situation, and DO concentrations ($p = 0.0188$) additionally decreased (Table 5). Furthermore, lake DOC concentrations declined back to initial levels after the impoundment had lasted for four to 6 years. The opposite occurred with DO concentrations, which increased. The concentration of N, P and pH did not show any significant changes.

No clear beaver-impoundment effect was found in the downstream lakes. The values of the chemical variables under evaluation (DOC, N, P, DO, and pH) did not differ in these lakes between the years when beavers were present or absent in upstream lakes (Table 6).

Table 2 Characteristics of the beaver and non-beaver lakes

	DOC (mg/l)	N (μg/l)	P (μg/l)	DO (mg/l)	pH
Beaver lakes					
Mean	**17.29**	**751.5**	**39.65**	**3.52**	**5.82**
Min	8.53	439.0	10.11	0.75	4.82
Max	24.46	1301.0	81.50	8.72	6.32
Non-beaver lakes					
Mean	**11.89**	**556.9**	**25.15**	**4.55**	**5.78**
Min	2.94	318.0	5.37	1.29	4.34
Max	22.72	775.0	62.05	8.44	6.27

Mean values in bold

Table 3 Differences between beaver and non-beaver 1st and 2nd order lakes

	Value	SE	DF	t-value	p value
DOC					
Lake (intercept)	−0.334	1.742	638	−0.192	0.848
Beaver lake	3.205	2.328	21	1.377	0.183
N					
Lake (intercept)	48.021	55.003	477	0.873	0.383
Beaver lake	127.388	73.513	21	1.733	0.098
P					
Lake (intercept)	−1.628	6.192	475	−0.263	0.793
Beaver lake	10.203	8.284	21	1.232	0.232
DO					
Lake (intercept)	−1.292	0.661	508	−1.954	0.051
Beaver lake	−0.434	0.881	21	−0.493	0.627
pH					
Lake (intercept)	−0.195	0.150	644	−1.297	0.195
Beaver lake	0.132	0.200	21	0.661	0.516

The value represents the coefficient of the lake type, SE denotes standard error, DF the degrees of freedom, t-value the test value, and p value the statistical significance

Table 4 Comparison of beaver impoundment years and non-beaver lakes

	Value	SE	DF	t-value	p value
DOC					
Lake (intercept)	−0.3279	2.0060	330	−0.1634	0.8703
Beaver lake	**7.3792**	**2.9193**	**19**	**2.5277**	**0.0205**
N					
Lake (intercept)	48.0010	51.8987	252	0.9249	0.3559
Beaver lake	129.5435	79.9905	18	1.6195	0.1227
P					
Lake (intercept)	−1.6296	6.0280	253	−0.2703	0.7871
Beaver lake	9.5657	9.1822	18	1.0418	0.3113
DO					
Lake (intercept)	−1.2916	0.6212	262	−2.0793	0.0386
Beaver lake	−0.4006	0.9195	18	−0.4357	0.6682
pH					
Lake (intercept)	−0.1944	0.1431	330	−1.3586	0.1752
Beaver lake	0.1357	0.2137	19	0.6352	0.5329

The value represents the coefficient of the lake type, SE denotes standard error, DF the degrees of freedom, t-value the test value, and p value the statistical significance

Significant results in bold

Discussion

In our study area beavers usually chose first- and second-order lakes as their habitats, while clearly avoiding groundwater lakes. DOC concentrations were higher in the beaver lakes during the impoundment when compared to the non-beaver lakes, which suggest clearly that beavers were involved in the biogeochemical cycling of DOC in that landscape. The damming and subsequent water level increase in the lakes appeared to be key processes as Hill and Duval (2009) have earlier proposed.

Because beavers in our study area mostly modified initial lakes and usually did not create them, we could compare the biogeochemistry of the beaver lakes during the impoundment years with the antecedent years. DOC concentration clearly increased during the first three beaver-impoundment years when compared to the pre-impoundment situation, which indicated that beavers seem to have a clear effect on DOC. The concentration furthermore reverted to initial levels after the impoundment had lasted for four to 6 years. In boreal lakes organic carbon concentration can be high and occur predominantly in the form of DOC (Tranvik et al. 2009).

Table 5 The beaver-impoundment effect before and after beaver occupation

	Value	SE	DF	t-value	p value
DOC					
Before flood (intercept)	4.1223	2.1814	170	1.8898	0.0605
Early beaver-flood years	**3.3145**	**1.2349**	**170**	**2.6840**	**0.0080**
Late beaver-flood years	−0.9442	1.2396	170	−0.7617	0.4473
N					
Before flood (intercept)	155.8024	42.1763	114	3.6941	0.0003
Early beaver-flood years	62.3210	48.3283	114	1.2895	0.1998
Late beaver-flood years	69.6740	48.3283	114	1.4417	0.1521
P					
Before flood (intercept)	10.0672	9.4721	91	1.0628	0.2907
Early beaver-flood years	13.0334	8.4225	91	1.5474	0.1252
Late beaver-flood years	10.2443	8.4225	91	1.2163	0.2270
DO					
Before flood (intercept)	−0.1604	0.6447	110	−0.2488	0.8040
Early beaver-flood years	**−0.9596**	**0.4024**	**110**	**−2.3847**	**0.0188**
Late beaver-flood	−0.0307	0.4073	110	−0.0754	0.9401
pH					
Before flood (intercept)	0.0555	0.0847	169	0.6547	0.5135
Early beaver-flood years	−0.0726	0.0629	169	−1.1547	0.2498
Late beaver-flood years	−0.0262	0.0629	169	−0.4171	0.6771

The situation before the beaver flood was set as a baseline (intercept). Beaver occupation was divided into two categories: the early (1st–3rd) and late (4th–6th) years of occupation. The value represents the coefficient of the flood category, SE denotes standard error, DF the degrees of freedom, t-value the test value, and p value the statistical significance

Significant results in bold

Table 6 The effect of beaver impoundment on downstream non-beaver lakes

	Value	SE	DF	t-value	p value
DOC					
Before flood (intercept)	−0.3506	1.0092	107	−0.3474	0.7290
Early beaver-flood years	1.3610	1.4301	107	0.9517	0.3434
Late beaver-flood years	−0.0122	1.4301	107	−0.0085	0.9932
N					
Before flood (intercept)	−37.4765	80.2578	23	−0.4670	0.6449
Early beaver-flood years	41.8579	85.7074	23	0.4884	0.6299
Late beaver-flood years	−4.6368	84.6155	23	−0.0548	0.9568
P					
Before flood (intercept)	−9.6144	3.8557	23	−2.4935	0.0196
Early beaver-flood years	−2.7440	5.9421	23	−0.4618	0.6482
Late beaver-flood years	−1.5667	5.7478	23	−0.2726	0.7874
DO					
Before flood (intercept)	2.1516	0.7431	95	2.8957	0.0047
Early beaver-flood years	−0.3971	0.4381	95	−0.9063	0.3671
Late beaver-flood years	0.2632	0.3974	95	0.6623	0.5094
pH					
Before flood (intercept)	0.1944	0.0753	91	2.5799	0.0115
Early beaver-flood years	−0.0043	0.0904	91	−0.0475	0.9622
Late beaver-flood years	0.0108	0.0904	91	0.1192	0.9054

The situation before the beaver flood occurred in an upstream beaver lake was set as a baseline (intercept). Beaver occupancy was divided into two categories: the early (1st–3rd) and late (4th–6th). The value represents the coefficient of the lake type, SE denotes standard error, DF the degrees of freedom, t-value the test value and p value the statistical significance

Interestingly, in contrast to Mulholland (2003) we did not find any relationship between DOC concentration and lake depth. Beaver damming effect did not extend to the downstream lakes, as no significant differences were found between the DOC, N or P concentrations before and during the impoundment. It therefore appears that within a lake-chain beaver has only a local effect on water chemistry.

Beavers can be viewed as producers of biogeochemical hot spots and hot moments in a landscape. Hot spots are patches that show exceptionally high reaction rates when compared to surrounding regions. Hot moments, on the other hand, are described as short moments with outstandingly high reaction rates (McClain et al. 2003). According to McClain et al. (2003), hot spot and hot moment activity is more profound in locations where terrestrial and aquatic habitats meet, such as the flooded areas around lakes and ponds. Carbon and nitrogen cycles demonstrate the hot spot phenomenon, and beaver activity itself is a good example of a hot moment in the riparian zone (Naiman et al. 1988; Nummi and Kuuluvainen 2013).

Beaver-created hot spots wander in a landscape, because beavers move from one lake to the next one, and often return to their previous locations within ca. 10 years (Fryxell and Doucet 1990; Fryxell 2001; Hyvönen and Nummi 2008). Although the duration of a beaver-created nutrient pulse is relatively short (1–3 years), the effect of this hot moment on major biogeochemical cycles, and on surrounding catchment soils and forest areas usually continues after beaver abandonment (Hyvönen and Nummi 2008; Nummi and Kuuluvainen 2013).

As a result of the increasing amount of organic material caused by beavers, carbon dioxide (CO_2) and methane (CH_4) fluxes into the atmosphere will increase (Ford and Naiman 1988; Huotari et al. 2013) and/or may settle down to the bottom sediments (see Einola et al. 2011). Both Wohl (2014) and Johnston (2014) showed that beaver created wetlands store lots of carbon. Equally with DOC, N and P in boreal lakes largely originate from terrestrial ecosystems. In certain circumstances beavers may increase nutrient inflow to the lakes (Naiman et al. 1986; Maret et al. 1987; Correll et al. 2000), although in our beaver lakes no clear increase in N or P concentrations was observed.

During the first impoundment year the main source of carbon in beaver wetlands is vegetation (plants and trees) and litter, which provide DOC for microbes. In contrast, in the following impoundment years a major proportion of organic carbon may originate from soil where DOC comprises mostly of high-molecular-weight humic and fulvic acids (Stevenson 1994). This may explain why beaver lakes may act as sediment traps (Fracz and Chow-Fraser 2013).

The effects of beaver may endure much longer than the animals inhabit the site, because the dams usually exist for several years after the disappearance of the animals. In addition, recovery of the previously flooded area may also take a long time. As a consequence the landscape easily becomes a mosaic of non-beaver and beaver sites of different age (Wright et al. 2002; Hyvönen and Nummi 2008), a fact that increases heterogeneity in the landscape. In the long-term beavers can modify both the morphology and hydrology of a drainage network (cf. Naiman et al. 1994), and influence the ecosystems therein (Nummi 1989; Ray et al. 2001; Little et al. 2012).

In agreement with previous studies (Ford and Naiman 1988; Wohl 2013; Johnston 2014), our results emphasized that the beaver is among the important animals that affect the carbon balance of the boreal zone. In contrast to the previous studies which were carried out in stream and coastal systems, our study lakes were initial boreal lakes before the beaver impoundment. Thus beavers did not strongly alter the discharge patterns in our lakes, although they extended their size by creating floods. The lake network of our study is very typical in many parts of the boreal. Similar lake ecosystems can be found in vast areas of western Eurasia as well as in Canada (Henriksen et al. 1997; Lehrer and Döll 2004; Downing et al. 2006), and therefore our study gives new insights into how beavers influence the carbon balance in small boreal lakes. Further research is needed, however, to clarify the effects of beavers on carbon emission into the atmosphere and carbon cycling at different spatial scales.

Acknowledgments Funding for data analysis (MV) was kindly provided by the Maj and Tor Nessling Foundation, and for the long-term study, including sampling and chemistry analyses, by the Lammi Biological Station, University of Helsinki, and the Finnish Game and Fisheries Research Institute. Special thanks to Antti Nykänen for map illustration and to Stella Thompson for grammatical corrections. Two anonymous referees are thanked for their useful comments on improving the manuscript.

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1

See Table 7.

Table 7 The 37 study lakes and their basic characteristics

Lake no.	Lake name	SA	Depth (m)	Hydrology	Soil type	Lake order	Beaver occupation (1st impoundment begun)
1	Alinen Rautjärvi	45.0	12	SW	S	10	No
2	Alinen Mustajärvi	0.7	7	GW	S	0	No
3	Haarajärven Valkjärvi	3.5	12	SW	T	1	No
4	Haarajärvi	12.1	14	SW	T	2	Yes (1992)
5	Halsjärvi	4.8	6	SW	S/T	2	No
6	Haukilampi	2.3	8	SW	S/T	1	Yes (1980)
7	Hautajärvi	7.7	11	SW	T	1	No
8	Hokajärvi	10.3	6	SW	T	2	Yes (1991)
9	Horkkajärvi	1.1	12	SW	T	1	No
10	Huhmari	1.6	8	SW	S	2	Yes (1990)
11	Iso-Keltajärvi	3.9	6	SW	T	3	Yes (1982)
12	Iso-Mustajärvi	1.0	5	SW	S	2	No
13	Iso-Ruuhijärvi	16.6	7	SW	T	2	Yes (1984)
14	Iso-Valkjärvi (limed part)	3.9	8	SW	S	1	No
15	Iso-Valkjärvi (unlimed part)	3.9	8	SW	S	1	No
16	Kaitalampi	2.1	4	SW	S	2	Yes (1998)
17	Karhujärvi	0.8	8	SW	T	1	No
18	Keskinen Rautjärvi	14.9	6	SW	S	9	No
19	Löytjärvi	1.7	9	SW	T	2	Yes (1986)
20	Majajärvi	3.9	12	SW	S/T	2	Yes (1980)
21	Mekkojärvi	0.3	3	SW	T	1	Yes (1983)
22	Möläkkä	0.9	15	GW	S	0	No
23	Nimetön	0.4	11	SW	T	1	Yes (1980)
24	Onkimajärvi	6.3	4	SW	S/T	2	No
25	Pitkänniemenjärvi	14.4	10	SW	S	7	No
26	Rahtijärvi	13.2	13	SW	S/T	6	No
27	Rieskalampi	1.9	4	SW	T	1	Yes (2005)
28	Ruuttanajärvi	1.0	7	SW	S	1	No
29	Savijärvi	16.6	12	SW	T	5	No
30	Sorsajärvi	15.0	13	SW	T	3	No
31	Syrjänalunen	0.9	8	Spring	S	−1	No
32	Särkijärvi	1.8	3	SW	S	1	Yes (1991)
33	Tavilampi	0.8	7	SW	S/T	1	Yes (2005)
34	Valkea Mustajärvi	13.9	10	GW	S	0	No
35	Vähä-Keltajärvi	2.5	4	SW	T	4	Yes (1978)
36	Vähä-Valkjärvi	2.3	4	GW	S	0	No
37	Ylinen Rautjärvi	19.3	12	SW	S	8	No

SA surface area of the lake (ha), *SW* surface water-fed lake, *GW* groundwater-fed lake, *S* sandy deposit and *T* till deposit

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