

Ecological and Biogeochemical Implications of the Recovery of Eurasian Beavers

Oded Levanoni

*Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Sciences and Assessment
Uppsala*

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2016

Acta Universitatis agriculturae Sueciae

2016:93

Cover: Two beavers arriving from Norway during the reintroduction of beavers to Sweden in 1922.

(Illustration: Oded Levanoni)

ISSN 1652-6880

ISBN (print version) 978-91-567-8688-6

ISBN (electronic version) 978-91-567-8689-3

© 2016 Oded Levanoni, Uppsala

Print: SLU Repro, Uppsala 2016

Ecological and Biogeochemical Implications of the Recovery of Eurasian Beavers

Abstract

In pre-industrial times beavers, ecosystem engineers, inhabited most of the Holarctic. Intensive exploitation over the last millennium, particularly in Europe during the 18th and 19th centuries, led to a dramatic decline in beaver populations. By the end of the 19th century the Eurasian beaver (*Castor fiber*) was at the verge of extirpation in many regions of Eurasia. However, during the 20th century, changes in management policy and reintroductions have resulted in a fast recovery of the species. Presently, Eurasian beavers are colonizing large parts of their former distribution range, and their population is still growing. Once again, beaver engineering and its outcomes are becoming prominent features of many streams in the boreal landscapes.

The goal of this thesis was to investigate how the reintroduction and population recovery of Eurasian beavers might affect ecosystem functioning at local and landscape scales. The work was based on measurements from 12 beaver systems of various colonization histories (pioneer and recolonized) in Swedish boreal forests. Based on water chemistry measurements together with field and lab experiments, I evaluated the effect of beavers on processes of mercury methylation, litter decomposition, and the growth and respiration of benthic biofilms. I also investigated how beavers alter the nutrient limitation of biofilm activity. To assess the environmental effects of the reintroduction of beavers at the landscape scale, this empirical approach was complemented by a meta-analysis of 76 published studies on a total of 16 environmental factors. The results showed that beavers increased MeHg concentrations, decreased algal biomass accrual, and sometimes increased litter decomposition rates downstream compared to upstream beaver systems. However, distinct contrasting patterns were observed in pioneer and recolonized systems: While all the above effects were prominent in pioneer systems, they were moderate or absent in recolonized systems. Albeit algal accrual and community respiration were nutrient limited, beaver systems had no effect on the degree of limitation. Based on the meta-analysis, this thesis demonstrates that, when compared to a reference site, beavers can potentially affect all studied factors. The meta-analysis also identified gaps in knowledge regarding the dependency of beaver effects on different stages of age and colonization history.

In conclusion, this thesis highlights: a) the importance of incorporating the successional stage and the colonization history of beaver systems when considering the effects of reintroducing beavers into stream ecosystems; and b) the lack of knowledge regarding these issues.

Keywords: beaver, beavers, beaver pond, pond, reintroduction, castor fiber, ecosystem functioning, algae, nutrient limitation, decomposition

Author's address: Oded Levanoni, SLU, Department of Aquatic Sciences and Assessment, P.O. Box 7050, 750 07 Uppsala, Sweden
E-mail: oded.levanoni@slu.se

Dedication

To all the hard-working engineers that work days and nights (but mostly nights) to make our forests a better place!

מסעות מאטים את קצב הזמן ומאריכים את החיים, כי מה שקובע זה לא האורך האמיתי שלהם אלא
הזיכרונות...
הזיכרונות...

(Journeys make time pass more slowly and life longer; because, what counts is not the length of time lived but the memories garnered...)

This was a Journey worth taking!

Contents

List of Publications	8
Abbreviations	10
1 Introduction	11
1.1 Beavers as ecosystems engineers	12
1.1.1 Dam building	13
1.1.2 Digging	15
1.1.3 Tree felling and selective feeding	15
1.2 Cycles of colonization, abandonment and recolonization	15
1.3 The effect of beavers on ecosystem functioning	17
1.4 The fall and rise of the Eurasian beaver (<i>Castor fiber</i>)	19
1.5 The extirpation and reintroduction as an opportunity for understanding the past and predicting the future	20
2 Framework and objectives	22
3 Methods	23
3.1 Study sites (Paper I-III)	23
3.2 Study design (Paper I-III)	23
3.3 Age and colonization history classification (Paper I-III)	23
3.4 Stream abiotic parameters (Paper I-III)	24
3.5 Mercury in water (Paper I)	25
3.6 Benthic species community and functional traits (Paper II)	25
3.7 Assessing leaf litter decomposition rates (Paper II)	26
3.8 Assessing algal accrual rates (Paper II-III)	26
3.9 Assessing nutrient limitation with nutrient diffusing substrate (NDS) (Paper III)	27
3.10 Meta-analysis of beaver effects (Paper IV)	28
3.11 Statistical analysis	28
4 Results and discussion	30
4.1 Beaver reintroduction affects water MeHg concentrations in pioneer but not in recolonized beaver systems (Paper I)	30
4.1.1 The effect of beavers on MeHg concentrations	30
4.1.2 Temporal variation in MeHg and the relation to abiotic predictors	32

4.2	Leaf litter decomposition and algal accrual can be affected by beavers, but mainly in pioneer systems (Paper II-III)	33
4.2.1	The effect of beavers on leaf litter decomposition	33
4.2.2	The effect of beavers on autotrophic and heterotrophic biofilms	35
4.2.3	Algal productivity and community respiration were nutrient limited but not affected by beavers	38
4.3	Landscape effect of beaver dams – a meta-analysis of published studies (Paper IV)	41
4.4	Short- and long-term effects of beaver systems following recolonization	43
4.5	Beavers and beaver reintroductions in Europe’s managed landscapes	45
5	Concluding remarks and future perspective	48
5.1	Future perspective	49
	References	50
	Acknowledgments	58

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Levanoni, O., Bishop, K., McKie, B., Hartman, G., Eklöf, K. & Ecke, F. (2015). Impact of beaver pond colonization history on methylmercury concentrations in surface water. *Environmental Science & Technology*, 49(21), pp. 12679-12687.
- II Levanoni, O., Ecke, F., Hartman, G. & Mckie, B. G. Responses of stream ecosystem functioning to the recovery of Eurasian beaver (*Castor fiber*). (*Manuscript*).
- III Levanoni, O., Sponseller, R., Hartman, G., Ecke, F. & Mckie, B. G. Nutrient limitation of autotrophic and heterotrophic biofilms in boreal streams colonized by Eurasian beaver (*Castor fiber*). (*Manuscript*).
- IV Ecke, F., Levanoni, O., Audet, J., Carlsson, P., Eklöf, K., Hartman, G., McKie, B. G., Ledesma, J.L.J., Segersten, J., Truchy A. & Martyn Futter. Meta-analysis of environmental effects of beaver and artificial dams. (*Manuscript*).

Paper I (open access) reproduced with the permission of the publishers.

The contribution of Oded Levanoni to the papers included in this thesis was as follows:

- I Planned the study together with co-authors. Carried out the selection of the study sites and sampling. Had the main responsibility for data handling, data analysis, interpretations, writing and publishing.
- II Planned the study together with co-authors. Carried out the experiments and sampling. Had the main responsibility for laboratory sample handling, data handling, data analysis, interpretations and writing the manuscript.
- III Planned the study together with co-authors. Carried out the experiments and sampling. Had the main responsibility for laboratory sample handling, data handling, data analysis, interpretations and writing the manuscript.
- IV Planned the study together with co-authors. Contributed to data extraction. Contributed to writing the manuscript.

Abbreviations

AFDM	Ash Free Dry Mass
AIC	Akaike's Information Criteria
ANOVA	Analysis Of Variance
CR	Community Respiration
CWM	Community-level Weighted Mean
D/U	Downstream/Upstream
DD	Degree Days
DO	Dissolved Oxygen
DOC	Dissolved Organic Carbon
F-Dispersion	Functional Dispersion
GLMM	Generalized Mixed effect Modeling
Hg	Mercury
MeHg	Methylmercury
N	Nitrogen
NDS	Nutrient Diffusing Substrate
NO ₂ ⁻	Nitrite
NO ₃ ⁻	Nitrate
P	Phosphorous
PLS	Partial Least-Squares regression
PO ₄ ³⁻	Phosphate
SRB	Sulphate Reducing Bacteria
TOC	Total Organic Carbon

1 Introduction

Even though rivers and lakes hold less than 1% of the Earth's water, they are a crucial resource for many animals (including humans) and plants. Maintaining the ecological health of these sources of water, particularly with a continuously growing human population, is an ongoing and fundamental management challenge (Vörösmarty *et al.*, 2010; Meyer, 1997). Effective conservation and restoration often involves integrating some aspect of habitat complexity (Kovalenko *et al.*, 2012; Tokeshi & Arakaki, 2012). This increases according to theory biodiversity and biotic interactions, which in turn, also potentially enhances ecological stability (Tilman *et al.*, 1996) and ecosystem resilience (Truchy *et al.*, 2015; Peterson *et al.*, 1998). Spatial heterogeneity can be linked to diversity and resilience (Virah-Sawmy *et al.*, 2009) and (sometimes) can also be achieved by introducing disturbance agents (Lepori & Hjerdt, 2006).

Many of the rivers and lakes in the northern hemisphere are home to millions of beavers (*Castoridae*), who have the extraordinary ability to build dams (and impound water), dig burrows and channels, and fell large trees. The ability to modify ecosystems entitled beavers as “ecosystem engineers” – a species that can create, modify and maintain ecosystems (Jones *et al.*, 2010; Wright & Jones, 2006; Jones *et al.*, 1994). Beavers have also been described as a keystone species – a species that affects the environment disproportionately to its abundance (Jones *et al.*, 1994). Therefore beavers, which can extensively alter and affect aquatic ecosystems, may be an important disturbance agent that can help promote the conservation goals of these systems (Nummi & Kuuluvainen, 2013; Burchsted *et al.*, 2010a).

Following near extirpation in Europe and Asia during the last centuries, populations of reintroduced beavers are now growing and, once again, colonizing territories that were inhabited by beavers during pre-extirpation periods. Today, beavers are colonizing stretches of streams where they were absent for hundreds of years (Halley *et al.*, 2012; Naiman *et al.*, 1988). In many cases, these streams have been modified by forestry and agriculture and

much of what we currently regard as pristine aquatic ecosystems is based on evidence from the era when beavers were absent from most of these aquatic ecosystems. Therefore, what we regard as pristine today may not represent pre-extirpation pristine conditions (Tornblom *et al.*, 2011; Ford & Naiman, 1988). Recent studies suggest that the recolonization of beavers in aquatic ecosystems can assist in achieving the restoration of aquatic ecosystems towards more pristine conditions (Curran & Cannatelli, 2014).

1.1 Beavers as ecosystems engineers

Beavers are one of the largest rodents in the world. They are semiaquatic and territorial; they spend large parts of their time in water and they mark and protect their territories. Palaeontologists have suggested that tree exploitation and swimming behaviour evolved to survive cold, harsh winters (Korth & Rybczynski, 2003). Fossil records, of roughly 30 genera, suggest that the beaver family evolved during the early Miocene period ca. 24 million years ago (Rybczynski, 2007).

As herbivores, beavers feed on aquatic and terrestrial vegetation in the water and riparian zones that surround their territories. While they evolved as excellent swimmers, on land they remain relatively easy prey for predators. Therefore, to secure their nests (a lodge made of wood and mud or an underground burrow) and access food, they modify their environments to maintain sufficient water levels. Dams and channels keep the water level constant and high enough to cover the lodge entrance, and provide access and escape routes to their foraging sites. The increased water level is also used for floating and transporting heavy wood material from foraging areas and to submerge food cache (Naiman *et al.*, 1988).

Today, the genus *Castor* is comprised of two species (and several subspecies): 1. The American beaver (*Castor canadensis*) - located natively in North America; and 2. The Eurasian beaver (*Castor fiber*) – located in Europe and Asia (Collen & Gibson, 2001). Both species are morphologically and behaviourally similar with slight differences in life span and reproduction, and are therefore expected to have a similar impact on the ecosystem (reviewed in Parker *et al.*, 2012; Collen & Gibson, 2001). The millions of years during which beavers have been modifying riverine ecosystems may have also affected the evolutionary paths of other species in associated communities. For example, animals such as woodpeckers (Soto *et al.*, 2012), birds that breed in shrub habitats (Chandler *et al.*, 2009), and amphibians (Hossack *et al.*, 2015) may have benefited from beaver-created habitats. Therefore, it is likely that

beaver modifications of ecosystems have significance for the wellbeing of other species (Jones *et al.*, 1997).

The ecosystem engineering function of beavers and their alteration of stream ecosystems is primarily due to four activities: dam building, digging, felling large trees, and selective feeding.

1.1.1 Dam building

The construction of dams demands significant energy. Beavers avoid building dams, if possible, by colonizing lakes and rivers with stable and sufficient water levels. If construction is needed to gain the desired water level properties (ca. 1m, Hartman & Tornlov, 2006), beavers build a dam of wood (trunks, branches and twigs), mud, soft vegetation and sometimes stones weaved together. The dam is a strong and stable structure that in extreme cases can be over 100 m long and several meters in height; it has the potential to flood vast areas (reviewed by Gurnell, 1998).

The transformation of lotic (moving water) habitats into (semi-) lentic (still water) ones is probably the most significant beaver-induced alteration to stream ecosystems. This transformation has the potential to affect the system's hydro-geomorphology and biogeochemical cycles, biota in the beaver systems and their surroundings, as well as the ecosystem functions the species mediate (Nummi & Kuuluvainen, 2013).

Hydrogeomorphology - the dam is built to create sufficient and stable water table. During events of high water flow the dam might also store water. The water is then gradually released throughout the following period of lower flow. Therefore, the overall effect of beaver dams is maintaining higher water levels behind the dam and as a result, reducing variability in discharge below it.

One single beaver dam might not have a significant effect on overall stream discharge, but a system of cascading dams can significantly affect water retention within a river reach (Andersen & Shafroth, 2010) and on surface-groundwater interactions (Janzen & Westbrook, 2011). The changes in hydrology also commonly affect fluvial geomorphology. These effects apply not only when beavers are colonizing the system, but also upon abandonment. The load of accumulated sediments and the remains of dam structures will continue to create low-gradient surfaces that result in a complex channel network (Polvi & Wohl, 2012).

By altering discharge regime, beavers change sediment loads and physical elements that define the structure of streams. Beavers have an important role in shaping stream planforms and generating complexity and discontinuities along

rivers. According to geomorphological evidence, these were the prehistoric common conditions in streams (Polvi & Wohl, 2013; Burchsted *et al.*, 2010b).

Biogeochemical cycles – As a result of beaver activities, the biogeochemical conditions (including flow, temperature, oxygen concentrations, sediment type and load, and pH) in beaver ponds often differ upstream from those downstream. These changes in conditions potentially affect several biogeochemical cycles within ponds and downstream beaver systems. Two primary biogeochemical processes that often studied are cycles of macronutrients (mainly nitrogen and phosphorous) and carbon (reviewed in Nummi & Kuuluvainen, 2013; and in Rosell *et al.*, 2005). These two processes are particularly affected by the inundation of riparian zones (which includes nutrient and carbon-rich soils, trees, and other terrestrial vegetation) upon the construction of dams. The flooded terrestrial vegetation dies and large volumes of dead wood are added to the system (Thompson *et al.*, 2016).

Decay processes start quickly, consuming the organic soils and woody debris, adding dissolved carbon and nutrients to the water column while reducing oxygen (Vehkaoja *et al.*, 2015). The intensity is usually greatest in the first several years following inundation, due to the large volume of dead wood and extensive digging in carbon rich soils. With time, the volume of dead carbon decreases. Then, the main carbon source is supplied by excretion of waste products of feeding and the carbon production within ponds (Nummi & Kuuluvainen, 2013). In such an environment, the extreme decay processes that characterize pioneer ponds are likely to decrease and make place for more stable processes.

The above changes in biogeochemical conditions have the potential to further affect the availability of important resources at the base of the food web, such as primary production, microbial production and invertebrates (Anderson & Rosemond, 2010).

Biota – the transformation of stream sections into wetlands and ponds can affect the biota by altering the environmental conditions, *viz.* habitat diversity, dead wood dynamics, changes in sediment load and structural properties. These conditions can also affect areas above, within and below the impoundments. Structural alterations might be especially substantial in managed landscapes, where the natural structure of streams has been altered by forestry and/or agriculture.

Overall, beaver dams increase biodiversity by the creation of suitable habitats for species which cannot colonise lotic (stream) environments (reviewed in Romero *et al.*, 2015). They have the potential to directly or indirectly affect inhabiting species (plants, invertebrates, fish, amphibians,

reptiles, birds and mammals) within ponds or in the adjacent environment (recently reviewed by Stringer & Gaywood, 2016).

1.1.2 Digging

Beavers are excellent diggers and even in prehistoric times (30-7 million years ago) some beavers evolved as burrowing specialists (Samuels & Van Valkenburgh, 2009). They use their front paws and even their incisors to dig burrows and channels, dig and add mud to the dam and lodges, and to deepen their ponds.

In the first years of inundation, digging activities might have a substantial effect due to the disturbance of riparian soils rich in organic carbon (Ledesma *et al.*, 2015). Most of the disturbance to riparian zones by beavers digging takes place in the first stage of pond creation and substantially decreases as the pond ages. Nevertheless, digging activity helps maintain water levels and wetted areas in periods of low flow (Anderson *et al.*, 2015), it also provides movement corridors for amphibians, and increases landscape connectivity (Anderson *et al.*, 2015; Hood & Larson, 2015).

1.1.3 Tree felling and selective feeding

Using their strong, sharp incisors, beavers can fell even large trees for feeding on twigs, branches and bark, and/or for using as building materials for dams and lodges (reviewd in Collen & Gibson, 2001). By felling big trees, beavers affect tree size and age distribution of both preferred and non-preferred tree and shrub species surrounding their territories (Johnston & Naiman, 1990b).

Beavers also selectively browse on aquatic vegetation within ponds and terrestrial vegetation in their territory. This selective browsing affects species composition and age structure, and the successional processes of aquatic and riparian vegetation (Wright, 2009).

1.2 Cycles of colonization, abandonment and recolonization

Beaver systems show spatial and temporal variability, and in particular go through successional stages in their structural and functional development. The formation of the first single pond is commonly followed by the creation of a set of ponds and channels that form the beaver system and the premise for future cycles of abandonment and recolonization. As previously framed, beaver systems are “a shifting mosaic of environmental conditions, [that] depend upon pond age and size, successional status, substrate, hydrologic characteristics, and resource inputs” (Naiman *et al.*, 1988).

Rarely discussed (including in Naiman *et al.*, 1988.) is the **first** (or “**pioneer**”) stage of inundation of a stream that was void of beaver activities for hundreds of years as a result of beaver extirpation (where the stream has returned to the state of a stream channel unaltered by beavers). During this “pioneer” stage, the flooding of riparian vegetation and soils rich in carbon, nutrients and other elements forms special conditions in a relatively still water environment. The large volume of generated dead organic matter eventually decays and its products are washed out or buried in the sediments.

The **second**, and less dramatic stage, is the natural “aging” of the ponds, with relatively stable successional shifts in biogeochemical conditions and biota (e.g. Nummi & Kuuluvainen, 2013; Ray *et al.*, 2001).

Eventually, in the **third** stage, beavers will abandon their territory in response to predation, hunting, natural mortality, and/or food limitation (Petrosyan *et al.*, 2013; Fryxell, 2001). Beaver-created structures such as dams and channels generally continue influencing a stream’s hydrogeomorphology even after system abandonment (see Gurnell, 1998). The result is commonly a braided and meandering stream with a flat bed of sediments rich in nutrients and organic matter; introducing a unique form of habitat, termed the “beaver meadow” (Polvi & Wohl, 2012; Naiman *et al.*, 1988). During the successional stage of a beaver meadow, forest regeneration takes place (Nummi & Kuuluvainen, 2013; Wright, 2009; Wright *et al.*, 2003) and food sources become adequate to support beavers again.

In the **fourth** stage, a new individual or family of beavers will recolonize the abandoned beaver meadow and form a **recolonized** beaver system. In this stage, beavers will restore the old dam structures (often still functioning even though abandoned), deepen the ponds, build new dams, and/or dig new channels. Food and/or habitat availability and population dynamics control the duration of each stage in the beaver colonization cycle (figure 1 and figure 2).

The magnitude of the overall effect of beavers is also influenced by the scale in focus – whether it relates to a beaver pond, beaver system or a landscape scale. A single **beaver pond** can have a local impact that can also be affected by succession. A **beaver system** combines several different ponds and the stretches of stream in between and therefore includes both spatial and temporal heterogeneity. The landscape scale, represented by different catchments with one or **several beaver systems** that will undergo cycles of abandonment and recolonization. At a landscape scale, the shifting mosaic of beaver systems includes fluctuating densities of pioneer, old or abandoned beaver systems.

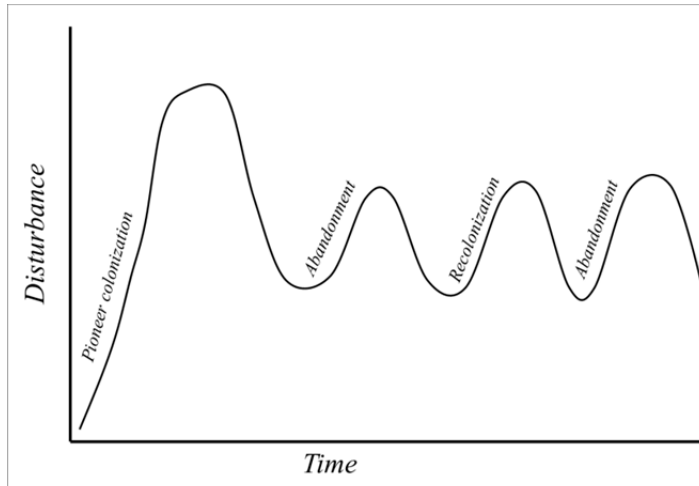


Figure 1. Illustration of the magnitude of disturbance of stream ecosystems by beaver colonization cycles. The highest magnitude is expected upon first inundation following the absence of beavers from the landscape. Then, cycles of abandonments and recolonizations potentially result in less significant disturbance.

1.3 The effect of beavers on ecosystem functioning

Ecosystem functioning describes the linkage between biological, geochemical and physical processes that sustain an ecosystem (Reiss *et al.*, 2009). Healthy functioning ecosystems involve complex interactions and feedbacks of abiotic drivers, biodiversity and biotic interactions (reviewed in Truchy *et al.*, 2015). Increased biodiversity and biotic interactions can potentially enhance ecosystem functioning even above the level expected based on the specific function of individual species (e.g. Cardinale, 2011), particularly in complex spatiotemporal environments. Moreover, ecosystem functioning and biotic interactions are also linked with ecosystem resilience as a response to disruptions (reviewed in Truchy *et al.*, 2015). As a keystone species and due to their engineering activities, beavers potentially enhance overall biodiversity (reviewed in Romero *et al.*, 2015), and therefore can play an important role in shaping ecosystem functioning and resilience (Peterson *et al.*, 1998).

In stream ecosystems, decomposition of organic matter and primary production are the two most widely studied processes (Gessner & Chauvet, 2002; Bunn *et al.*, 1999). Decomposition of leaf litter is a key process regulating the flow of allochthonous organic matter and nutrients, into the stream. The decomposition of leaf litter is primarily mediated by macroinvertebrates and microbes. Primary production is a key process fixing nutrients and atmospheric carbon. These two processes are sensitive to local

environmental conditions such as hydrologic conditions, pH, nutrient concentrations, habitat availability and biotic interactions (Feio *et al.*, 2010); all can be influenced by beaver engineering (Stringer & Gaywood, 2016). The products of these processes regulate an important energy sources at the base of aquatic food webs (e.g. invertebrates); however, their impact also extends to higher levels of the food web (e.g. fish).

Another key process of particular importance in wetland ecosystems is the methylation of mercury (Hg). This is predominantly a microbial process mediated by the activity of sulphate reducing bacteria (SRB); its final product is methylmercury (MeHg). In stream ecosystems this process is not as fundamental as decomposition and primary productivity. However, its product, *viz.* MeHg, is of great environmental concern (reviewed in Ullrich *et al.*, 2001). MeHg is one of the most toxic forms of Hg that can potentially bioaccumulate in aquatic food webs. It can also compromise human health through the consumption of exposed fish (EU, 2008; JECFA, 2004). The methylation process is influenced by the availability of Hg, organic carbon, sulphate, redox (reduction-oxygenation reaction) conditions and temperature (Tjerngren *et al.*, 2012). These conditions often occur in wetlands and ponds, and therefore, beaver systems, have the potential to increase MeHg concentrations (Painter *et al.*, 2015; Roy *et al.*, 2009a).

The effect of beavers on these three fundamental processes might also be depending on the successional stage of the beaver system. Following the construction of dams, decay processes of carbon generally induce higher levels of nitrogen, phosphorous and dissolved organic carbon (DOC) but lower concentrations of dissolved oxygen. These conditions characterize new beaver ponds in particular, and might have a greater potential to effect ecosystem functioning. However, with time, the impact of beaver ponds might change with ongoing successional processes within the ponds, and beaver systems can become either source or sink for these factors (reviewed in Nummi & Kuuluvainen, 2013). Despite the potential effects of beaver engineering activities on ecosystem processes, and the impact they can have on stretches downstream, only a few studies have quantified the influence of beavers on benthic algal productivity (Painter *et al.*, 2015; Bledzki *et al.*, 2011; Coleman & Dahm, 1990), litter decomposition (Anderson & Rosemond, 2007) or methylation (Painter *et al.*, 2015; Roy *et al.*, 2009b; Roy *et al.*, 2009a). Furthermore, out of these only few addressed pond age (in relation to methylation); however, none addressed the effects of colonization history.

1.4 The fall and rise of the Eurasian beaver (*Castor fiber*)

The earliest fossil record of the Eurasian beaver date to the Late Miocene, ca. 11 million years ago. Shifting distribution from north to south Eurasia and back during glaciation cycles, Eurasian beavers constantly modified the landscape with their semiaquatic, woodcutting and burrowing behaviour that we still witness today (Rybczynski, 2007; Ducroz *et al.*, 2005). Taking into account the long history of shaping forested stream ecosystems and habitat creation (Polvi & Wohl, 2013; Polvi & Wohl, 2012), Eurasian beavers might have played an important role in the evolution of riparian zones and the biota that benefit from the special habitats beavers create and shape.

The demographic history of Eurasian beavers in the last centuries is an extraordinary and dramatic story associated with human-induced over-exploitation of natural resources (beavers), followed by a last minute awakening. In the early days of European and Asian human history, millions of beavers colonized large parts of continental Eurasia ranging from Kamchatka in the east, Great Britain in the west and the Mediterranean in the south. However, during the 17th -19th centuries, demand for quality beaver pelts by the fashion markets resulted in the over-hunting of Eurasian beavers (by this time already extirpated in many parts of southern Europe), significant decreases in population size, and near extirpation in the less inhabited areas of northern Eurasia. The quest for beaver pelts, highly valued in Europe, was also a motivator for French and British traders to establish the North American-European fur trade, which resulted in the near extirpation of the largest population of beavers at that time, the American beaver (*C. canadensis*). By the end of the 19th century Eurasian beavers were on the verge of extirpation. About 1200 individuals of eight small populations managed to survive the over-exploitation in some isolated areas in Norway, France, Germany, Russia, Belarus, Ukraine, Mongolia and China (Nolet & Rosell, 1998).

Towards the end of the 19th century interest in restoring the Eurasian beaver population began to grow. Norway, the first country to protect beavers by law (1845), was followed by Finland (1868), Sweden (1873) and other countries in the early 20th century. But, in many cases the beaver population was already extirpated and other conservation measures were needed. Sweden was the first country to reintroduce 80 Eurasian beavers from Norway in 1922-1939. And other countries soon followed (Nolet & Rosell, 1998). Today, the Eurasian beaver populations are flourishing, colonizing most of their historic distribution range while reintroduction programs are still in action in several European countries (Halley *et al.*, 2012).

1.5 The extirpation and reintroduction as an opportunity for understanding the past and predicting the future

In aquatic ecosystems, beavers are a classic example of a keystone species. The term keystone is an analogue to the key stone at the top of an arch; while the key stone experiences the smallest pressure of all stones, the arch will collapse once the key stone is removed. For some aspects in aquatic ecosystems, extirpation of beavers may have analogous consequences as the removal of the arch key stone.

The removal of beavers, may have a significant impact on species composition and ecosystem processes (Jones *et al.*, 1994). Ecosystem alterations by beavers can have beneficial and/or detrimental effects on aquatic and terrestrial biota. Therefore, the removal of a keystone species is likely to have substantial effect at various spatial scales. The extirpation and reintroduction of keystone species, such as beavers, following decades or even centuries of absence, provides a unique opportunity to study the species' role in landscape-level processes before, during and after their extirpation.

By comparing beaver systems to **reference** streams/sites that had no beaver activities since extirpation we can study the consequences of the absence beaver from the landscape. **Pioneer** systems enable us to study the temporary responses of processes and biota following the return of beavers after many decades or even centuries in which the ecosystem might have changed during the absence of this keystone species. Finally, the study of **recolonized** systems (including spatial and temporal shifts of the landscape mosaic of beaver systems) enables us to study the current and future effects of beavers. Recolonized systems can also contribute to the understanding of the structure and function of northern hemisphere stream ecosystems, prior to the extirpation of a keystone species that shaped the aquatic landscape and network of streams (e.g. Hood & Larson, 2015; Johnston & Naiman, 1990a). However, it is difficult to determine if the recovery of beavers can restore stream ecosystems to their original conditions or if these ecosystems have changed irrevocably in the absence of beavers.

The beaver system cycle of colonization

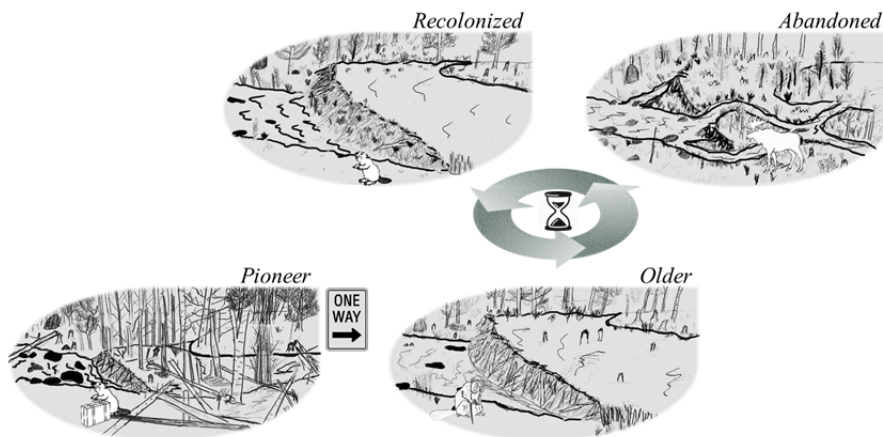


Figure 2. Illustration of the succession beaver systems undergo following pioneer colonization and inundation. A natural succession ends in older ponds, which upon abandonment, transform into beaver meadows and eventually are recolonized. The system will then undergo cycles of colonization – aging – abandonment – colonization etc., while pioneer systems will only be formed once in one and the same system

2 Framework and objectives

The focus of this thesis is on how biogeochemical conditions and ecosystem functioning in streams is affected by the recolonization of beavers in Sweden. The novelty of this work is the distinction between the effects of pioneer systems, which are assumed to be ephemeral and more extreme, and those of the recolonized systems, which carry potential long-term effects that can persist during cycles of abandonment and recolonization.

This thesis was conducted as part of a project funded by the Swedish Research Council Formas and aimed to assess if the reintroduction of European beavers is a plus for biodiversity or detrimental for the environment.

The overall objective of this thesis was to assess how ecosystem functioning in streams is affected by the recolonization of beavers in Sweden. The thesis further aimed to infer on the landscape scale effects of beavers based on studies available in the scientific literature.

The specific objectives of the thesis were to:

- Quantify the effect of beavers on MeHg concentration in water (paper I) and how it is affected by colonization history.
- Assess the effect of beavers on the process of leaf litter decomposition and benthic algal productivity, and examine potential underlying drivers of variation in these processes (paper II).
- Explore the role of nutrient availability and limitation for control of activity of benthic biofilms in beaver systems (paper III).
- Investigate if there are consistent environmental effects of beavers in stream ecosystems throughout their distribution range (paper IV).

3 Methods

This thesis is based on a series of water sampling, field and laboratory experiments complemented with a meta-analysis of published studies.

3.1 Study sites (Paper I-III)

In this thesis 12 beaver systems were studied; six were located in northern Sweden and six in south-central Sweden. The *limes norrlandicus*, a major biogeographical discontinuity in Scandinavia, was used to define the border between the northern and southern region. The six sites in the southern region were located between latitude 59.2° to 59.8°N, whereas the six northern were located between latitude 62.2° to 66.5°N. All catchments of the study sites were dominated by coniferous forest (51-66 % of the total land cover). For more details see paper I.

3.2 Study design (Paper I-III)

At each beaver system three sites were studied: (1) An *upstream reference* site which was located upstream to the first pond in the beaver system. This site showed no beaver activity and represented the pre-reintroduction conditions, (2) A *pond* site representing the largest pond in the system. For all systems it was also the pond where the lodge was constructed, and (3) A *downstream* site which was located directly downstream the last dam in the beaver system.

3.3 Age and colonization history classification (Paper I-III)

Age and colonization history of the 12 beaver systems in the study were estimated from aerial photographs complemented by interviews with the local land owners. The aerial photographs were taken by the Swedish Mapping,

Cadastral and Land Registration Authority (*Lantmäteriet*) between 1973 and 2012 with 2-12 years intervals. The images were screened for signs of beaver activity (e.g. dams, dead trees, flooded areas, fallen trees) from the newest to the oldest image available. The age limit of each beaver system was determined as the time between the oldest image with signs of beaver activity and the following one (e.g. if signs of beavers were not present in an image from 2008 but were present in an image from 2012 the system age was 1-4 years old).

Information from the aerial photographs, regional authorities, land owners or locals, complemented by observation in the field was combined to classify the beaver systems into two colonization history categories; **pioneer systems**, which were new systems with no signs of previous activities of beavers, and **recolonized systems**, which were either new or old systems but with signs of previous colonization periods. For more details see paper I.

3.4 Stream abiotic parameters (Paper I-III)

Water samples were taken during November 2011 and thereafter I collected water samples approximately every second month during the ice free season from April 2012 (aiming to catch the spring floods) to November 2013. Additionally, water samples were collected during winter 2012 (February) when the streams and ponds were ice-covered. In total 10 water samples were collected per site. Samples were taken at 20-30 cm depth except when total depth was less than 20 cm, samples were taken 5 cm above the stream bottom. For each sample the following abiotic parameters were analysed: Total Hg, MeHg, dissolved organic carbon (DOC), total organic carbon (TOC), pH, total nitrogen (total-N), total phosphorous (total-P), nitrite + nitrate ($\text{NO}_2^- + \text{NO}_3^-$).

An optical dissolved oxygen sensor (HDO, resolution 0.01 mg/l or ± 1 % saturation) was used in situ to measure dissolved oxygen (DO) and optical fluorometer sensor (resolution 0.01 $\mu\text{g/L}$ accuracy ± 3 % of full scale) to measure chlorophyll-a concentration in water. Both sensors were mounted on a Eureka Manta2™ multiparameter water quality recorder (Eureka Water Probes LTD).

For every four hrs, water level and temperature (average for the four hrs and point) were logged using TruTrack WT-HR Water Height Data Loggers (resolution ± 1 mm or ± 1 % of full scale and repeatability ± 0.1 °C).

Canopy cover was calculated using a model of radiative transfer in vegetative canopies from measurement above and below canopy. Canopy cover was calculated from five repeated measurements in five different specific locations within 5 m of stream at each site. For more details see paper I.

3.5 Mercury in water (Paper I)

Total Hg analyses were performed at the Swedish Environmental Research Institute (IVL) following the US Environmental Protection Agency standards (EPA, 2002) with detection limit of 0.04 ng/L and limit of quantitation (LOQ) of 0.1 ng/L. Methylmercury (MeHg) in water was analysed based on the procedure described in Lambertsson and Björn (2004) by ALS Scandinavia AB (certified by SWEDAC reg no. 2030) with detection limit of 0.01 ng/L and LOQ of 0.03 ng/L. To quantify the effect of beaver activities on the concentrations of MeHg, the ratio of MeHg between down- and upstream of the beaver systems (D/U MeHg ratio) was calculated for each beaver system. Methylation efficiency was then calculated as the relative concentration of MeHg out of the Total Hg following Roy *et al.* (2009a).

3.6 Benthic species community and functional traits (Paper II)

Macroinvertebrate samples were collected at all sites between mid-October to mid-November 2013 using a Hess sampler with a height of 40 cm, mesh size of 500 μm and bottom cover area of 0.086 m^2 . Four replicates were taken at each site, preserved in 75 % ethanol, and sorted and identified to the lowest possible taxonomic level (species or genus).

Feeding trait information compiled in the Freshwater Ecology database (Schmidt-Kloiber, 2015) was used to assign each species to one or several feeding groups. For the analysis of the effect of macroinvertebrates on litter decomposition, I pulled the leaf “shredders” species out of the total species, which represent the main group impacting leaf litter decomposition. For the analysis of the effect of macroinvertebrates on algal productivity I pulled out the biofilm “grazers” species which represent the main group impacting algal accrual. For each group I calculated Shannon diversity index and Pielou’s evenness index. Shannon and Pielou indexes were calculated using the R package *vegan* (Oksanen *et al.*, 2015).

Species within these two groups (shredders and grazers) may have variation in the degree in which they are exclusively dependant on leaf litter/algae or may choose to feed on other sources of energy as well. To evaluate variation in the dominant feeding traits within these two groups, I further calculated for each site the Functional Dispersion (F-Dispersion). F-Dispersion is the degree of dissimilarity among feeding traits and abundances (Laliberté & Legendre, 2010). Community-level Weighted Mean (CWM) is the mean trait value of all species presented in the community and weighted by their relative abundance (Lavorel *et al.*, 2008) (see details in the methods section of paper II). F-Dispersion and CWM were calculated using R package *FD* (Laliberté, 2015).

3.7 Assessing leaf litter decomposition rates (Paper II)

To evaluate leaf litter decomposition rates, pairs of litterbags filled with 4.2 ± 0.05 g of air-dried silver birch (*Betula pendula*) leaves was used. Each pair consisted of one a) fine mesh bag ($\phi = 0.5$ mm) which excludes shredding macroinvertebrates and therefore decomposition rates represent an estimation of the microbial contribution and b) coarse mesh bag ($\phi = 6$ mm) which allows both macroinvertebrates and microbes to access the litter and therefore quantifies total decomposition rates mediated by both groups together. I deployed five pairs of litterbags in each site arranged along a riffle with approximately 2-3 m between pairs. The litterbags were exposed in the streams for 50-55 days between September to November 2013 to allow ca. 50 % mass loss and then retrieved and kept frozen at -20°C . Within three months from retrieval the litterbags were defrosted and insects were removed from the sample. The litter was dried at 105°C and weighted to determine dry mass loss. The dry litter was then further burned at 550°C to remove all organic matter. The initial and the final ash free dry mass (AFDM) was then calculated for each litterbag. Leaching losses were determined from a 24 h laboratory experiment and the initial AFDM was corrected for leaching. For each of the coarse and fine bags decomposition rates were calculated relative to the average daily temperature above zero (Benfield, 2006; Gessner & Chauvet, 2002). Temperature-corrected decomposition rates were calculated as:

$$-k = \frac{\ln(M_t/M_0)}{DD} \text{ gr/degree - day}$$

With M_t = final AFDM, M_0 = initial AFDM corrected for leaching losses (determined from a 24h laboratory trial) and DD (degree days) is the sum of average daily water temperature above zero.

Decomposition attributable to invertebrates was calculated for each pair of litter bags (fine and coarse) in the same way as the overall decomposition rate but with reducing the AFDM loss of the fine mesh bag from the initial AFDM of the paired coarse bag.

3.8 Assessing algal accrual rates (Paper II-III)

Algal accrual rates were assessed by exposing ceramic tiles for ca. 30 days during July-August 2012, at a standard depth of 20-30 cm and 5 cm above the stream substrate. At each of the study sites I exposed four pairs of tiles, each pair comprised one tile with a 2 cm Vaseline band at the edges to exclude grazers and one tile without the Vaseline treatment. At the end of the exposure period algal accrual was measured in the field using BenthosTorch (bbe

Moldaenke GmbH, Schwentinal, Germany) which allows real-time quantification of benthic algal by measuring the in-vivo fluorescence of algal cells. To account for the regional temperature differences, I calculated algal accrual rates relative to the average daily temperature above zero as:

$$K = \frac{\text{Total chlorophyll} - a}{DD} \text{ ng/cm}^2 / \text{day}$$

Where DD (degree days) is the sum of average daily water temperature for the exposure period (see details in the methods section of paper II).

3.9 Assessing nutrient limitation with nutrient diffusing substrate (NDS) (Paper III)

Nutrient limitation and how it is affected by beavers was assessed using the NDS method following Johnson *et al.* (2009) with small modifications. Due to the logistic constraints imposed by the large geographical range of the study I chose three pioneer and five recolonized beaver systems for the NDS experiment. In the lab I filled 60 mL containers with 2 % agar solution enriched with NaNO₃ (N treatment), KH₂PO₄ (P treatment), both nutrients (N+P treatment) and a container with no nutrient enrichment (control). Each container was topped with either organic birch veneer disc or inorganic glass microfiber filter. Each unit of the NDS experiment comprised eight containers (one for each treatment (control, N, P and N+P; n=4 organic and n=4 inorganic) attached to plastic L-bar. Four replicates of the NDS experiment units were attached in comparable riffles at the upstream and the downstream sites of the beaver systems in August 2013. At the end of the experiment (after exposure of 20-24 days in the streams) I removed the experimental units and algal accrual was quantified in the field using the BenthosTorch (bbe Moldaenke GmbH, Schwentinal, Germany) in the same way as in the algal tile experiment (Paper II). For transportation to the lab, I removed the filters from the NDS experiment unit and placed them in 60 mL containers filled with unfiltered stream water. In the lab the containers were emptied and refilled with unfiltered stream water at room temperature, shaken to contain 100% oxygen saturation, sealed with transparent Parafilm "M"® (Bemis) and incubated in the dark at 19°C. After three hours of incubation dissolved oxygen (DO) measurements were taken using an optical DO sensor (FireString O2, Pyroscience). The DO measurements were corrected for water temperature and surrounding pressure. Community respiration (CR) was calculated as the differences between the initial 100 % DO saturation corrected for water temperature during the final measurement, and the final DO measurement (see details in the methods section of paper III).

3.10 Meta-analysis of beaver effects (Paper IV)

Peer-reviewed literature that is also listed in Journal Citation Reports was extracted from Web of Science™ on 22 April 2016. The word “beaver” and the different factors of interest as title keywords combined with adjacent relevant keywords were used. The factors of interest were: concentrations of N, P, carbon, DO, Hg in water and biota, methane release, water temperature, hydrology (velocity, water area and volume), sedimentation, dead wood, ecosystem functioning, macroinvertebrates and fish. The meta-analysis only included studies that allowed for the comparison between impacted (i.e. affected by beavers) and non-impacted sites (i.e. before beaver colonization, after removal or collapse of beaver dams, or upstream sections unaffected by beavers). Impacted sites were further classified as either ponds or downstream sections and the data were arranged in pairs of Upstream-Downstream, Upstream/Reference-Pond and Pond-Downstream. If available, potential explanatory variables (e.g. system age and beaver species; see paper IV for details) were also extracted. Based on the above criteria 76 relevant scientific articles were selected, representing studies from 11 countries. For some factors differences between artificial dams and beaver dams were also investigated, however this information is not presented in this thesis (see paper IV for details).

The impact of the beaver systems was assessed by calculating the effect size for each factor as suggested in Osenberg et al. (1997) (see methods paper IV).

In total 1366 effect sizes were calculated from beaver systems for the 16 environmental factors. Factors with less than three effect sizes were excluded. (For more details regarding the literature survey and the factors see methods of paper IV).

3.11 Statistical analysis

The effect of beavers on MeHg concentrations, algal accrual, decomposition rates, nutrient limitation, abiotic parameters and the interactive effect of colonization history (all papers), geographical region (paper I-II), season (paper I-II) and year (paper I) were investigated using Analysis of Variance (ANOVA). Response variables were natural log-transformed to satisfy parametric assumptions. I tested for all fixed factors and the interactions between them (crossed and nested). All ANOVAs were conducted using JMP (SAS, 2012). All mean values are presented in this thesis as mean \pm 1 SE.

Differences in variance among categories were assessed with Levene’s test and Wilcoxon signed-rank test was used to determine significant differences

between groups when the normality assumption was not met (paper I). Both tests were conducted using R (*R development core team*, 2014).

Partial least-squares regression (PLS) was used to evaluate the importance of different predictors for explaining the variation in the effect of beavers on MeHg concentrations (paper I). PLS was conducted using SIMCA-P (UMETRIX, 2012).

To explore the influence of potential predictors on differences in ecosystem functioning between and within streams, I used generalized mixed effect modeling (GLMM) in R package nlme (Pinheiro, 2015) (paper II). The best model was selected by stepwise forward selection of parameters and had the lowest Akaike's Information Criteria (AIC). I verified the results using R package gmulti (Calcagno, 2015), which finds the best models among all possible models based on the AIC. The gmulti package uses a genetic algorithm which allows a large set of predicting parameters to be addressed (Calcagno & de Mazancourt, 2010). I further calculated marginal R^2_{GLMM} (represents the variance explained by the fixed factors) for the final mixed effect model using R package MuMIn (Bartoń, 2015).

4 Results and discussion

4.1 Beaver reintroduction affects water MeHg concentrations in pioneer but not in recolonized beaver systems (Paper I)

4.1.1 The effect of beavers on MeHg concentrations

Overall, pioneer systems increased MeHg concentrations downstream; particularly in the warmer periods of the year. In contrast, recolonized systems had no overall effect on MeHg concentrations and only showed occasionally a slight increase during summer. In pioneer systems, during the entire study period the overall downstream MeHg concentrations were significantly higher than upstream, particularly in the summer when MeHg concentrations downstream were up to 3.5 fold higher than upstream (figure 3). In pioneer systems, the effect size (Downstream/Upstream (D/U) ratio) was significantly higher than the 1:1 ratio for all seasons with the exception of spring (possibly due to a dilution effect by spring floods). In contrast, in recolonized systems the D/U ratio was higher than 1:1 only in summer (figure 3). In beaver systems ponds serve as hot spots for methylation and are potentially the source of MeHg downstream (Roy *et al.*, 2009a). Overall, pioneer ponds showed a tendency for higher methylation efficiency compared with recolonized ponds, and during summer (July to September), when methylation is at its highest rates (Ullrich *et al.*, 2001), pioneer ponds had significantly higher methylation efficiency than the recolonized ponds.

Pioneer beaver inundation of a stream by constructing a dam combined with digging in riparian soils (Naiman *et al.*, 1986) rich in organic carbon (Ledesma *et al.*, 2015) expose a large volume of organic material to degradation processes. Resulting from the oxygen consumption of organic matter degradation, a pioneer pond might become an anoxic or subanoxic environment with reducing conditions, particularly at the sediment – water interface. These conditions combined with high availability of degradable

carbon for methylating microorganisms, might increase methylation rates in pioneer ponds and therefore elevate MeHg concentrations downstream.

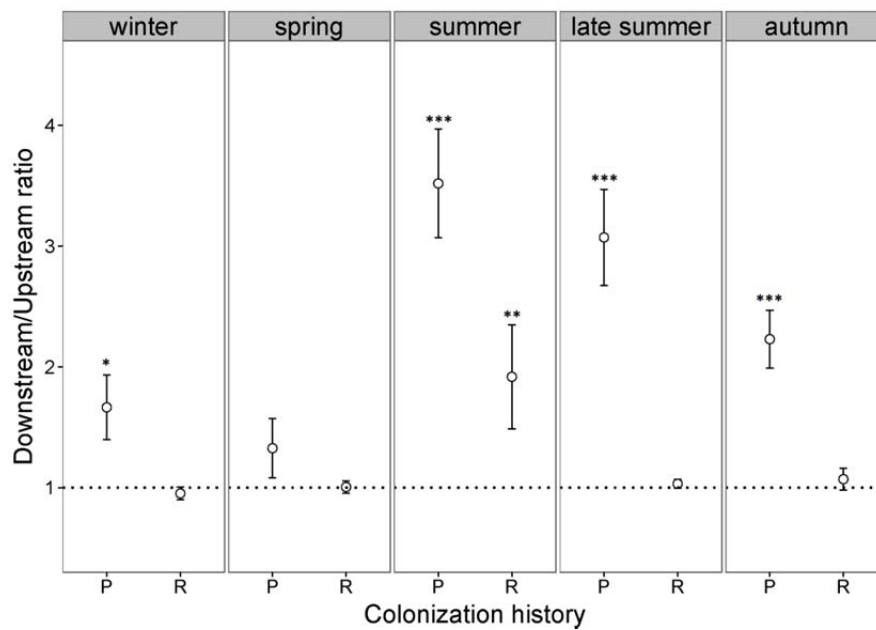


Figure 3. Mean D/U (downstream/upstream) MeHg ratios (± 1 Standard Error) in pioneer (P, n = 5) and recolonized (R, n = 7) beaver systems during five seasons from November 2011 to November 2013. Please note that I only sampled one winter season (February-March 2013). The dashed line denotes the 1:1 ratio. Asterisks above whisker plots denote a D/U ratio higher than 1:1 (*** P<0.001, ** P<0.01, *P<0.05).

The reducing conditions in pioneer beaver ponds are apparently different from those in older ones (Roy *et al.*, 2009a). While colonizing their territory, beavers will continue to maintain high water level but with lower supply of dead wood (Nummi & Kuuluvainen, 2013) and newly flooded soils compared to the pioneer period. Presumably, in older ponds the lower availability of labile carbon and less reducing environment results in less favorable conditions for methylating organisms.

Eventually, beavers will abandon their territory but the structures they created might still persist and affect the hydrology, stream planform and the vegetation (Hood & Larson, 2015; Polvi & Wohl, 2013; Wright, 2009; Naiman *et al.*, 1988). When recolonized, the newly re-flooded beaver ponds have assumingly lower volumes of dead wood and beavers dig less compared with pioneer inundation, which potentially triggers less intensive decay processes and lower methylation rates. Indeed, previous studies also found higher MeHg

D/U ratios in young beaver ponds compared to older ones (Roy et al., 2009a; Roy et al., 2009b; Driscoll et al., 1998). However, these studies focused solely on the pond age without accounting for the differences between new pioneer ponds and recolonization of previously abandoned beaver systems.

4.1.2 Temporal variation in MeHg and the relation to abiotic predictors

In this study, pond methylation efficiency varied seasonally; peaking in the summer in all the study sites but more evidently in pioneer compared to recolonized systems (figure 3). In pioneer beaver ponds, warmer water temperature in combination with the availability of organic matter most likely generates a reducing environment. Such combination in stream ecosystems has shown to increase the activity of sulphate reducing bacteria and stimulate methylation (Tsui & Finlay, 2011). In contrast, lower concentrations and less labile organic material in combination with light-induced (photolytically-driven) demethylation processes at the surface of large open water bodies associated with older beaver ponds, may have induced lower methylation efficiency in recolonized ponds during summer (Lehnerr *et al.*, 2012; Hammerschmidt *et al.*, 2006; Sellers *et al.*, 1996). Nevertheless, the occasional increase in MeHg concentrations downstream of recolonized ponds during the summer, suggests that these systems can sometimes be sites for methylation, albeit at lower rates compared to pioneer ponds.

In this study, PLS analysis showed that dissolved oxygen was the main predictor of D/U MeHg ratios, with higher MeHg concentrations associated with lower oxygen concentrations. The found relation between methylation and dissolved oxygen is in agreement with previous studies (reviewed in Ullrich *et al.*, 2001) and shown for beaver ponds by Roy *et al.* (2009b). Chlorophyll-*a*, total-P and levels of $\text{NO}_2^- + \text{NO}_3^-$ were also valuable predictors for D/U MeHg ratios, reflecting the prominence of nutrient availability in promoting biological activity, which is also enhanced in the summer and can be related to higher methylation rates (Ullrich *et al.*, 2001).

Altogether, temporal variation of MeHg in beaver ponds is the outcome of the relation between methylation (mostly in the sediment layer) which is related to oxygen concentrations, temperature and nutrient concentrations, and demethylation (mostly in the upper surface layer) which is affected by the availability of organic matter and radiation. These results are supported by Tjerngren *et al.* (2012) that in a comparative study of boreal wetlands found that restored wetlands (i.e. re-flooded areas that have previously been natural wetlands) affected MeHg mostly in the first period after flooding. They suggested that increased open water area by flooding (which can be comparable to the old and recolonized beaver systems in this thesis) may result

in decreased net MeHg production. Further studies are needed to reveal in detail the effect of recolonization history on the balance between methylation and demethylation processes in beaver ponds.

4.2 Leaf litter decomposition and algal accrual can be affected by beavers, but mainly in pioneer systems (Paper II-III)

To assess the effect of beavers on ecosystem functioning, rates of leaf litter decomposition, algal accrual and community respiration were compared in comparable riffles downstream and upstream beaver systems. Algal accrual was consistently higher upstream compared with downstream sites for both the algal tiles experiment and the controls of the NDS experiment. In contrast, community respiration measured during the NDS experiment on both organic and inorganic substrates was not affected by beavers. The GLMM analysis suggests that it is the combination of DOC and pH that controls rates of algal accrual, which is reduced when DOC levels are elevated. Furthermore, pioneer beaver systems affected algal accrual stronger than recolonized systems. In contrast to algal accrual, litter decomposition was generally not affected by beaver systems except for significantly faster decomposition rates in three pioneer systems in the southern region (but not in the two pioneer systems in the northern region). These findings demonstrate that algal productivity is consistently lower downstream beaver systems with this effect diminishing – but not disappearing – in older beaver systems and that leaf decomposition downstream beaver systems can sometimes be affected, but most likely in pioneer beaver systems and not in recolonized ones. In summary, the results highlight the potential of beavers in the different colonization phases to alter key ecosystem processes, which potentially can further affect stream food webs.

4.2.1 The effect of beavers on leaf litter decomposition

Overall decomposition rates did not differ between downstream and upstream beaver systems for microbial-derived and total decomposition rates. The only significant difference in decomposition rates between downstream and upstream sites was recorded in the southern pioneer systems where overall decomposition rates were faster downstream compared to upstream, mainly due to faster invertebrates-derived decomposition rates. In general, invertebrate-derived decomposition rates were not different downstream compared to upstream except in the pioneer systems of the southern region (figure 4).

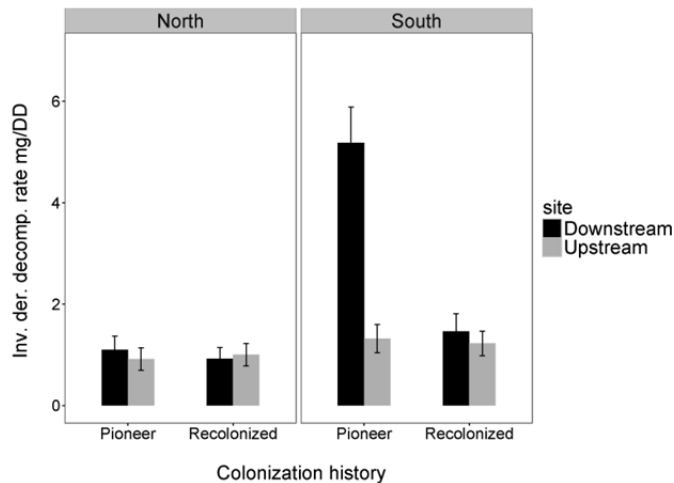


Figure 4. Mean (\pm 1 Standard Error) of invertebrate-derived decomposition rate (mg/DegreeDay) in downstream and upstream reaches of pioneer ($n = 5$) and recolonized ($n = 7$) beaver systems in the northern ($n=6$) and southern ($n=6$) regions.

Although invertebrate-derived decomposition rates were higher downstream for all three pioneer systems in the southern ecoregion, it appears that different mechanisms were behind these differences in decomposition rates. In one system, it was related to shredder functional dispersion that increased markedly downstream compared to the upstream site. In another system, faster decomposition rates were related to lower N/P ratio downstream compared to upstream. The GLMM analysis indicated that total-N or alternatively total-P produced the best model for invertebrate-derived decomposition both (but not together) explaining ca. 25 % of the variance in invertebrate-derived decomposition. The general response to nutrients is in agreement with previous studies that showed that increased decomposition rates can be associated with elevated nutrient concentrations (Woodward *et al.*, 2012; Young *et al.*, 2008; Gessner & Chauvet, 2002). Changes in detritivore community assemblages and feeding traits did not affect decomposition rates, but might have contributed to some of the elevated decomposition rates at the downstream sites of southern pioneer systems.

Altogether, The results of this study suggest that when a beaver dam is built in a landscape that was not subjected to beaver activity for many decades or even centuries, (i.e. pioneer inundation), the effect of such inundation on decomposition rates is determined primarily by the environmental conditions and ecosystem characteristics. This effect might be local or temporarily limited and might be mediated by beaver-induced changes in nutrient balance, shredder community and possible physical alteration (e.g. flow and sediments)

in the pioneer systems. However, the results from the recolonized systems suggest that with time and upon abandonment and recolonization, systems will stabilize and decomposition rates downstream will no longer be affected.

4.2.2 The effect of beavers on autotrophic and heterotrophic biofilms

The effect of beavers on autotrophic biofilms

By quantifying algal accrual on ceramic tiles followed by an NDS experiment, this thesis assesses the effect of beavers on autotrophic and heterotrophic biofilms. On ceramic tiles, algal accrual rates were higher upstream than downstream in all the beaver systems. Furthermore, upstream-downstream differences in pioneer systems were larger than in recolonized ones (figure 5). There were no differences between the northern and the southern beaver systems and these findings were consistent throughout all the systems in the study.

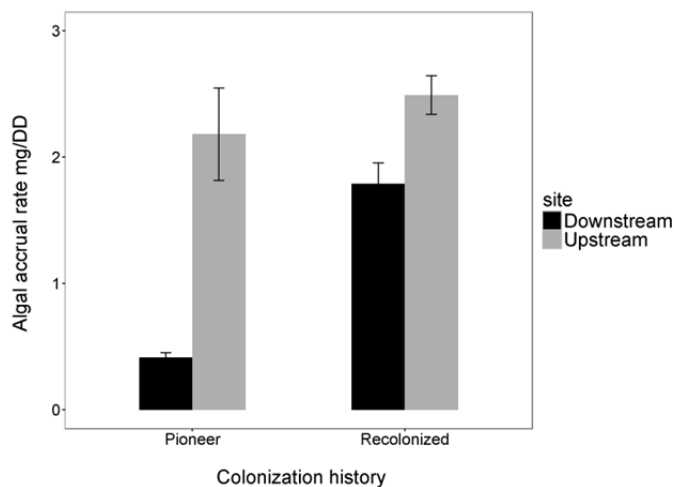


Figure 5. Mean (± 1 Standard Error) of algal accrual rates (mg/DegreeDay) in downstream and upstream reaches of pioneer ($n = 4$) and recolonized ($n = 7$) beaver systems.

When fitting a GLMM model, DOC and pH produced the best model (highest AIC), and explained 55 % of the variance in algal accrual rates. An alternative model including pH and total-P as fixed factors produced a similar AIC and explained variance. Algal accrual rates in this study were positively related to pH and negatively related to DOC. However, algal accrual rates were also negatively related to total-P. The other biotic (grazer abundance, feeding traits) and abiotic (temperature, canopy cover, water level, flow, tile depth, total-N and $\text{NO}_2^- + \text{NO}_3^-$) factors did not improve the model.

As implied from the GLMM analysis, the consistent decrease in algal accrual rates downstream the beaver systems is linked to variation in DOC. The negative effect of DOC on algal accrual rates can be related to reduced light penetration as DOC concentrations rise (Leavitt *et al.*, 1999). This is supported by previous studies in boreal lakes, where the effect of DOC on algal productivity has shown to be even more important than nutrient availability (Seekell *et al.*, 2015; Karlsson *et al.*, 2009). However, information regarding the effect of DOC on algal accrual through light inhibition in streams is lacking in the scientific literature.

In agreement with the algal accrual experiment (paper II), the control containers of the inorganic substrate (a substrate that resembles the ceramic tiles) of the NDS experiment that was conducted one year later (paper III) followed the same pattern; consistently lower algal accrual downstream compared to upstream. The results from the NDS experiment also supported the association between DOC concentrations and algal accrual with significant negative correlation between average D/U ratio of algal accrual and those of DOC (figure 6).

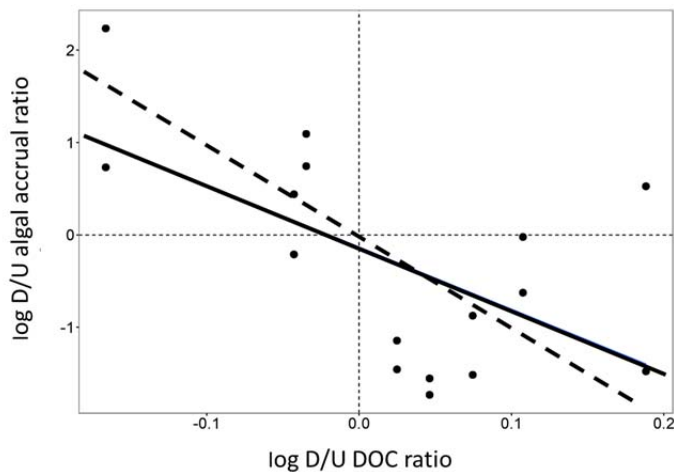


Figure 6. Relationship between downstream/upstream (D/U) ratio of algal accrual and D/U ratio of DOC. The black line shows best fit for the regression ($n=16$, $R^2 = 0.35$, $P = 0.015$) and the dash line represents best fit after removing one outlier ($R^2 = 0.57$, $P = 0.001$). Dotted lines represent the zero intercepts of the X and Y axis.

Although The GLMM identified an association between pH and algal accrual, there were no differences in pH between downstream and upstream sites during the experiment. Therefore, although there are some mechanisms where pH can

affect algal productivity (see details in paper II), it is likely that the differences in algal accrual were not driven by pH.

Apart from DOC, GLMMs also identified total-P as a predictor of algal accrual and the D/U ratio of N/P ratio was a significant predictor of the D/U ratio of algal accrual, explaining 38 % of the variance (ANOVA $F_{1,8} = 5.57$, $P = 0.04$). Surprisingly, although algal accrual was expected to respond positively to increased nutrient availability (Johnson et al., 2014; Johnson & Hering, 2009; Stevenson et al., 2008), in this study, algal accrual declined as total-P increased. Here, the most bioavailable form of P, i.e. PO_4^{3-} , was not measured and the measure of total-P might have primarily captured variation in less bioavailable forms of P. This might explain why increased total-P was not related to increased algal accrual (see details in paper II).

The D/U ratio of total-N or total-P was not related to the D/U ratio of algal accrual. Still, the N/P ratio might partly explain the variation in D/U algal accrual rates since it was lower downstream pioneer systems compared to upstream and might also have some role in the reduction of algal accrual, particularly in pioneer systems.

The effect of beavers on heterotrophic biofilms

Community respiration (CR) was measured on organic and inorganic substrates of the NDS experiment (paper III) in order to assess the effect of beavers on microbial activity. In control substrates, CR was not different downstream compared to upstream or in pioneer compared to recolonized systems for neither organic nor inorganic substrates. However, the ratio between CR and algal accrual (CR /algal accrual) was higher downstream compared to upstream for inorganic substrates (figure 7). This relationship between algal accrual and CR suggests that autotrophic biofilms on inorganic substrate were affected by beaver activity while heterotrophs on the same substrate were not affected or even benefited. Elevated concentrations of DOC that affected autotrophs (both on ceramic tiles and on inorganic substrates of the NDS experiment) might affect heterotrophs differently. While a higher quantity of DOC downstream negatively affected algal productivity, the quality of the organic matter downstream positively affected heterotrophic productivity (see details in paper III). The effect of the availability of labile carbon on biofilms is supported by laboratory experiments. Several studies found that additional labile DOC stimulates uptake of N and P by heterotrophs and as a result suppresses the growth of autotrophs (Bechtold *et al.*, 2012; Johnson *et al.*, 2009; Stets & Cotner, 2008; Thingstad *et al.*, 2008).

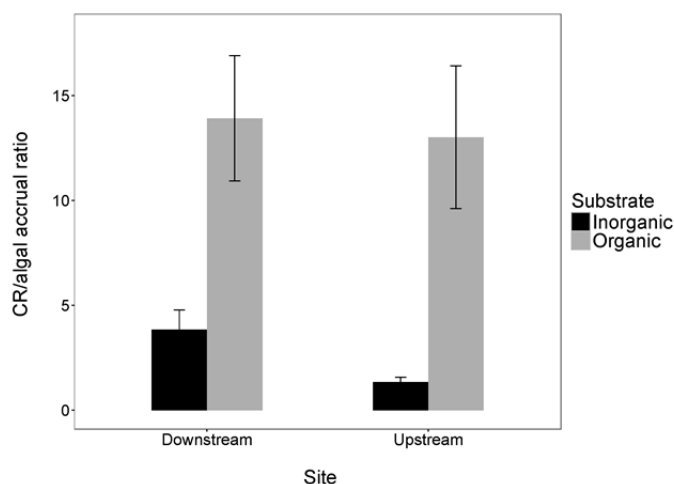


Figure 7. Means (± 1 Standard Error) of the ratio between community respiration and algal accrual rates in downstream and upstream reaches and on organic and inorganic substrates.

In summary, these results suggest that the suppression of algal accrual downstream beaver ponds might reflect a complex interaction between quantity and quality of DOC, nutrient balance and possibly reduction in pH. Conversely, beaver systems had no effect on microbial biofilms and potentially even increased microbial activity on inorganic substrates. The primary causes of the beaver-induced changes in DOC, nutrients and pH are potentially the flooding of riparian vegetation and soils upon the creation of beaver ponds. Inundation and other activities (e.g. digging, feeding) increase the runoff of nutrients and DOC which potentially reduce pH and alter N/P ratio. The results indicate that the negative effect of these changes on algal productivity is greater during pioneer inundation; however this effect extends beyond the phase of pioneer ponds, to also impact algal accrual in older, recolonized systems. More research is needed to elucidate potential mechanisms affecting the decrease in algal accrual downstream beaver systems.

4.2.3 Algal productivity and community respiration were nutrient limited but not affected by beavers

Primary producers (mainly algae) as well as bacteria and fungi are typically limited by N or P or both (Harpole *et al.*, 2011; Elser *et al.*, 2007; Francoeur, 2001). Beavers can affect N and P concentrations in water, and as shown in section 4.2.2, by altering nutrient balance downstream, beavers can also affect autotrophic and heterotrophic biofilms. Therefore, it was also expected that the degree of nutrient limitation will be affected by beavers. To elaborate the role

of nutrient limitation in algal productivity and microbial respiration and how beavers affect nutrient limitation, an NDS experiment was applied (paper III).

In the NDS experiment, algal accrual was consistently N-limited for both organic and inorganic substrates with higher algal accrual on N and N+P treatments when compared to controls (figure 8). Algal accrual N limitation was not different downstream compared to upstream and no effect of colonization history was observed.

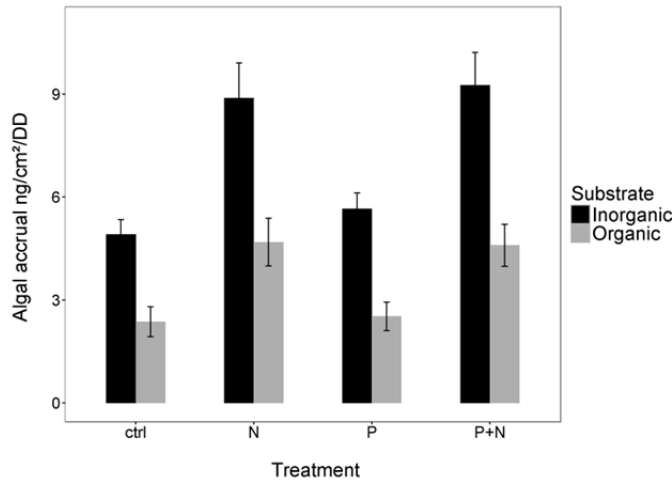


Figure 8. Means (± 1 Standard Error) of algal accrual ($\mu\text{g}/\text{cm}^2$) for controls (ctrl), N, P and N+P treatments on organic and inorganic substrates.

The average RR of algal accrual to N and N+P on both organic and inorganic substrates was negatively correlated to total-N, $\text{NO}_2^- + \text{NO}_3^-$ and DOC. No correlation between RR of algal accrual and the remaining predictors (temperature, canopy cover or N/P ratio) was found. The correlation between RR of N and the concentrations of N in the water column is intuitive since it is expected to have stronger response when the limiting nutrient is less available. Surprisingly, beaver systems had no effect on the magnitude of the response. The combined results from the NDS and the algal accrual experiment suggest that although N was the limiting factor of algal productivity, it was mainly the beaver effect on DOC concentration, and not N or P, which controls the reduction in algae accrual downstream beaver systems. To understand how DOC limits algal productivity and how this limitation is affected by beavers, future NDS experiments should consider including a carbon-diffusing treatment as well as N and P to address the combined control of these three limiting factors.

Community respiration (CR) was consistently inhibited by additional P on both organic and inorganic substrates with lower CR in the P and N+P treatments compared to controls (figure 9). There were no differences between downstream and upstream for any of the treatments and no effect of colonization history or substrate was observed. Since the inhibition of CR was not followed by increased autotrophic productivity it is not likely that autotrophs suppressed the growth of heterotrophs. For primary producers, there are only few records in the scientific literature for P inhibition, and such results are commonly not discussed in the scientific literature (Tank & Dodds, 2003). I could not find studies reporting P inhibition for heterotrophic biofilms but in a meta-analysis of 641 studies on autotrophic biofilms, Harpole *et al.* (2011) found that 15 % of the studies showed negative response to P. In my study it is likely that the reduced respiration resulted from either stoichiometric imbalance or alteration in species composition of heterotrophs as a result of P addition. Average RR of CR to P and N+P on organic substrate was positively correlated to $\text{NO}_2^- + \text{NO}_3^-$ concentrations and there was no relationship between RR of CR to the other available predictors (temperature, canopy cover, total-N, total-P, DOC or N/P ratio). The reduced P inhibition as a result of additional bioavailable N from the water column supports the assumption that it might have been the effect of internal stoichiometric imbalance that was controlling P inhibition. Further NDS experiments enriched with different N:P ratios may help to explain P inhibition of microbial biofilms.

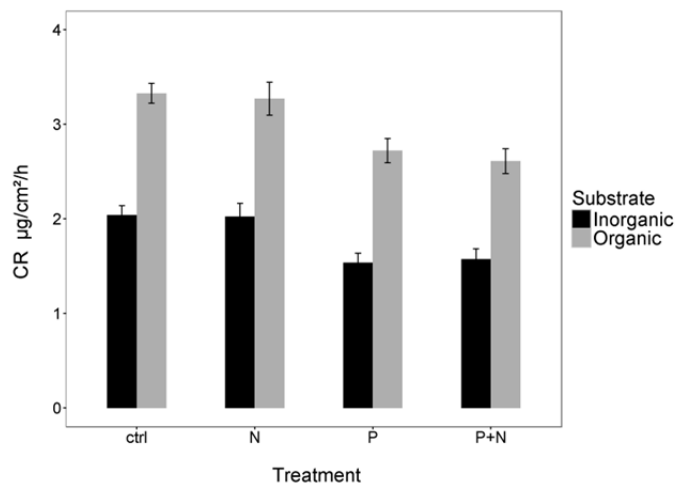


Figure 9. Means (± 1 Standard Error) of community respiration ($\mu\text{g O}_2 / \text{cm}^2 \text{ h}^{-1}$) for controls (ctrl), N, P and N+P treatments on organic and inorganic substrates.

4.3 Landscape effect of beaver dams – a meta-analysis of published studies (Paper IV)

In papers I, II and III, I found that the effect of beavers on different processes in stream ecosystems not only depend on the biogeochemical settings of the systems but also on successional stages and colonization history of the various ponds in the beaver system which also regulates the way downstream reaches are affected. In Paper IV, a meta-analysis of 1366 effect sizes from 76 published studies assessed the overall effect of beavers on 16 factors related to biogeochemistry, hydrogeomorphology, biodiversity and ecosystem functioning.

Although the aim was to address overall ecosystem functioning, at the time of performing the meta-analysis (July 2016) the only beaver effect related to ecosystem functioning that was found published in the scientific literature was regarding water column concentrations of chlorophyll-a. Overall, chlorophyll-a in water increased in impoundments compared with upstream and with downstream but not when comparing upstream with downstream. The meta-analysis also showed that overall, beaver dams did not affect nutrient concentrations (N and P). However, when considering system age, young beaver systems (≤ 10 years) were a source of P while P retention was observed in older beaver systems (> 10 years). In contrast, water carbon concentrations (mainly DOC and TOC) were higher in ponds compared to downstream and upstream and higher downstream compared to upstream.

Altogether, the results from the experiments (paper II and III) and the meta-analysis suggest that beaver systems might affect algal productivity downstream not primarily by altering nutrient concentrations but mainly by increasing dissolved carbon concentrations in the water. The meta-analysis further suggests that the relation between pond age and P also can play a role in regulating algal productivity downstream beaver systems.

The results from the meta-analysis also support the beaver effect on Hg and the relation to beaver system colonization history (or age) that was found in paper I. Overall beaver systems were a source of Hg and especially MeHg when comparing upstream with downstream however; it was the young and not the old systems that were the source of Hg when comparing upstream with ponds. The meta-analysis also identified beaver ponds as a source for methane emission when compared with upstream and downstream sites. Beavers transfer streams into ponds and wetlands with characteristics which are commonly recognized as a source of Hg, MeHg (Tjerngren *et al.*, 2012; Galloway & Branfireun, 2004) and Methane (Pickett-Heaps *et al.*, 2011) in the boreal landscape. Therefore, it is likely that beavers affect these factors as long as they maintain constant water level in the ponds and sustain the conditions

favouring these factors. The results from this study suggest that during the recovery stage of beavers, methane, mercury and particularly MeHg concentrations will increase at the landscape scale. However, since old and recolonized systems only slightly increase MeHg concentrations (or not at all), it is not evident to which extent the recovery of beavers will affect the background levels of MeHg in e.g. wetlands and peatlands. There are no studies on how recolonized/old ponds affect methane emission compared to pioneer ponds. At this stage, it is therefore not possible to conclude about the effect of colonization history on methane emissions.

As expected from previous descriptive reviews (Nummi & Kuuluvainen, 2013; Rosell *et al.*, 2005; Collen & Gibson, 2001), the meta-analysis showed that beavers affect hydrogeomorphology by increasing water area and volume while reducing flow. Changes in flow conditions and water volume in impoundments may lead to the overall decrease in dissolved oxygen and increased temperature in ponds and downstream compared with upstream. The above alterations to the hydrogeomorphology also resulted in finer sediments and higher amount of dead wood in the beaver impoundments compared with the upstream and downstream sites.

When assessing the effect of beavers on macroinvertebrates and fish diversity and abundance, both factors decreased downstream compared with upstream. However, the average effect size was not affected by damming as indicated by the effect ratios between impoundments and upstream and downstream, respectively. These results reflect the way beaver impoundments also can affect stretches downstream by altering the biogeochemical conditions and resources at the base of the aquatic food web, potentially affecting also higher trophic levels.

Overall, the meta-analysis showed that beavers have the potential to affect all analysed factors. When compared to a reference site, significant effects were found (1) in both beaver ponds and downstream reaches for: hydromorphology (water volume, area and flow) as well as for concentrations of dissolved oxygen, mercury and carbon, (2) in ponds but not downstream for: volume of dead wood, sediment structure (fine and coarse), methane emission, concentrations of N and chlorophyll-a, and (3) in downstream reaches but not ponds for: fish and macroinvertebrates (species diversity and abundance) and temperature (figure 10). Beaver ponds were a source for P in young systems but a sink in old ones, potentially resulting in no overall effect. The example of beaver effects on P demonstrates the importance of the age of the system/pond since with time the effect of beavers on some factors might increase, decrease, or even be inverted. Unfortunately, it was not possible to assess the effect of beaver system succession on most of the factors due to lack of information

regarding age and colonization history in most of the published literature. Paper I-III demonstrates the importance of these factors and future studies should consider them when evaluating landscape scale and long-term environmental effects of beavers.

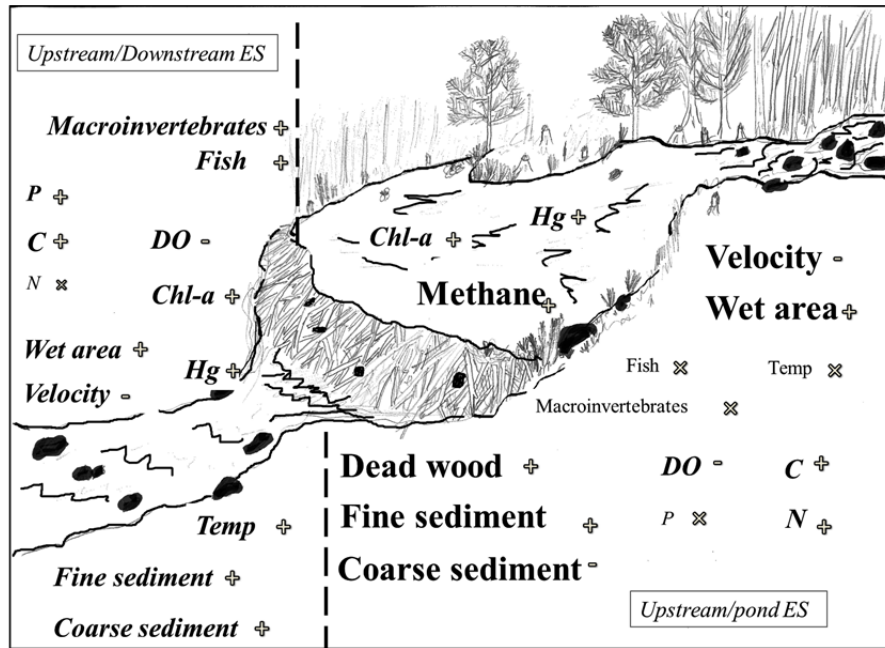


Figure 10. Average effect size (ES) of the factors studied in the meta-analysis. ES comparing downstream with upstream sites and ponds with upstream sites are presented to the left and right, respectively. Positive (+), negative (-) and indifferent (x) ES are shown. Bold normal text represents ES larger than ± 1 , bold italic text represents ES between ± 0.1 to ± 0.99 and small normal text represents ES between 0 to ± 0.09 .

4.4 Short- and long-term effects of beaver systems following recolonization

One of the most striking results of this thesis is the regular occurrence of differences in the way pioneer impoundments affect ecosystem processes and functioning compared to old or recolonized systems. For the 12 beaver systems that were the focus of this study, colonization history was an important factor that regulates the effect of beavers on nutrients (N and P), organic carbon, dissolved oxygen, methylation rates and MeHg concentrations, algal accrual and leaf litter decomposition. The meta-analysis confirmed the effect of system age on Hg concentrations and P retention.

This thesis further demonstrates how processes resulting from beaver engineering in stream ecosystems and the cyclic nature of beaver colonization periods can regulate three key ecosystem processes: Hg methylation; algal productivity; and leaf litter decomposition.

When upscaling the results to the landscape scale, beaver systems affect forested stream ecosystems, particularly as pioneer systems. However, the pervasiveness of pioneer systems in the Swedish landscape is itself predominantly the result of the recovery of the beaver populations following near extirpation. The absence of beavers and beaver engineering in freshwater ecosystems – in some instances for centuries – followed by their reintroduction and recovery, potentially created a landscape mosaic scattered with pioneer systems (as in Johnston & Naiman, 1990a).

As long as beaver populations recover by expanding distribution ranges and increasing population size (Halley *et al.*, 2012), pioneer beaver systems will be relatively common. However, most pioneer systems eventually mature (colonized for potentially several decades), will be abandoned, and most likely recolonized at a later phase. Hence, it is likely that old and recolonized beaver systems will dominate future beaver-impacted landscapes (as example in Little *et al.*, 2012; Cunningham *et al.*, 2006). If this thesis were to be re-run 50 to 100 years from now, it is likely that many of the effects observed here would be weaker or non-existent at the landscape scale due to the decrease in pioneer systems.

Even though the importance of temporal aspects for the way beavers affect ecosystems has been recognized for 30 years (Naiman *et al.*, 1988; Naiman *et al.*, 1986), only a few published studies address the age aspect of beaver systems (e.g. Vehkaoja *et al.*, 2015; Roy *et al.*, 2009a; Stevens *et al.*, 2006; Wright *et al.*, 2003; Ray *et al.*, 2001). I am also unaware of any studies that consider the effect of colonization history. The ongoing debate related to new reintroduction plans in parts of Europe often involves various experts and may also incorporate public opinion – such as in the case of the Scottish beaver trial (trust, 2016) and Welsh beaver project (wales, 2012).

Therefore, when considering reintroduction it is important to present to decision makers, managers and the public the potential costs and benefits of such programs (e.g. Stringer & Gaywood, 2016). This thesis highlights the importance of separating short-term effects of pioneer systems from long-term effects of established populations when evaluating the overall effect of beaver reintroduction programs.

Finally, the definition of reference conditions to which an impacted site (pond, downstream or the entire system) is compared to, is an important issue when assessing the effect of beaver reintroduction on stream ecosystems.

While some studies used temporal references (comparing conditions before beaver colonisation with those after colonization), others used spatial references (comparing conditions in a reference stream without active beaver colonization or in most cases an upstream reach of the same stream) (see Paper IV for different approaches used in the literature).

A temporal reference approach will, most likely, examine pioneer systems. This is because the study will often be conducted in the first years after inundation (unless the study continues for many years following inundation). Applying a spatial reference approach hosts several challenges since reference sites might: (1) be located downstream of another beaver system that is situated upstream of the focal beaver systems, or might represent an abandoned beaver system, and therefore might also represent an “affected site”; and (2) represent post extirpation or managed conditions (this means it will not accurately represent pristine conditions).

Therefore, it is challenging to evaluate the effect of beavers in freshwater ecosystems, without defining the proper reference conditions and whether this includes beavers.

4.5 Beavers and beaver reintroductions in Europe’s managed landscapes

About 27,000 streams run through the Swedish landscape, with a total length of ca. 192,000 km (SMHI, 2010). In 1939, shortly after the reintroduction of beavers in Sweden, the total population was 80 beavers. About 70 years later the population of beavers was estimated at 130,000-140,000 (Hartman, 2011b) inhabiting most of Sweden (except for the southern parts), but not yet all suitable habitats (Hartman, 2011a). It is likely that, with time, beaver colonies of different colonization status (pioneer, abandoned and recolonised) will be present in most suitable streams in Sweden. Therefore, it is important to consider the profound ecosystem changes caused by beavers, and their effects when implementing watershed and landscape management programs, such as the European Water Framework Directive (WFD) (EU, 2000) and hunting policy.

The WFD was established in 2000, with the goal that all water bodies in Europe achieve at least good ecological status (EU, 2000). Ecological status encompasses the quality and functioning of aquatic ecosystems. Good ecological status can be achieved if the conditions in the waterbody are not significantly different from the conditions which are expected with minimal anthropogenic impact (i.e. reference conditions). Since beavers were historically present in large parts of Europe, the conditions of stream

ecosystems, which we now regard as “pristine”, were to a great extent shaped by beavers.

The WFD, however, does not include the impact of beavers. For example, this exclusion is evident in the discussion of hydro-geomorphological status, which accounts for stream modifications in the form of fragmentation, continuity, variation in flow, alterations in water level, volume of dead wood, and stream straightening. All of these can also be affected by beaver engineering activities (Tornblom *et al.*, 2011).

At a landscape scale, boreal forests and wetlands might have adapted to beaver engineering activity over millions of years of co-existence (Rybczynski, 2007). Due to anthropogenic pressure during the latest centuries, this link was broken, and the absence of beavers from the landscape – together with drainage of forests – has driven comprehensive changes to boreal freshwater ecosystems (Nummi & Kuuluvainen, 2013). Moreover, today, reintroduction of beavers is regarded as a “natural restoration” of pre-historic conditions (e.g. Curran & Cannatelli, 2014; DeVries *et al.*, 2012).

This thesis suggests that following beaver reintroduction, and as long as the population is growing, beavers might strongly affect present-day functioning of stream ecosystems. However, since recolonized systems, even if very recent, are expected to have comparable effects as natural wetlands, with time the overall effect of beavers will potentially be comparable to pre-extirpation.

Since the activities and impacts of beavers often interfere with human practices (such as forestry, agriculture and recreation), large populations of beavers may become a subject of controversy. In the absence of natural predators (mainly wolves) beavers are controlled by habitat availability, food regeneration, natural mortality and hunting.

In 1992 Eurasian beavers were included as an Annex II species (species of community interest whose conservation requires the designation of special areas of conservation) in the European Habitats Directive (EU, 1992). However, due to population recovery, since 2008 the Eurasian beaver is classified as “of least concern”, with an increasing population trend according to the International Union for Conservation of Nature Red List of Threatened Species (Batbold, 2008). In Scandinavia and the Baltic countries, hunting is no longer for pelts trading or meat supply, but rather for mitigation and damage control or for sport, and is mainly limited only by season or not at all.

In Sweden, hunting is allowed throughout the open hunting season (October–May) without any regulation, control or recommendations. The removal of dams and hunting for damage control is generally associated with the conflict between beavers and agriculture or forestry, since beaver dams cause the flooding of productive land and damage access roads.

The absence of management plans for beaver populations holds the risk for local over exploitation. Several methods to control beaver populations and damage control have been suggested. This includes fertility control, restoration of adequate buffer riparian zones, fencing trees, overflow pipes, chemical repellents, and compensation schemes for farmers and foresters (Reviewed in Nolet & Rosell, 1998).

Considering the profound ecological effects of beavers, there is a need for a management plan towards maintaining landscapes of spatially and temporally shifting mosaics that comprise new, old, abandoned and recolonized beaver systems. According to the results of this thesis, such a management plan has the potential to reduce the environmental burden of MeHg and to restore pre-industrial ecosystem functioning of streams.

5 Concluding remarks and future perspective

This thesis is based on the study of 12 pioneer and recolonized beaver systems along a latitudinal gradient in Sweden, complemented by a meta-analysis of published studies. This setting made it possible to study how damming by beavers affects stream ecosystems, and also to distinguish between short-term effects in pioneer systems and long-term effects in recolonized ones.

Overall, this thesis emphasizes the importance of incorporating temporal aspects of the “beaver cycle” when assessing the environmental effects of beavers, particularly following reintroduction. The main conclusions of this thesis are:

- Overall, the effect of beavers on ecosystem processes and biotic or abiotic conditions is stronger in recently colonized pioneer beaver systems than in old or recolonized ones.
- Beaver systems can potentially increase MeHg concentrations in ponds and immediately downstream of the dam systems. This increase is expected in pioneer beaver systems, but not in recolonized systems.
- Beaver systems are likely to decrease algal accrual in reaches immediately downstream beaver ponds – this effect is larger in pioneer than in recolonized systems. The reduction in algal accrual is primarily related to increased concentrations of dissolved organic carbon.
- The degree of nutrient limitation of algal productivity and community respiration is probably not affected by beaver systems.
- Rates of leaf litter decomposition are not expected to be affected by beaver systems. However, in pioneer systems, decomposition rates might be faster due to variations in nutrient concentrations and changes in macroinvertebrate communities downstream compared to upstream.

- Overall, beavers can potentially affect all 16 factors that were in the scope of the meta-analysis study but the effect may differ from ponds to downstream reaches and between young and old ponds. This thesis also identifies the gap in knowledge in the scientific literature regarding the potential variation in beaver effects related to different stages of age and colonization history.

5.1 Future perspective

This thesis stresses the importance of future studies to focus on the succession of beaver systems. Of particular importance is differentiating between the effects of pioneer systems and how it is changing as systems enter the “beaver cycle” (comprising old, abandoned, and recolonized systems).

Between 1922 and 1939, Sweden reintroduced the Eurasian beaver and was the first country to do so in Europe and Asia (followed by many others). Today, almost 100 years later, the Swedish beaver population is still growing, nonetheless, beavers are still absent from many available, suitable habitats. Hence, as long as the beaver population is expanding, beaver landscapes will be characterized by pioneer systems. Information regarding differences of beaver effects between pioneer and recolonized systems is crucial for the ability to assess present and future landscape effects of beaver reintroduction plans in Sweden and in other countries where beaver populations are still recovering.

At present, such information is limited and future scientific efforts should therefore be directed to fill this gap in knowledge.

References

- Andersen, D.C. & Shafroth, P.B. (2010). Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology*, 3(3), pp. 325-338.
- Anderson, C.B. & Rosemond, A.D. (2007). Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, 154(1), pp. 141-153.
- Anderson, C.B. & Rosemond, A.D. (2010). Beaver invasion alters terrestrial subsidies to subantarctic stream food webs. *Hydrobiologia*, 652(1), pp. 349-361.
- Anderson, N.L., Paszkowski, C.A. & Hood, G.A. (2015). Linking aquatic and terrestrial environments: can beaver canals serve as movement corridors for pond-breeding amphibians? *Animal Conservation*, 18(3), pp. 287-294.
- Bartoń, K. (2015). *MuMIn: Multi-Model Inference; R package* (Version: 1.15.1) [Computer Program].
- Batbold, J., Batsaikhan, N., Shar, S., Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G. & Palomo, L.J. (2008). Castor fiber. The IUCN Red List of Threatened Species.
- Bechtold, H.A., Marcarelli, A.M., Baxter, C.V. & Inouye, R.S. (2012). Effects of N, P, and organic carbon on stream biofilm nutrient limitation and uptake in a semi-arid watershed. *Limnology and Oceanography*, 57(5), pp. 1544-1554.
- Benfield, E.F. (2006). Decomposition of leaf material. In: Lamberti, F.R.H.G.A. (ed. *Methods in Stream Ecology*. 2nd. ed. San Diego, CA: Academic press, pp. 711-720.
- Bledzki, L.A., Bubier, J.L., Moulton, L.A. & Kyker-Snowman, T.D. (2011). Downstream effects of beaver ponds on the water quality of New England first- and second-order streams. *Ecohydrology*, 4(5), pp. 698-707.
- Bunn, S.E., Davies, P.M. & Mosisch, T.D. (1999). Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology*, 41(2), pp. 333-345.
- Burchsted, D., Daniels, M., Thorson, R. & Vokoun, J. (2010a). The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. *Bioscience*, 60(11), pp. 908-922.
- Burchsted, D., Daniels, M.D. & Thorson, R.M. (2010b). *Restoring the river discontinuum: looking at the example of beaver dams*. (Proceedings of the World Environmental and Water Resources Congress 2010, Providence, Rhode Island, USA, 16-20 May, 2010.

- Calcagno, V. (2015). *gmulti: Model selection and multimodel inference made easy. R package.* (Version: 1.0.7) [Computer Program].
- Calcagno, V. & de Mazancourt, C. (2010). gmulti: An R Package for Easy Automated Model Selection with (Generalized) Linear Models. *Journal of Statistical Software*, 34(12), pp. 1-29.
- Cardinale, B.J. (2011). Biodiversity improves water quality through niche partitioning. *Nature*, 472(7341), pp. 86-89.
- Chandler, R.B., King, D.I. & DeStefano, S. (2009). Scrub-shrub bird habitat associations at multiple spatial scales in beaver meadows in massachusetts. *Auk*, 126(1), pp. 186-197.
- Coleman, R.L. & Dahm, C.N. (1990). Stream geomorphology - effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society*, 9(4), pp. 293-302.
- Collen, P. & Gibson, R.J. (2001). The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. *Reviews in Fish Biology and Fisheries*, 10(4), pp. 439-461.
- Cunningham, J.M., Calhoun, A.J.K. & Glanz, W.E. (2006). Patterns of beaver colonization and wetland change in Acadia National Park. *Northeastern Naturalist*, 13(4), pp. 583-596.
- Curran, J.C. & Cannatelli, K.M. (2014). The impact of beaver dams on the morphology of a river in the eastern United States with implications for river restoration. *Earth Surface Processes and Landforms*, 39(9), pp. 1236-1244.
- DeVries, P., Fetherston, K.L., Vitale, A. & Madsen, S. (2012). Emulating Riverine Landscape Controls of Beaver in Stream Restoration. *Fisheries*, 37(6), pp. 246-255.
- Driscoll, C.T., Holsapple, J., Schofield, C.L. & Munson, R. (1998). The chemistry and transport of mercury in a small wetland in the Adirondack region of New York, USA. *Biogeochemistry*, 40(2-3), pp. 137-146.
- Ducroz, J.F., Stubbe, M., Saveljev, A.P., Heidecke, D., Samjaa, R., Ulevicius, A., Stubbe, A. & Durka, W. (2005). Genetic variation and population structure of the Eurasian beaver *Castor fiber* in Eastern Europe and Asia. *Journal of Mammalogy*, 86(6), pp. 1059-1067.
- EU (1992). *on the conservation of natural habitats and of wild fauna and flora*: Council Directive 92/43/EEC.
- EU (2000). *Directive 2000/60/EC of the European Parliament and of the Council establishing a framework for the Community action in the field of water policy*: EU.
- EU Directive 2008/105/EC of the European Parliament and of the Council of 16 December 2008 on environmental quality standards in the field of water policy (2008). EU.
- Feio, M.J., Alves, T., Boavida, M., Medeiros, A. & Graca, M.A.S. (2010). Functional indicators of stream health: a river-basin approach. *Freshwater Biology*, 55(5), pp. 1050-1065.
- Ford, T.E. & Naiman, R.J. (1988). Alteration of carbon cycling by beaver - methane evasion rates from boreal forest streams and rivers. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 66(2), pp. 529-533.
- Fryxell, J.M. (2001). Habitat suitability and source-sink dynamics of beavers. *Journal of Animal Ecology*, 70(2), pp. 310-316.
- Galloway, M.E. & Branfireun, B.A. (2004). Mercury dynamics of a temperate forested wetland. *Science of the Total Environment*, 325(1-3), pp. 239-254.

- Gessner, M.O. & Chauvet, E. (2002). A case for using litter breakdown to assess functional stream integrity. *Ecological Applications*, 12(2), pp. 498-510.
- Gurnell, A.M. (1998). The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, 22(2), pp. 167-189.
- Halley, D., Rosell, F. & Saveljev, A. (2012). Population and Distribution of Eurasian Beaver (*Castor fiber*). *Baltic Forestry*, 18(1), pp. 168-175.
- Hammerschmidt, C.R., Fitzgerald, W.F., Lamborg, C.H., Balcom, P.H. & Tseng, C.M. (2006). Biogeochemical cycling of methylmercury in lakes and tundra watersheds of Arctic Alaska. *Environmental Science & Technology*, 40(4), pp. 1204-1211.
- Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B. & Smith, J.E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, 14(9), pp. 852-862.
- Hartman, G. (2011a). *The beaver (Castor fiber) in Sweden*. (Restoring the European beaver: 50 Years of experience.)
- Hartman, G. (2011b). *The case of the Eurasian beaver in Sweden: re-introduction project carried out before the existence of re-introduction guidelines!* (Global re-introduction perspectives: 2011. More case studies from around the globe.)
- Hartman, G. & Tornlov, S. (2006). Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*). *Journal of Zoology*, 268(2), pp. 127-131.
- Hood, G.A. & Larson, D.G. (2015). Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. *Freshwater Biology*, 60(1), pp. 198-208.
- Hossack, B.R., Gould, W.R., Patla, D.A., Muths, E., Daley, R., Legg, K. & Corn, P.S. (2015). Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation*, 187, pp. 260-269.
- Janzen, K. & Westbrook, C.J. (2011). Hyporheic Flows Along a Channelled Peatland: Influence of Beaver Dams. *Canadian Water Resources Journal*, 36(4), pp. 331-347.
- JECFA (2004). *Evaluation of certain food additives and contaminants Sixty-first report of the Joint FAO/WHO Expert Committee on Food Additives*. Geneva: World Health Organization.
- Johnson, L.T., Tank, J.L. & Dodds, W.K. (2009). The influence of land use on stream biofilm nutrient limitation across eight North American ecoregions. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(7), pp. 1081-1094.
- Johnson, R.K., Angeler, D.G., Moe, S.J. & Hering, D. (2014). Cross-taxon responses to elevated nutrients in European streams and lakes. *Aquatic Sciences*, 76(1), pp. 51-60.
- Johnson, R.K. & Hering, D. (2009). Response of taxonomic groups in streams to gradients in resource and habitat characteristics. *Journal of Applied Ecology*, 46(1), pp. 175-186.
- Johnston, C.A. & Naiman, R.J. (1990a). Aquatic patch creation in relation to beaver population trends. *Ecology*, 71(4), pp. 1617-1621.
- Johnston, C.A. & Naiman, R.J. (1990b). Browse selection by beaver - effects on riparian forest composition. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 20(7), pp. 1036-1043.
- Jones, C.G., Gutierrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G. & Talley, T.S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, 119(12), pp. 1862-1869.

- Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69(3), pp. 373-386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78(7), pp. 1946-1957.
- Karlsson, J., Bystrom, P., Ask, J., Ask, P., Persson, L. & Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, 460(7254), pp. 506-U80.
- Korth, W.W. & Rybczynski, N. (2003). A new, unusual castorid (rodentia) from the earliest miocene of Nebraska. *Journal of Vertebrate Paleontology*, 23(3), pp. 667-675.
- Kovalenko, K.E., Thomaz, S.M. & Warfe, D.M. (2012). Habitat complexity: approaches and future directions. *Hydrobiologia*, 685(1), pp. 1-17.
- Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), pp. 299-305.
- Laliberté, E.L., Pierre, Shipley, Bill (2015). *FD: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package.* (Version: 1.0.12) [Computer Program].
- Lambertsson, L. & Björn, E. (2004). Validation of a simplified field-adapted procedure for routine determinations of methyl mercury at trace levels in natural water samples using species-specific isotope dilution mass spectrometry. *Analytical and Bioanalytical Chemistry*, 380(7-8), pp. 871-875.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. (2008). Assessing functional diversity in the field – methodology matters! *Functional Ecology*, 22(1), pp. 134-147.
- Leavitt, P.R., Findlay, D.L., Hall, R.I. & Smol, J.P. (1999). Algal responses to dissolved organic carbon loss and pH decline during whole-lake acidification: Evidence from paleolimnology. *Limnology and Oceanography*, 44(3), pp. 757-773.
- Ledesma, J.L.J., Grabs, T., Bishop, K.H., Schiff, S.L. & Kohler, S.J. (2015). Potential for long-term transfer of dissolved organic carbon from riparian zones to streams in boreal catchments. *Global Change Biology*, 21(8), pp. 2963-2979.
- Lehnherr, I., St Louis, V.L., Emmerton, C.A., Barker, J.D. & Kirk, J.L. (2012). Methylmercury Cycling in High Arctic Wetland Ponds: Sources and Sinks. *Environmental Science & Technology*, 46(19), pp. 10514-10522.
- Lepori, F. & Hjerdt, N. (2006). Disturbance and Aquatic Biodiversity: Reconciling Contrasting Views. *Bioscience*, 56(10), pp. 809-818.
- Little, A.M., Guntenspergen, G.R. & Allen, T.F.H. (2012). Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. *Ecoscience*, 19(3), pp. 246-257.
- Meyer, J.L. (1997). Stream health: Incorporating the human dimension to advance stream ecology. *Journal of the North American Benthological Society*, 16(2), pp. 439-447.
- Naiman, R.J., Johnston, C.A. & Kelley, J.C. (1988). Alteration of North -American streams by beaver. *Bioscience*, 38(11), pp. 753-762.
- Naiman, R.J., Melillo, J.M. & Hobbie, J.E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor-Canadensis*). *Ecology*, 67(5), pp. 1254-1269.

- Nolet, B.A. & Rosell, F. (1998). Comeback of the beaver *Castor fiber*: An overview of old and new conservation problems. *Biological Conservation*, 83(2), pp. 165-173.
- Nummi, P. & Kuuluvainen, T. (2013). Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. *Boreal Environment Research*, 18, pp. 13-24.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, R.P., O'Hara, R.B., Simpson, L.G., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015). *vegan: community ecology; Ordination methods, diversity analysis and other functions for community and vegetation ecologists. R package*. (Version: 2.2.1) [Computer Program].
- Osenberg, C.W., Sarnelle, O. & Cooper, S.D. (1997). Effect size in ecological experiments: The application of biological models in meta-analysis. *American Naturalist*, 150(6), pp. 798-812.
- Painter, K.J., Westbrook, C.J., Hall, B.D., O'Driscoll, N.J. & Jardine, T.D. (2015). Effects of in-channel beaver impoundments on mercury bioaccumulation in Rocky Mountain stream food webs. *Ecosphere*, 6(10), p. art194.
- Parker, H., Nummi, P., Hartman, G. & Rosell, F. (2012). Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and a strategy for eradication. *Wildlife Biology*, 18(4), pp. 354-365.
- Peterson, G., Allen, R.C. & Holling, S.C. (1998). Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, 1(1), pp. 6-18.
- Petrosyan, V.G., Golubkov, V.V., Goryainova, Z.I., Zav'yalov, N.A., Al'bov, S.A., Khlyap, L.A. & Dgebuadze, Y.Y. (2013). Modeling of the Eurasian beaver (*Castor fiber* L.) population dynamics in the basin of a small Oka River tributary, the Tadenka River (Prioksko-Terrasnyi Nature Reserve). *Russian Journal of Biological Invasions*, 4(1), pp. 45-53.
- Pickett-Heaps, C.A., Jacob, D.J., Wecht, K.J., Kort, E.A., Wofsy, S.C., Diskin, G.S., Worthy, D.E.J., Kaplan, J.O., Bey, I. & Drevet, J. (2011). Magnitude and seasonality of wetland methane emissions from the Hudson Bay Lowlands (Canada). *Atmos. Chem. Phys.*, 11(8), pp. 3773-3779.
- Pinheiro, J.B., Douglas, DebRoy, Saikat, Sarkar, Deepayan; (2015). *nlme: Linear and Nonlinear Mixed Effects Models; Fit and compare Gaussian linear and nonlinear mixed-effects models. R package*. (Version: 3.1.122) [Computer Program].
- Polvi, L.E. & Wohl, E. (2012). The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. *Earth Surface Processes and Landforms*, 37(3), pp. 332-346.
- Polvi, L.E. & Wohl, E. (2013). Biotic Drivers of Stream Planform: Implications for Understanding the Past and Restoring the Future. *Bioscience*, 63(6), pp. 439-452.
- R development core team* (2014). (Version: 3.1.0) [Computer Program]. Viena, Austria: R foundation for statistical computation. Available from: <http://www.R-project.org/>.
- Ray, A.M., Rebertus, A.J. & Ray, H.L. (2001). Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 79(4), pp. 487-499.
- Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, 24(9), pp. 505-514.
- Romero, G.Q., Goncalves-Souza, T., Vieira, C. & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, 90(3), pp. 877-890.

- Rosell, F., Bozser, O., Collen, P. & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35(3-4), pp. 248-276.
- Roy, V., Amyot, M. & Carignan, R. (2009a). Beaver Ponds Increase Methylmercury Concentrations in Canadian Shield Streams along Vegetation and Pond-Age Gradients. *Environmental Science & Technology*, 43(15), pp. 5605-5611.
- Roy, V., Amyot, M. & Carignan, R. (2009b). Seasonal methylmercury dynamics in water draining three beaver impoundments of varying age. *Journal of Geophysical Research-Biogeosciences*, 114.
- Rybczynski, N. (2007). Castorid phylogenetics: implications for the evolution of swimming and tree-exploitation in beavers. *Journal of Mammalian Evolution*, 14(1), pp. 1-35.
- Samuels, J.X. & Van Valkenburgh, B. (2009). Craniodental Adaptations for Digging in Extinct Burrowing Beavers. *Journal of Vertebrate Paleontology*, 29(1), pp. 254-268.
- SAS (2012). *JMP*. (Version: 10.0) [Computer Program].
- Schmidt-Kloiber, A.H., D. (2015). www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 6.0.
- Seekell, D.A., Lapierre, J.-F., Ask, J., Bergstroem, A.-K., Deininger, A., Rodriguez, P. & Karlsson, J. (2015). The influence of dissolved organic carbon on primary production in northern lakes. *Limnology and Oceanography*, 60(4), pp. 1276-1285.
- Sellers, P., Kelly, C.A., Rudd, J.W.M. & MacHutchon, A.R. (1996). Photodegradation of methylmercury in lakes. *Nature*, 380(6576), pp. 694-697.
- SMHI, S.M.a.H.I. (2010). *FAKTABLAD 44 - Sveriges vattendrag*: SMHI.
- Soto, G.E., Vergara, P.M., Lizama, M.E., Celis, C., Rozzi, R., Duron, Q., Hahn, I.J. & Jimenez, J.E. (2012). Do beavers improve the habitat quality for Magellanic Woodpeckers? *Bosque*, 33(3), pp. 271-274.
- Stets, E.G. & Cotner, J.B. (2008). The influence of dissolved organic carbon on bacterial phosphorus uptake and bacteria phytoplankton dynamics in two Minnesota lakes. *Limnology and Oceanography*, 53(1), pp. 137-147.
- Stevens, C.E., Paszkowski, C.A. & Scrimgeour, G.J. (2006). Older is better: Beaver ponds on boreal streams as breeding habitat for the wood frog. *Journal of Wildlife Management*, 70(5), pp. 1360-1371.
- Stevenson, R.J., Hill, B.H., Herlihy, A.T., Yuan, L.L. & Norton, S.B. (2008). Algae-P relationships, thresholds, and frequency distributions guide nutrient criterion development. *Journal of the North American Benthological Society*, 27(3), pp. 783-799.
- Stringer, A.P. & Gaywood, M.J. (2016). The impacts of beavers *Castor* spp. on biodiversity and the ecological basis for their reintroduction to Scotland, UK. *Mammal Review*, pp. n/a-n/a.
- Tank, J.L. & Dodds, W.K. (2003). Nutrient limitation of epilithic and epixylic biofilms in ten North American streams. *Freshwater Biology*, 48(6), pp. 1031-1049.
- The Scottish wildlife trust . *Scottish beaver trial*. <http://www.scottishbeavers.org.uk/>.
- Thingstad, T.F., Bellerby, R.G.J., Bratbak, G., Borsheim, K.Y., Egge, J.K., Heldal, M., Larsen, A., Neill, C., Nejtgaard, J., Norland, S., Sandaa, R.A., Skjoldal, E.F., Tanaka, T., Thyraug, R. & Topper, B. (2008). Counterintuitive carbon-to-nutrient coupling in an Arctic pelagic ecosystem. *Nature*, 455(7211), pp. 387-390.

- Thompson, S., Vehkaoja, M. & Nummi, P. (2016). Beaver-created deadwood dynamics in the boreal forest. *Forest Ecology and Management*, 360, pp. 1-8.
- Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379(6567), pp. 718-720.
- Tjerngren, I., Meili, M., Björn, E. & Skyllberg, U. (2012). Eight Boreal Wetlands as Sources and Sinks for Methyl Mercury in Relation to Soil Acidity, C/N Ratio, and Small-Scale Flooding. *Environmental Science & Technology*, 46(15), pp. 8052-8060.
- Tokeshi, M. & Arakaki, S. (2012). Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia*, 685(1), pp. 27-47.
- Tornblom, J., Angelstam, P., Hartman, G., Henrikson, L. & Sjöberg, G. (2011). Toward a Research Agenda for Water Policy Implementation: Knowledge about Beaver (*Castor fiber*) as a Tool for Water Management with a Catchment Perspective. *Baltic Forestry*, 17(1), pp. 154-161.
- Truchy, A., Angeler, D.G., Sponseller, R.A., Johnson, R.K. & McKie, B.G. (2015). Chapter Two - Linking Biodiversity, Ecosystem Functioning and Services, and Ecological Resilience: Towards an Integrative Framework for Improved Management. In: Guy, W. & David, A.B. (eds) *Advances in Ecological Research* Volume 53) Academic Press, pp. 55-96.
- Tsui, M.T.K. & Finlay, J.C. (2011). Influence of Dissolved Organic Carbon on Methylmercury Bioavailability across Minnesota Stream Ecosystems. *Environmental Science & Technology*, 45(14), pp. 5981-5987.
- Ullrich, S.M., Tanton, T.W. & Abdrashitova, S.A. (2001). Mercury in the aquatic environment: A review of factors affecting methylation. *Critical Reviews in Environmental Science and Technology*, 31(3), pp. 241-293.
- UMETRIX (2012). *SIMCA-P*. (Version: 13.0) [Computer Program].
- US EPA (2002). Mercury in water by oxidation, purge and trap, and cold vapor atomic fluorescence spectrometry. *Method 1631: Measurement of Mercury in Water*. United States Environmental Protection Agency, Washington.
- Vehkaoja, M., Nummi, P., Rask, M., Tulonen, T. & Arvola, L. (2015). Spatiotemporal dynamics of boreal landscapes with ecosystem engineers: beavers influence the biogeochemistry of small lakes. *Biogeochemistry*, 124(1-3), pp. 405-415.
- Virah-Sawmy, M., Gillson, L. & Willis, K.J. (2009). How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar. *Ecological Monographs*, 79(4), pp. 557-574.
- Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467(7315), pp. 555-561.
- Wildlife trust Wales. *Welsh beaver project*. <http://www.welshbeaverproject.org>.
- Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graca, M.A.S., Fleituch, T., Lacoursiere, J.O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M., Vadineanu, A., Vought, L.B.M. & Chauvet, E. (2012). Continental-Scale Effects of Nutrient Pollution on Stream Ecosystem Functioning. *Science*, 336(6087), pp. 1438-1440.

- Wright, J.P. (2009). Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. *Ecology*, 90(12), pp. 3418-3429.
- Wright, J.P., Flecker, A.S. & Jones, C.G. (2003). Local vs. landscape controls on plant species richness in beaver meadows. *Ecology*, 84(12), pp. 3162-3173.
- Wright, J.P. & Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *Bioscience*, 56(3), pp. 203-209.
- Young, R.G., Matthaei, C.D. & Townsend, C.R. (2008). Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *Journal of the North American Benthological Society*, 27(3), pp. 605-625.

Acknowledgments

I do not understand why this page is the last if most of the readers anyway start reading from this page (and many of the readers never continue...). I need to send it to print and people I should thank keep coming up in my mind – so, I first want to thank all those who I will forget to thank bellow!!

This journey would have not been the same if I was to do it alone! Lots of people comes and goes during the time of PhD (and now also me) - so first of all I want to thank all the people (and animals) that were there for me – at home, at work, in my life and in my heart!

Special thanks to my supervisors! As a group you complemented each other and together assembled a very good supervision team. **Frauke**, for giving me the freedom (and the financial support) to find the answers I was looking for in my own way, and for teaching me the meaning of small details and accuracy... **Brendan**, for lighting my way in the darkness of the scientific writing and for making the functioning part function...**Göran**, for infecting me with the enthusiastic love for those lovely big fat rats and for opening the world of beavers for me, and **Kevin**, for connecting me to the scene and the people of methylmercury and for making everything sound complicated but so simple at the same time.

Ryan Sponseller, not supervisor but definitely great advisor when it comes to biofilms (and probably other things), thank you for your time and guidance.

It's a good opportunity to thank the **amazing lab team** that supported this entire thesis; to take samples is nice, but without making it into data it's impossible to get the answers we are looking for. So, thank you people of the geochemistry and benthic fauna lab for all the help.

And if lab mentioned – special thank you to **Elin** that was forced to volunteer into analyzing all the DOC-TOC samples. **Kristina**, that helped me in lab and in field work in crisis moments. **Fredrik** that was my remote hand in

Luleå, **Jenny** (my svägerska), **Jenni** (the Finn), **Amelie**, and others that helped me in the field or in preparation to field work.

Thank you administration team – **Annika**, **Maria**, **Catarina**, **Hasse** and **Ronald**! I never experienced such a helpful and friendly administration team.

For all the helping hands in the department – **Micke** for knowing where, what and how, **Anders** and **Tommy** (workshop) for sharing their calendar with me and building strange machines that I invented for my field and lab work. **The researchers of the department** for being so helpful and happily discuss different ideas when I needed. **Herman**, for healing my computer. **Andreas** and **Anders**, for executing extra projects. **André**, my traits trainer. **Jose**, for writing this thesis template and advising in the countdown.

All young researchers (known these days as the YR's) in the past and the present, for all the fun – it's a great group of people that can support in hard times and in good times – keep holding it together with fun activities and discussions – it makes a huge difference!

Special thanks for my roomies – **Peter** (who introduced me to this department to begin with), **Kristina** and **Amelie** (and shortly **Emma** and **Richard**), it was fun opening the office door, knowing that you were there (though I knew that from the corridor...). Next PhD we should try to talk about the research too.

Kristina – thank you for being Kristina – for being there to help at any time and anything needed, for distracting my mind when needed, for the wall art, for the door art, for the candies and the chocolates, for introducing me to Frisbee and improving my Ping-Pong skills...

Thank you **Taryn** (which goes under family also) for spending valuable time of your Swedish vacation on improving the text of this thesis.

Off course- **My father, mother and brothers**, that showed me one way but encouraged me to choose my own way.

And my own special beloved family, Marie, Samuel and Alma, for giving me the support and the challenge I need in life, without you everything would have been just too easy 😊