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Beaver in the drainage basin: an ecosystem engineer restores wetlands in the boreal landscape

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Academic dissertation

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Wetland and deadwood loss have had a profound effect on boreal aquatic and terrestrial ecosystems and their biodiversity. Deadwood-dependent species are one of the most endangered organism groups in the world, while amphibians on the other hand excellently represent the ecological state of wetlands. The boreal region contains a large proportion of the world's wetlands, which have undergone two major alterations during the last 500 years: first the extirpation of beavers and secondly draining during the 20th century.

Beavers are well-known ecosystem engineers of the Northern Hemisphere. They modify their surroundings by damming water systems. Damming raises flood waters into the surrounding riparian forest and changes environmental conditions both on land and in water. Ecosystem processes are altered when beavers turn a lotic water system into a lentic one, but the alteration is also evident when beavers modify initially lentic water systems. Organic matter and nutrients are transferred into a wetland from beaver-felled trees and vegetation killed by flooding. The amount of dissolved organic carbon increases during the first three impoundment years, which enhances the growth of aquatic vegetation and the abundance of phyto- and zooplankton, thereby also increasing invertebrate abundances. Luxuriant vegetation and ample plankton and invertebrate populations facilitate frogs, which become abundant in beaver wetlands. The moor frog in particular favours beaver-created wetlands.

Flooding and beavers kill trees, producing high amounts of deadwood. The riparian forests of beaver wetlands include much higher deadwood levels than wetlands without beavers. Increased deadwood creates substrate resources for deadwood-dependent species. Snags are a typical deadwood type in beaver wetlands. Calicioids are deadwood-dependent species particularly specialised in inhabiting standing deadwood.

The comeback of beavers has aided the restoration of wetlands and deadwood. Beaver wetlands can be seen as carbon and biodiversity hot spots that increase the heterogeneity and hydraulic connectivity of the boreal landscape.

Keywords: anurans, biodiversity, calicioids, deadwood, dissolved organic carbon, riparian forest

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LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to in the text by their Roman numerals. Articles I–III are reprinted with kind permission of the publishers, while article VI is the author's version of the submitted manuscript.

I 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: 405–415.
http://dx.doi.org/10.1007/s10533-015-0105-4

II Thompson S., Vehkaoja M., Nummi P. (2016). Beaver-created deadwood dynamics in the boreal forest. Forest Ecology and Management 360: 1–8. http://dx.doi.org/10.1016/j.foreco.2015.10.019

III Vehkaoja M., Nummi P. (2015). Beaver facilitation in the conservation of boreal anuran communities. Herpetozoa 28 (1/2): 75–87.

IV Vehkaoja M., Nummi P., Rikkinen J. (2016). An ecosystem engineer creates vacant habitats in boreal forests: beavers and calicioid diversity. Manuscript.

Author's contribution

The contributions of the Author (Mia Vehkaoja) to the papers included in this thesis were as follows:

Mia Vehkaoja (MV) is fully responsible for the summary of this doctoral thesis and she is the main author of two papers and one submitted manuscript. MV, Petri Nummi (PN) and Lauri Arvola (LA) were responsible for the original idea and study plan of paper I. MV analysed the data and was responsible for the writing. All co-authors commented on the manuscript. In study II, PN was responsible for the original idea and planning of the study along with MV and Stella Thompson (ST). The data were collected by MV and ST, and analysed by MV. Although ST was responsible for writing the manuscript, MV also participated in the writing process. PN commented on the manuscript. In study III, MV was responsible for the original idea and planning the study, in addition to collecting and analysing the data and preparing the manuscript. PN commented on the manuscript. In manuscript IV, MV planned the study with PN and Jouko Rikkinen (JK). The data were collected and analysed by MV. MV performed species identification in collaboration with JR. Although MV was responsible for writing the manuscript, all co-authors participated in the writing process.

TABLE OF CONTENTS

INTRODUCTION 9
Wetlands — the Earth's kidneys 9
Beaver's wetland engineering 10
Boreal carbon cycle 11
Deadwood – a fading resource in boreal forests 12
Patterns of biodiversity loss in boreal wetlands and forests 13

THESIS AIMS 14

MATERIAL AND METHODS 15

RESULTS AND DISCUSSION 16
Beaver engineering alters the carbon cycle 16
Beavers modify the habitat structure of riparian forests 17
Beavers benefit aquatic and terrestrial biodiversity 19
Beaver-inhabited lakes increase anuran diversity 19
Caliciales hot spots in the boreal landscape 20
The location of beaver-created hot spots and hot moments shifts in the landscape 20

CONCLUSIONS AND MANAGEMENT IMPLICATIONS 22

REFERENCES 23

INTRODUCTION

Biological diversity decreases with declining genetic diversity, species extirpation and habitat loss. As a result of anthropogenic pressure, the number of endangered species is increasing worldwide. However, biodiversity provides ecosystems with the means to be functional and also to produce ecosystem services. Because of ecosystem and species loss, developing new methods for securing biodiversity and ecosystem services on Earth is necessary. According to the European Union's (EU) water framework directive, member states must maintain and improve the ecological conditions of inland waters and ensure the conservation of their inland waters, including wetlands.

Wetlands — the Earth's kidneys

Wetlands are one of the world's most important ecosystems. Unfortunately, the world has lost approximately half of its wetlands, and Europe alone has destroyed and changed two-thirds of its wetlands. As the "Earth's kidneys", wetlands mitigate both floods and drought, purify waters and recharge groundwater stores. Furthermore, they offer habitat for thousands of species.

Finland is located in the boreal region, which is the world's largest forest ecosystem, extending throughout the Northern Hemisphere. A large proportion of the world's wetlands are located in the boreal (Table 1), which also stores large amounts of carbon. Generally speaking, boreal ecosystems are under considerable stress. The climate is severe and often unpredictable, which produces additional challenges for wetland conservation. Furthermore, nearly 14 million hectares of wetlands have been drained for forestry in northern Europe (Paavilainen and Päivänen 1995; Suislepp et al. 2011). Finland alone has drained more than 5.5 million hectares of wetlands and forests (Peltomaa 2007), most of them during the last 50 years. Ditches drain excess surface water, which influences the quality and processes of aquatic ecosystems, resulting in reduced wetland diversity (Suislepp et al. 2011).

Another reason behind the deterioration of boreal wetlands is the near extinction of beavers in in both Eurasia and North America during the 19th century. Before the extirpation, probably ca. 100 million beavers roamed the boreal region (in North America and Eurasia) (Naiman et al. 1988; Nolet and Rosell 1998). The boreal therefore abounded with beaver-created wetlands in addition to other types of wetlands. The last European beaver (Castor fiber; Linnaeus 1758) of Finland was shot in 1868, but the main population was hunted down as early as the late 1500s (Lahti and Helminen 1974). Only eight small isolated populations remained in Europe, with approximately 1200 animals in total (Halley and Rosell 2002).

During the last 500 years, boreal wetlands have thus undergone two major changes: firstly, the loss of beavers and secondly, draining. Both processes have had an extensive effect on boreal wetlands. After destroying wetlands, we are gradually beginning to recognise their value and working to restore them. Additionally, beaver populations have begun recovering from their near extinction. They have spread by both aided reintroductions and naturally, and currently inhabit most of their original range in both North America and Eurasia. European beavers were reintroduced to Finland in 1935, and North American beavers (Castor canadensis; Kuhl 1820) were introduced to Finland nearly concurrently (1937). At the time, science did not recognise the two as separate species (Parker et al. 2012). Nowadays both species inhabit different parts of Finland, and are spreading to new areas naturally.

Table 1. Current stage of the world's wetlands. Modified from Junk et al. (2013). Africa's figures are conservative estimates excluding Algeria, Egypt, Libya, Mauritania, Morocco, Tunisia and Western Sahara, and excluding wetlands along low-order rivers and coastal wetlands. Europe's figures include the European side of Russia, so the Russian figures are partly presented twice.

Region	Land area	Wetlands (tot.) (km2)	Wetland (%)
N. & C. America	24 900 000	2 490 000	10
Europe	10 000 000	500 000	5
Russia	17 075 400	>1 800 000	>10
China	9 600 000	684 900	7
South America	17 850 000	>3 000 000	>20
Africa	30 065 000	2 129 000	7
Sub-Saharan A.	23 004 000	2 073 000	9
Tropical Asia	14 536 000	687 000	2.8
Australia	7 692 000	230 000	3

Beaver's wetland engineering

The use of ecosystem engineers in conservation biology has recently received attention (Byers et al. 2006; Bartel et al. 2010). Ecosystem engineers are organisms that physically modify the environment through their activities. These activities feature digging, burrowing or damming, and they affect the environment on both the spatial and temporal scales. Ecosystem engineering is a widespread phenomenon including organisms from invertebrates and angiosperms to vertebrates, such as mammals (Wright and Jones 2006). In a way, ecosystem engineering can be used to widen our ecological thinking.

Ecological engineers can also substantially influence the input and export of materials (Gutiérrez and Jones 2006), modify chemical and microbial processes, alter direct biotic interactions (Jones et al. 1994; Gurney and Lawton 1996; France 1997), and enrich the biodiversity of systems (Bruno et al. 2003). Although all organisms affect their physical environments, the influences of ecosystem engineers are much more profound and protracted, as they operate on large spatial and/or temporal scales (Hastings et al. 2007).

Beavers act as ecosystem engineers in the Northern Hemisphere (Jones et al. 1994; Wright et al. 2002). They create and maintain special habitats by creating dams (Baker and Hill 2003). Damming changes both the abiotic and biotic conditions of a wetland. Tree felling and raising water into riparian forests transfer nutrients and energy from terrestrial environments to water ecosystems such as boreal lakes (Collen and Gibson 2001; Nummi and Kuuluvainen 2013). The beavers' modifications (damming, digging, felling trees) alter ecosystem structure and function. The degree of these large-scale effects depends on the patch dynamics that they create (Jones et al. 1994; Wright et al. 2004). Beavers alter the morphology and hydrology of drainage networks, thus creating a shifting patch mosaic of recurring successional phases. These occur with their own individual temporal wet-dry continuums (Naiman et al. 1994; Hyvönen and Nummi 2008). As a result, beavers can strongly impact landscape features in the long term, particularly because their dams may endure much longer than the animals actually inhabit a site. At the landscape level, the degree of beaver-induced effects depends on the size of the beaver population and the patch dynamics created by the animals (Jones et al. 1994; Wright et al. 2004), in addition to the landscape characteristics and aquatic topography.

Boreal carbon cycle

The boreal region contains huge pools of terrestrial and aquatic carbon, which play an important role in the global carbon cycle (Couture et al. 2012; Olefeldt et al. 2013; Moen et al. 2014). A large fraction of boreal landscapes is covered in lakes, which are probably more significant to the carbon cycle in boreal areas than in any other region. Atmospheric carbon sinks into boreal forests and peatlands (Apps et al. 1993; Weber and Flannigan 1997; Lavoie et al. 2005). Boreal lakes, on the other hand, receive their carbon inputs from terrestrial ecosystems (Benoy et al. 2007; Prairie 2008; Olefeldt et al. 2013), and most of their carbon is in the form of dissolved organic carbon (DOC), which is then mineralised, transformed and sedimented (Tranvik et al. 2009; Kortelainen et al. 2013). As a result, carbon accumulates in lake sediments (Sobek et al. 2005; von Wachenfeldt et al. 2008; Einola et al. 2011).

Beaver-flooded habitats alter the biogeochemical conditions of an ecosystem. Flooding enhances biogeochemical fluxes by transporting elements across space (McClain et al. 2003). To date, not a single beaver-related carbon study has been performed in Europe, and the studies conducted in North America have concentrated on aquatic ecosystems that change from lotic to lentic ones. These studies have shown beaver wetlands to act both as carbon sources and sinks (Fig. 1) (Naiman et al. 1986; Mitsch et al. 2013; Johnston 2014).

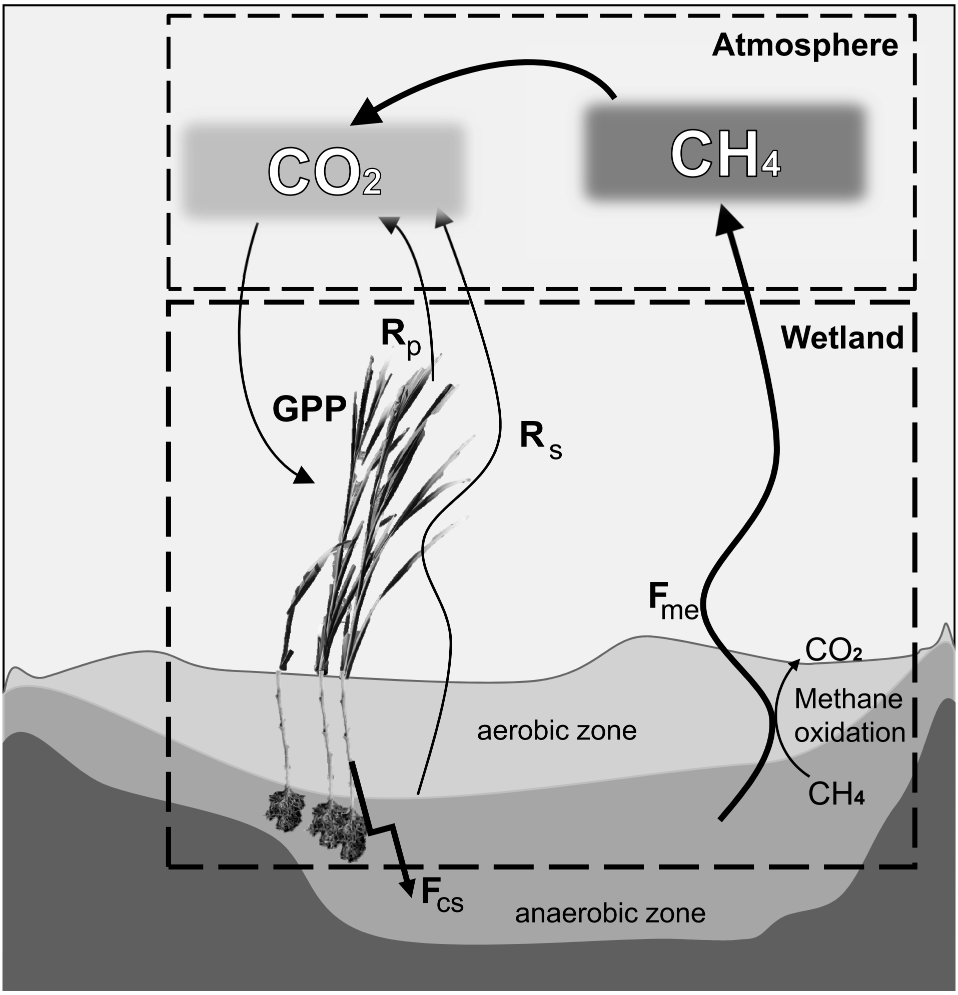

Figure 1. A typical wetland carbon cycle. Modified from Mitsch et al. (2013). Wetlands are usually seen more as carbon sinks than emitters. However, beaver-inhabited lakes and ponds act both as emitters and sinks. Abbreviations: CH_4 = methane, CO_2 = carbon dioxide, GPP = gross primary productivity, R_p = plant respiration, R_s = soil respiration, F_{cs} = carbon sequestration, F_{me} = methane emissions.

Deadwood – a fading resource in boreal forests

Humans have influenced boreal forests for centuries, but forestry practices have dramatically intensified forest utilisation during recent decades (Gamfeldt et al. 2013). Boreal forests have been conifer-dominated from approximately the end of the Pleistocene onwards, but forestry has reinforced this coniferous dominance. In addition, deadwood and deadwood-dependent species have become very rare (Linder and Östlund 1998; Stokland et al. 2012). Nowadays, Finnish and Swedish foresters at least are obligated to leave deadwood and retention patches in forests, although some loopholes still exist in these practices. Stumps are usually the most common deadwood type left in forests after forestry practices are performed (Green and Peterken 1997). Stumps probably have the smallest volume of all deadwood types. Additionally, they can only uphold quite restricted communities of deadwood-dependent species. Furthermore, the retention patches left as refugia during forestry practices are too small to support saproxylic community viability (Perhans et al. 2009).

Wildfires, wind, snow and pathogens are the main disturbances of boreal forests (Kuuluvainen 1994). However, stand-replacing disturbances nowadays occur very seldomly (Liu and Hytteborn 1991; Kuuluvainen 1994). Flooding is one of the main disturbances faced by riparian forests (Nummi and Kuuluvainen 2013). The moisture of riparian areas protects the trees from fires, and also from storms to some degree. Spring and autumn floods are common in Finland and in the boreal in general. Normally spring and autumn floods in Finland's inland water systems reach, on average, a few metres from the shoreline into a riparian forest (SYKE 2016). Water inundation because of flooding by beavers, on the other hand, can reach several dozen metres into a riparian forest (Nummi and Hahtola 2008), and have twofold impacts on it. The flood causes substantial tree mortality, and beavers felling trees to build dams, lodges and food caches add to this mortality. (Jones et al. 1994; Nummi and Kuuluvainen 2013). Deadwood amount is a limiting factor for several ecological processes and species (Stokland et al. 2012), thus it is a biodiversity indicator of boreal forests (Hahn and Christensen 2005; Stokland et al. 2012).

Patterns of biodiversity loss in boreal wetlands and forests

Anthropogenic actions are the primary threats to biodiversity (Jenkins and Joppa 2009; Bradshaw and Brook 2014), both on land and water. Wetlands, including those in the boreal region (Rooney et al. 2012), have declined during the last century due to anthropogenic factors. Although merely understanding the ecological processes of the ecosystem is important, we need to identify the factors upholding these processes and the biodiversity linked to them (Montoya et al. 2012).

Amphibians have experienced their share of anthropogenic impacts, and represent one important aspect of global biodiversity loss. Along with declining wetlands, approximately 30% of amphibian species globally are threatened with extinction (Crump 2010). The chytrid fungus (Batrachochytrium dendrobatidis) and anthropogenic habitat destruction are the key causes of this loss (Petranka et al. 2004; Gibbons et al. 2006; Whiles et al. 2006; Sayim et al. 2009). Amphibians are good indicators of habitat sustainability, especially for wetland habitats. Their life cycle commonly includes both aquatic and terrestrial phases. Anurans lay aquatic eggs, and the aquatic tadpoles metamorphose into terrestrial adults. Amphibians are additionally important to the energy flows and nutrient cycling of ecosystems; they function as both predators and prey (Crump 2010). Furthermore, the physical and chemical changes in the environment rapidly impact amphibians. The permeable skin and tadpoles' gills render anurans vulnerable to several alterations in environmental conditions (e.g. oxygen concentration and environmental toxins). As amphibians play diverse roles in natural ecosystems, they can be seen as bioindicators of wetland conditions (Matthews et al. 2002; Whiles et al. 2006). The moor frog (Rana arvalis; Nilsson 1842), as an EU inland water directive species, indicates the healthy state of wetlands.

On the other hand, deadwood-dependent species are declining and/or on the verge of extinction in boreal forests, even in regions where forest areas are increasing. They are one of the most globally threatened organism groups (Stokland et al. 2012). The disappearance of deadwood is associated with the decrease of deadwood-dependent species. In boreal Fennoscandia the average volume of coarse woody debris has decreased by 90–98%. We have concurrently lost, by default, more than 50% of the original saproxylic species (Siitonen 2001).

Forest management and the low prevalence rate and strong control of natural forest disturbances have made the living conditions and dispersion of saproxylic species challenging (Kruys et al. 1999; Junninen et al. 2006; Brunet and Isacsson 2009). In addition to habitat fragmentation, the characteristics of the individual habitat fragments significantly explain the decline of species (Hanski and Ovaskainen 2002). Forest management mainly produces stumps and coniferous deadwood, which as a whole influence the available deadwood substrate for saproxylic species towards a very narrow selection. Many saproxylic species indicate stand naturalness and the long-term continuity of deadwood, and are therefore used in conservation planning (Niemelä 2005; Jansson et al. 2009). Pin lichens (Caliciales), a form of saproxylic organisms, are considered sensitive biomonitors of forest ecosystem health (Selva 2003), and can be used to indicate snag abundance as they most commonly inhabit snags (Tibell 1992; Holien 1998; Lõhmus and Lõhmus 2011).

Beaver engineering influences riparian forests (Hyvönen and Nummi 2008; Nummi and Kuuluvainen 2013), and their activity increases both habitat and species diversity (Rosell et al. 2005). Beavers have been suggested to increase species richness at the landscape scale (Wright et al. 2002). They could, therefore, be used to ensure the conservation of several species.

THESIS AIMS

The main aim of this thesis was to identify the influence beavers have from a landscape perspective. Moreover, I studied the impacts of beavers' actions on:

1) water chemistry, especially carbon,
2) habitat structure in the form of produced deadwood, and
3) biodiversity.

Regarding biodiversity I studied the diversity of anurans and Caliciales as deadwood-dependent organisms.

Throughout my thesis I have evaluated the effects of beavers in initially lentic water systems. Most previous studies have focused on beavers changing lotic systems into lentic ones, but see e.g. Hood and Bailey 2009, Hood and Larson 2015 and Anderson et al. 2015. My thesis surveys the fundamental alterations beavers induce on boreal lentic wetlands. Based on this knowledge we can develop suggestions on how beavers could be used in wetland restoration and conservation.

MATERIAL AND METHODS

The work has been conducted in two forest landscapes in southern Finland: the Evo area (61°10'N, 25°05'E) and Nuuksio National Park (60°19'N, 24°28'E). Both areas belong to the southern boreal vegetation zone (Ahti et al. 1968). They consist of tens of small headwater lakes. A subset of these lakes was used in the different studies (I: 37 lakes each located in Evo; III: 20 lakes each located in Evo; II and IV: 18 lakes in total, 12 located in Evo and six located in Nuuksio). In addition, one study (**III**) also included six temporary ponds in Evo.

The altitude of the Evo area varies from 125 m to 185 m a.s.l, and Nuuksio from 27 m to 114 m a.s.l. The soils of both areas are low in nutrients, with glacial and sandy tills being the dominant soil types respectively. Both areas are predominantly coniferous with deciduous patches scattered in the landscape.

The Evo area was one of the places where the first European beaver reintroductions were performed in 1935. The North American beaver was introduced to Evo in the 1950s (Parker et al. 2012), and currently the area's beaver population consist solely of North American beavers. The beaver-inhabitated lakes at Evo are most commonly formed by the damming of an existing lake by beavers (Nummi and Hahtola 2008). Beavers usually occupy one site for an average of three years, and recolonise an abandoned patch after an average 10-year absence (Hyvönen and Nummi 2008). Neither species has colonised Nuuksio since their (re)introductions to Finland, which is why we considered the area a reference area to Evo.

Evo's lakes have been monitored for beavers every year since 1970 by surveying the lake/wetland perimeters. The beaver population distribution is, therefore, well documented. This information was used in all articles (**I–IV**).

Water chemistry data (**I**) were collected during years 1978–2013. The samples were taken twice a year, during early spring and late autumn. Total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), dissolved oxygen (DO) and pH were determined from the samples. In this study we were able to measure beavers' effects on water chemistry variables. We compared the situations in beaver-inhabited lakes and lakes downstream of them before, during and after beaver occupation.

Deadwood data (**II**) were collected during summer 2014. We calculated the type and amount of deadwood from two equal-sized sampling plots at each study site. The total area of each sampling plot was 0.04 ha. One sampling plot from each site was situated on the widest flood meadow section of the riparian zone and the other directly across from it on the opposite side of the lake. We recorded the species, diameter, length, decay stage and type (downed, standing, stump) of each deadwood sample. The total deadwood volume was calculated according to the formulas by Laasasenaho (1982).

The anuran abundance and diversity study (**III**) was performed in May 2010. Data were collected using anuran calling surveys. Each anuran species has a unique call so identification of the species was straightforward. To evaluate abundance I used the anuran calling index (ACI). See more details in article II. In addition to the anuran calling surveys, I measured six environmental variables: the extent of shallow water (< 0.6 m), water temperature, pH, dissolved oxygen concentration (DO), riparian canopy cover and emergent vegetation coverage.

Caliciales samples (**IV**) were gathered concurrently with the deadwood data (**II**). I randomly picked 10 dead trees from each sampling plot (i.e. 20 samples from each site) and took a sample of each distinguishably different Caliciales species. The species of each sample were identified by examining the anatomical details using dissecting and compound microscopes, and by testing for species-specific colour reactions in KOH solution from squash mounts of ascomata in water (Tibell 1999; Tuovila 2013).

RESULTS AND DISCUSSION

Although critics have argued that all organisms modify their surroundings to some degree, it is essential to determine those organisms that alter important ecosystem processes and biodiversity. In addition, Crain and Bertness (2006) perceived important ecosystem engineers as providers of limited resources, which will obviously lead to a greater impact on ecological communities benefitting from the resource enhancement.

Beaver engineering alters the carbon cycle

Beavers alter both terrestrial and aquatic environments, especially when a lotic system is transformed into a lentic one. But the impacts are also prominent when beavers modify an existing lake. We identified DOC peaks in beaver-inhabited lakes (**I**). All our study lakes had fairly similar DOC concentrations prior to the beavers' arrival. A DOC peak was seen during the first three beaver impoundment years, after which DOC returned back to its initial levels (Fig. 2). We observed a simultaneous but opposite effect with DO. During the first three impoundment years DO concentrations decreased significantly, but once the impoundment had lasted four to six years, DO returned back to its original concentrations. Similar changes did not occur in downstream non-beaver-inhabited lakes.

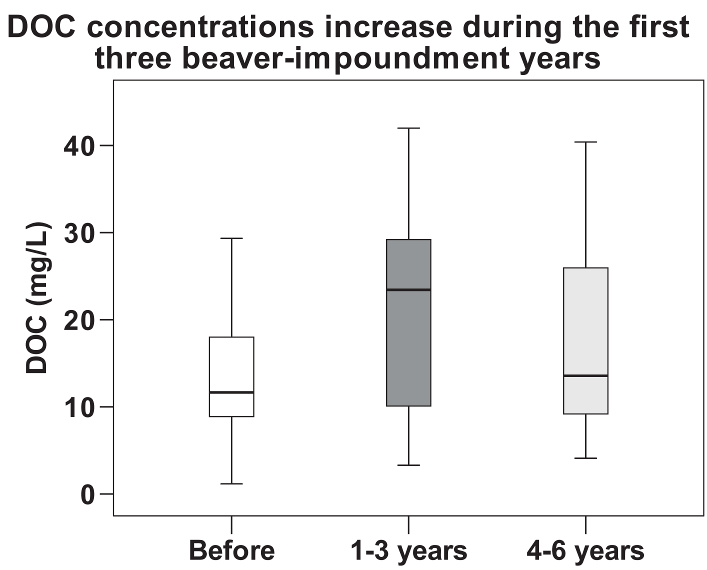

Figure 2. DOC concentrations increase during the first three beaver-impoundment years.

Our study demonstrated the effect of damming by beavers and water level increase on the biogeochemical cycling of DOC. This phenomenon has previously been studied in stream systems, where entire ecosystems may shift from one to another (lotic to lentic). Similar alteration is seen in our study in an initially lentic ecosystem. Although the duration and extent of a beaver-created nutrient pulse is both relatively short (1–3 years) and local, beavers can play an important role in the carbon cycle from the perspective of a landscape and the entire boreal region.

The DOC increase in beaver-inhabitated lakes is due to a rising water level, which releases organic carbon and nutrients from the soil and dying vegetation (Naiman et al. 1988; 1994). Flooding enhances the biogeochemical fluxes by transporting elements across space, and providing conditions that enhance biogeochemical cycling rates (McClain et al. 2003). Beaver ponds have open water and are often a mosaic of varying vegetative structures. Beaver-inhabited lakes and ponds have a twofold effect on the carbon cycle. They, equally with other wetlands, emit carbon gases into the atmosphere (Roulet et al. 1997; Mitsch et al. 2013), but can also store carbon into the bottom sediments (Wohl 2013; Johnston 2014). Beaver-pond deposits can be retained in pond sediments for thousands of years (Persico and Meyer 2013).

The boreal region with its numerous wetlands (lakes and extensive peatlands) contain large stores of carbon and thus plays an important role in the global carbon cycle (Couture et al. 2012, Olefeldt et al. 2013; Moen et al. 2014). Most of the carbon in boreal lakes originates from terrestrial ecosystems (Sarvala et al. 1981; Arvola et al. 1990; Olefeldt et al. 2013) in the form of DOC. Our observation of a relatively short DOC peak indicates that the carbon from terrestrial ecosystems is transferred either to the atmosphere and/or into sediment storages. Additionally, the amount of organic carbon may be limited due to several factors, including changes in redox conditions and the decomposition rate of organic matter. The nature of these processes undoubtedly calls for further studies.

Beavers modify the habitat structure of riparian forests

Beavers kill trees by flooding and felling. Our study is the first to measure the amount of deadwood created by beavers. Our results show that beavers produce large amounts of deadwood, particularly some rare types (**II**). We compared the deadwood amounts of riparian forests surrounding beaver sites and non-beaver sites. Beaver sites had significantly higher amounts of deadwood compared to the other two riparian forest types.

The beaver's importance as a creator of deadwood was further emphasised with their ability to produce rare types of deadwood (Fig. 3). Snags, fine woody debris (< 10 cm) and deciduous deadwood are the rarest types of deadwood in currently heavily-managed boreal forests (Sippola et al. 1998; Ekbom et al. 2006; Rudolphi et al. 2011); these are the elements particularly created by beavers. Moreover, these rare types of deadwood are important for several deadwood-dependent and -associated species (Stokland et al. 2012). Another key feature to consider is that the deadwood created by beavers is generally moist, and beaver-produced snags mostly stand in water. Their decomposition processes begin in fairly moist conditions, whereas the deadwood caused by other disturbances begin their decomposition as dry wood. This difference may be essential for deadwood-dependent species that live on moist deadwood and/or late decay stages (stages 4 and 5). In addition to the rare types of deadwood, beaver foraging and building activities produce large amounts of snags that were not so evident in our results due to the transect lines, which were located mostly in water.

Beavers, where they exist, are probably the main creators of stand-replacing disturbances in boreal riparian forests (Nummi and Kuuluvainen 2013). Floods kill trees over a long time period due to asphyxiation. Boreal tree species have different tolerances to asphyxiation and drowning, so some die almost immediately, while others may survive for several years (Nummi 1989). The cyclical nature of beaver occurrence, inhabiting, departing and returning to the original site, makes beavers continuous creators of deadwood. However, the effect of beaver lasts longer than the animal actually occupies a site. Dam collapse may take several years, and in addition beavers often return to the previous site, where wetland succession and deadwood creation will begin again.

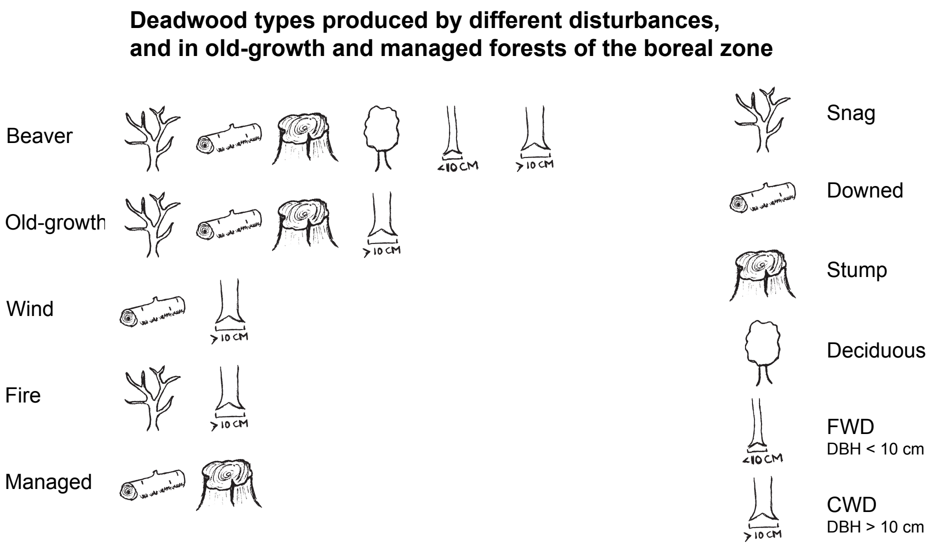

Figure 3. Deadwood types produced by different forest disturbances. FWD = fine woody debris, CWD = coarse woody debris, DBH = diameter at breast height.

Beavers benefit aquatic and terrestrial biodiversity

Beavers, as ecosystem engineers, are known to facilitate several species groups, such as water lice, ducks and bats (Nummi 1992; Nummi et al. 2011; Nummi and Holopainen 2014). Previous studies have shown the impact of beavers on groups of species that are dependent on or associated with aquatic ecosystems during certain periods in their lives. Generally speaking, prior to this thesis very little research has been conducted concerning beaver and deadwood organisms (bark beetles as pests, see Saarenmaa 1978), and no one has emphasised the biodiversity of organisms on beaver-created deadwood. Additionally, as frogs are associated with both aquatic and terrestrial systems and Finnish forests are heavily drained, I wished to study the effect of beavers on frogs in a fully drained landscape.

Beaver-inhabited lakes increase anuran diversity

Beaver wetlands have been shown to benefit frogs in Central Europe and North America (Dalbeck et al. 2007; Stevens et al. 2007). According to our study the situation appears similar in the boreal region. Beaver-inhabited lakes have higher anuran diversity than lakes and temporary ponds without beavers (**III**). Beavers particularly facilitate moor frogs, which favour more luxuriant habitats than common frogs (Rana temporaria; Linnaeus 1758) and common toads (Bufo bufo; Linnaeus 1758).

Flooding by beavers creates shallow water areas, and organic materials and nutrients washed out from shores support the growth of algae, benthic vegetation and animals. In addition, felled trees increase open canopies, thereby offering enhanced conditions for photosynthesis. The increased light penetration along with the dark-colouration of the water elevate the water temperature of beaver wetlands. These environmental changes benefit anurans, because warm water accelerates the hatching, development and metamorphosis of tadpoles. Luxuriant aquatic vegetation provides cover for tadpoles and adult anurans against predators. Nutrients and organic material, on the other hand, promote phyto- and zooplankton abundances, as well as invertebrates, which are food for tadpoles and adult frogs.

DOC may aid the survival of anuran tadpoles (Banks et al. 2007). DOC is considered important to amphibians because it reduces light penetration into water, which in turn reduces the penetration of UV-B radiation and its harmful effects on eggs and tadpoles (Carpenter et al. 2001; Diamond et al. 2005). In other words, DOC peaks during the first three years of beaver impoundment (**I**) could benefit anuran reproduction.

The depth features of beaver-created wetlands are typically versatile, with shallow and deeper water areas creating a mosaic structure, in addition, channels dug by beavers enhance the wetland area and act as dispersal corridors for amphibians (Anderson et al. 2015; Hood and Larson 2015). This increased habitat diversity makes them a suitable habitat for several anuran species. Common frogs prefer shallow habitats, whereas common toads prefer deeper ones. The moor frog is somewhere in between the two. Beaver wetlands can thus provide favourable habitats for the entire anuran community of Finland.

Beavers' actions clearly mitigate the negative impacts of draining. Beavers can create a wetland ecosystem in landscapes also containing drained areas, and the presence of moor frogs can be used to demonstrate the ecological significance of these wetlands. The moor frog is one of the EU directive species for inland waters, and an indicator of high quality ecosystems.

Caliciales hot spots in the boreal landscape

Deadwood-associated pin lichens flourish in beaver-created snags (**IV**). From all the recorded species in the study, 87% inhabited beaver sites. Furthermore, half of the recorded species occupied one single, particularly species-rich beaver site. The suitability of beaver sites for pin lichens is fairly discernible. The beaver sites proportionately increased Evo's regional pin lichen species pool by 62%.

Most pin lichens found from beaver sites occurred on snags standing in water (**IV**). Surrounding water bodies influence the microclimate conditions of pin lichens. Tibell (1992) and Selva (2003) have previously shown that most pin lichens favour considerable humidity and canopy cover. The moist deadwood substrate could be a key factor explaining why organisms that normally favour old-forest habitats have become so abundant in a completely different environment. Water is not a limiting factor on moist deadwood, and the lack of canopy cover offers favourable light conditions. Pin lichens usually have to balance between light availability and desiccation risk, while both resources are ample in beaver wetlands.

Beavers' habitat expansion and dispersal across the landscape could benefit pin lichen dispersal. Beavers create a continuum of deadwood habitats, which allow pin lichens to disperse. Other deadwood-dependent species, such as beetles and woodpeckers, might aid the dispersion of pin lichens, because spores and propagules could attach to their feathers, surface structures and hairs.

The location of beaver-created hot spots and hot moments shifts in the landscape

Beavers cause large and structurally mediated modifications in the landscape that last longer than the animals actually inhabit the sites. Their effects, therefore, occur at different spatial and temporal scales. Because beavers are spatially mobile engineers, they can return to previously inhabited sites and re-engineer them in our study area in approximately ten-year cycles. Several simultaneous and overlapping beaver wetlands of different age classes might, therefore, concurrently exist in the landscape, thereby producing temporal and spatial heterogeneity (Fig. 4).

The hot-spot phenomenon begins with a nutrient pulse in the early flood years (**I**), which leads to abundant plankton and invertebrate production (McDowell and Naiman 1986; Nummi 1989). Trees and other vegetation in the riparian zone (from 40 m to 100 m from the original shoreline of the wetland) concurrently begin to die. Conifers are the first to die. Some deciduous trees are more tolerant of flooding than others, but Salix species are usually the only deciduous trees to have survived after three impoundment years (Hyvönen and Nummi 2008). Disappearance of the canopy provides an opportunity for wetland and aquatic vegetation. Gradual tree mortality produces high amounts of deadwood (**II**), some of which is not evident until the water level has lowered to almost its initial levels. Anurans live in both younger and older beaver wetlands (**III**). The benefits of beavers to anuran communities can be argued to begin early on and frogs additionally disperse without difficulty to newly established beaver sites. In contrast, pin lichen dispersal to beaver wetlands will probably take at least a few years. They will nevertheless have to wait for the deadwood substrate to be produced (**IV**). As a result, beavers significantly contribute to the biodiversity of the boreal region, and have the capacity to produce a mosaic landscape.

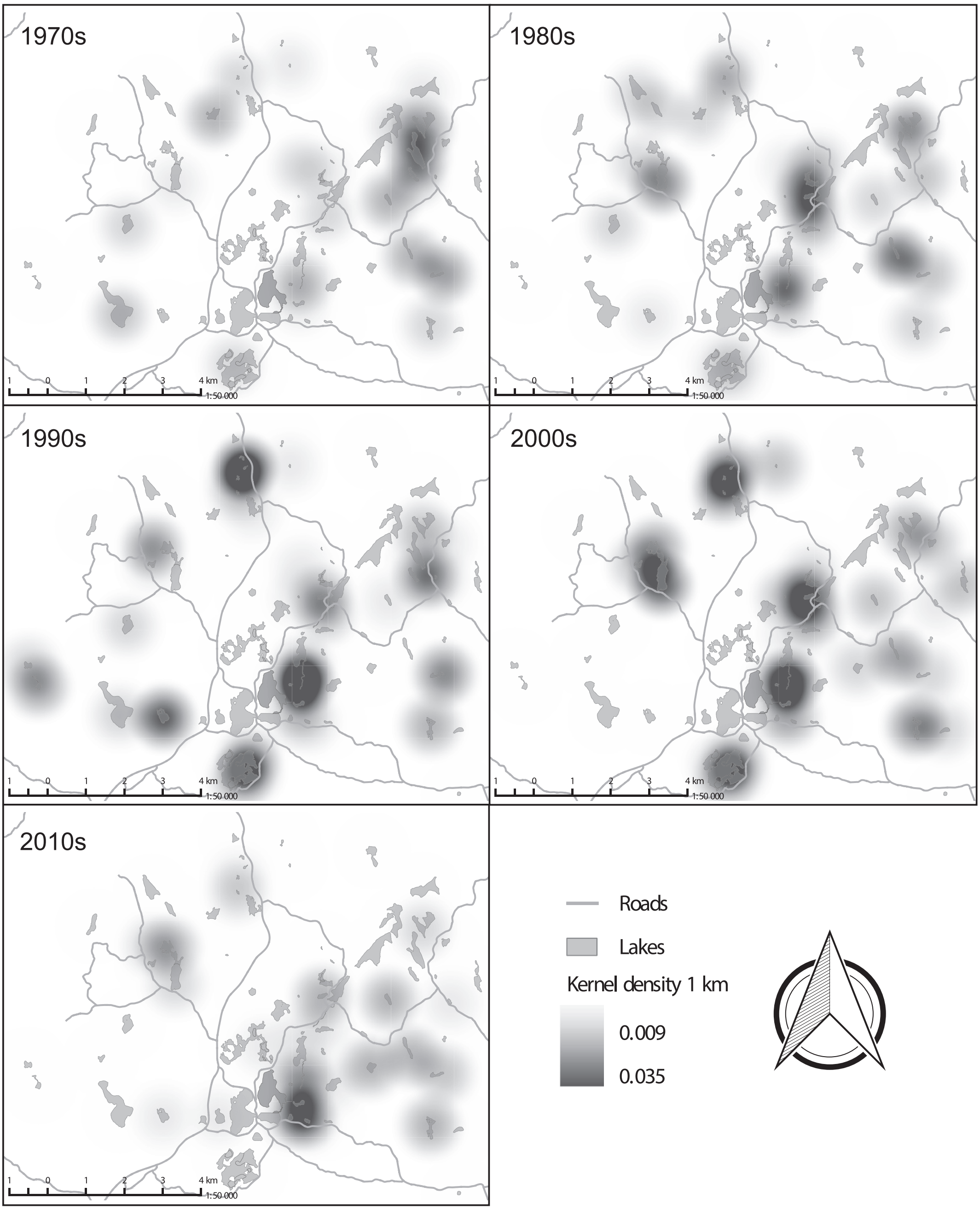

Figure 4. The population density of Evo's beavers in the 1970s, 80s, 90s, 2000s and 2010s. Population density is presented according to Kernel density. The beavers' mobility and wetland hot spot creation can be seen from the maps. Dark grey areas are beaver-induced biodiversity hot spots. (The Kernel density for the 2010s is not directly comparable to the other decades, because it only includes five years instead of 10.)

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This thesis provides new information of the beaver's effects on wetland carbon cycling, riparian forest structure and biodiversity. It is evident that the impacts of beavers extend from aquatic to terrestrial ecosystems. Wetland science is considered a unique discipline including terrestrial and aquatic ecology, chemistry, hydrology and engineering (Mitsch and Gosselink 2015). Wetlands can even be seen as a continuum between aquatic and terrestrial ecosystems, and are considered to increase hydrological connectivity in the landscape. Beavers seemingly alter wetland structure and conditions, which should be important when planning wetland restoration and conservation. Restoration projects should be aimed at identifying the providers of ecosystem services and biodiversity (Montoya et al. 2012).

Although beavers have both positive and negative effects on environments, they can be seen as important ecosystem engineers. They provide limited resources for several organisms (e.g. ducks, frogs, pin lichens, bats) both through habitat amelioration and resource enhancement.

Beaver wetlands were nearly absent throughout the Northern Hemisphere for several hundred years due to overhunting. Before their near extinction, 60–400 million beavers are estimated to have roamed North America (Seton 1929). An original population size estimate is missing for Europe, but would presumably be over ten million individuals. (This estimation is based on the following facts: a) there are 2.5 million and 500 000 wetlands in North America and Europe, respectively, so Europe's wetland number is 20% of the wetlands in N. America, and; b) approximately 30 million beavers currently live in North America (~8–50% of the original population size of 60–400 million estimated by Seton in 1929), while over one million currently inhabit Europe. From this we can infer two possible estimates for original beaver population sizes in Europe: a) 60 x 0.2 = 12 and 400 x 0.2 = 80, which would give an estimate of 12–80 million, and; b) an estimate of 2–17 million, assuming Europe currently has a similar percentage of beavers left as North America compared to original numbers (8–50%). An approximate value of 10 million beavers can then be estimated from these two valuations.)

After a long period of absence, beavers have returned to many parts of their former range. Currently there are over one million beavers in Eurasia and ca. 30 million in North America (Halley et al. 2012; Whitfield et al. 2015). Although beaver populations are still far from initial levels, they are heading towards the situation preceding overhunting. The comeback of beavers has definitely benefitted wetland conservation. Along with the beavers' increase, ca. 25 000 km^2 of new aquatic wetland habitat and 550 000 km of riparian interface have been created (Whitfield et al. 2015). As beaver populations are increasing in both North America and Europe (Halley et al. 2012; Whitfield et al. 2015), it is feasible to take into account the possibility of populations becoming too dense in some regions. This has been the case with other large herbivores lacking a top predator (Ritchie et al. 2012). Beaver floods can damage for example forestry and infrastructure, and in addition, the landscape can become one-sided with over-dense beaver population. A management plan for beavers should contain the species' value as an ecosystem engineer, but still aim to prevent potential conflicts caused by over-dense populations.

Understanding the main drivers maintaining ecosystem processes and biodiversity is essential for wetland restoration and conservation. We can learn a lot from beavers. One alternative would be to mimic beavers, but using these ecosystem engineers as aids to ecological restoration and managing them along with wetland conservation would probably be a better and more efficient way. Finland has implemented several wetland restoration projects during the last decade. The Life+ Return of Rural Wetlands, a recent well-funded (over 2 million euro) project, restored 47 wetlands in total. I argue that we could save conservation book-marked funds by just enhancing and conserving beaver-created wetlands. We could reintroduce European beavers to Finnish national parks and wilderness areas where it is currently extirpated, and concurrently we would contribute to our obligations dictated by the EU.

The EU water framework directive aims to maintain and improve the ecological conditions of inland waters. Every member state has to make great efforts to ensure wetland conservation. The beaver is a potential tool for EU wetland conservation. The EU could implement the use of beavers in the inland water directive, and design a management plan for the species. As Montoya et al. (2012) suggest for restoration projects, it is feasible to target the reintroduction of dominant key species, and use these key species to restore biodiversity-based ecosystem functions.

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