

Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes

Petri Nummi and Timo Kuuluvainen

Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland

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Natural disturbances are important for forest ecosystem dynamics and maintenance of biodiversity. In the boreal forest, large-scale disturbances such as wildfires and windstorms have been emphasized, while disturbance agents acting at smaller scales have received less attention. Especially in Europe beavers have long been neglected as forest disturbance agents because they were extirpated from most of their range centuries ago. However, now they are returning to many parts of their former distribution range. As a disturbance agent, beaver plays two roles: of an ecosystem engineer and of a herbivore. The engineering impact is realized through dam construction resulting in a transformation of an originally terrestrial ecosystem into an aquatic one. As herbivores, beavers affect stand structure and tree species composition by preferring deciduous trees over coniferous ones. After abandonment, a beaver pond gradually turns into a terrestrial habitat again. At well-drained sites, forest will return in due course, first dominated by deciduous trees. At poorly drained sites, moistness of beaver patches may result in fen development. We conclude that beaver has an important impact on ecosystem processes and biodiversity in boreal forest ecosystems because it creates and maintains a spatio-temporal mosaic of successional habitats and associated species communities that would otherwise not exist in the landscape.

Introduction

It is currently acknowledged that unmanaged forests across the circumboreal zone exhibit considerable variation in their native disturbance regimes (Kneeshaw *et al.* 2011). This variability is caused by various and often interacting abiotic and biotic disturbance factors. In addition to fire, which is conventionally considered the ‘primary’ disturbance factor in boreal forests, often a multitude of other disturbance agents, operating over a range of time and space scales, are active (Kuuluvainen 2002). These include wind, fungi, insects (both defoliating and bark beetles)

as well as large herbivores such as moose and beaver (Shorohova *et al.* 2009, Kuuluvainen and Aakala 2011).

Beavers are large semi-aquatic rodents which strongly affect the ecology of their habitat consisting of ponds, creeks and riparian forests (Baker and Hill 2003). The effects of beavers may be considered within many ecological conceptual frameworks: beavers can be viewed as herbivores (central place foragers) (Jenkins 1980), disturbance agents (Remillard *et al.* 1987), keystone species (Naiman *et al.* 1986), ecosystem engineers (Jones *et al.* 1994) and facilitators (Nummi and Hahtola 2008).

During most of the history of modern ecology and forest sciences, beavers have been extinct from most of their former potential-distribution sites. This is the case especially for the Eurasian beaver (*Castor fiber*). At the beginning of the 20th century, only around 1200 Eurasian beavers survived after a long period of over-hunting, and they were scattered across eight remnant populations in Europe and Asia (Halley *et al.* 2012). Also in North America, most of the Canadian beaver (*C. canadensis*) populations at middle and southern latitudes were depleted by the year 1900 (Baker and Hill 2003). It can be claimed that in the absence of beaver as an important natural disturbance agent, riparian landscapes have been in an “unnatural” state (Naiman *et al.* 1988).

With the aid of protection and active restocking beavers returned to most of their original range in North America by the end of the 1950s (Jenkins and Busher 1979). In Eurasia, beaver re-establishment — via dispersal and reintroductions — has taken more time and is still an ongoing process. The present Eurasian population is estimated to be at least one million animals, and the densest stocks are found in the eastern and northern parts of Europe (Sjöberg and Ball 2011, Halley *et al.* 2012). In connection with reintroductions of the Eurasian beaver in Finland, in the 1930s also Canadian beavers were released into the wild from where they dispersed to Russian Karelia in the 1950s (Lahti and Helminen 1974, Parker *et al.* 2012).

Despite the return of the beaver to many forested landscapes, it is barely even mentioned in the forest disturbance literature (Kneeshaw *et al.* 2011, but *see* Engelmark 1999), and we are not aware of any recent study specifically evaluating the role of beavers in boreal forest disturbance regimes (but for beaver foraging *see* Johnston *et al.* 1993, Donkor 2007). Hence, the purpose of this paper is first and foremost to review and evaluate the ecological role of the beaver as a disturbance agent in the boreal forest. We will also shortly discuss the implications of its role in ecological restoration. This is most pertinent concerning areas in Europe, where the beaver has been re-established quite recently (Halley *et al.* 2012), although most of the research on ecosystem impacts of beavers has been carried out in North America.

Beaver in boreal forest disturbance regimes

In forest ecosystems, the occurrence of disturbances can be considered to be partly stochastic and partly deterministic, so that the predictability of disturbances vary between agents within and among ecosystems. In the north European landscapes, this is most clearly expressed by the changing probability of occurrence of different disturbance factors along topographical and soil-fertility gradients, ranging from moist lowland herb-rich sites to nutrient-poor upland dry sandy heaths (Fig. 1). For example, forest fires have historically occurred more often at drier upland sites than at moister lowland sites (Zackrisson 1977), typically resulting at the landscape level in complex mosaics of burned and unburned patches (e.g. Wallenius *et al.* 2004).

Beaver as a disturbance agent in forested landscapes is interesting because as compared with that of fire, its impact is restricted to the opposite end of the topography-related moisture–soil-fertility gradient (Fig. 1). Beaver is active at moist lowland sites in the vicinity of flowing water or small waterbodies. These are usually relatively nutrient-rich and high-productivity sites, with high overall species diversity. Apart from having regular spring floods which usually do not kill trees, these lowland sites are relatively stable and exhibit long habitat continuity. This is because they are rarely perturbed by disturbance factors — such as fire (because of moistness) and wind (because of topographically sheltered location) — common at upland sites. Thus, beaver activity and associated tree mortality, concern a limited and specific part of the forest landscape that is void of major disturbance agents dominating the other parts of the landscape (e.g. Rouvinen *et al.* 2002). However, within their spatially-restricted range of activity, beavers can extensively affect and change the habitat (Naiman *et al.* 1988).

Beaver as a disturbance agent

As a disturbance agent, the beaver has two distinct roles: an ecosystem engineer and a herbivore. The peculiar aspect of beaver’s ecosystem engineering is that because of construction of

Gradient of decreasing site moisture and increasing probability of fire occurrence

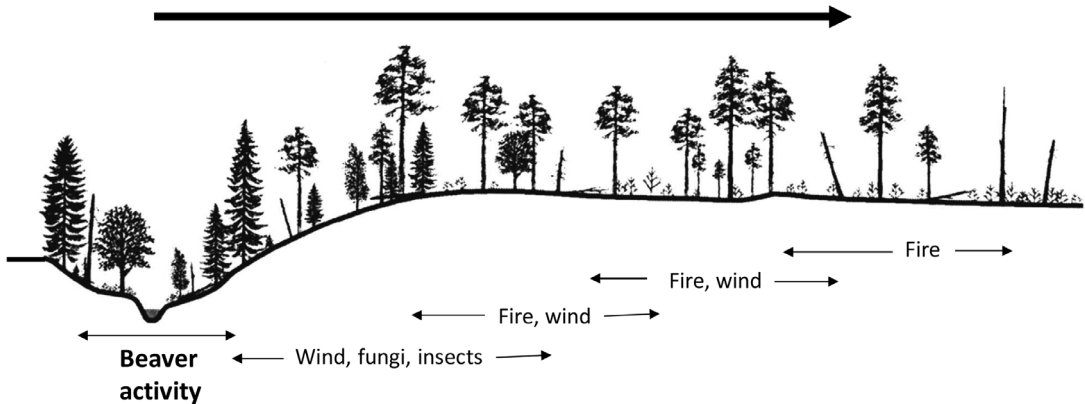


Fig. 1. Schematic presentation of the probability of occurrence of different disturbance factors along the topography-related site moisture gradient in boreal forest landscapes. Beaver disturbance is restricted to the moist end of the gradient, while fire probability is assumed to increase toward the dryer end of the gradient. Drawing by Janne Karsisto.

dams, an originally terrestrial ecosystem shifts to an aquatic one (Naiman *et al.* 1988). Depending on an area, there can be 2–16 beaver dams per kilometer of first- to fourth-order streams (Naiman *et al.* 1988). The ability to transform a terrestrial ecosystem into an aquatic one makes beaver a unique disturbance agent capable of creating habitats that would otherwise not exist in the landscape. This has far reaching implications for ecosystem functioning and species diversity in the boreal forest landscape.

The question whether the building activity of the two species, the Eurasian beaver and the Canadian beaver, differs has been debated. Initially Danilov and Kanshiev (1983), working in a region containing both Eurasian and Canadian beavers, reported that the two species were slightly different in their building activities. However, after being able to study the two species in similar habitats, they recently refuted their earlier findings and concluded that “the construction activity has no species-specific features, and is evidently determined by geomorphological and hydrographic settings in the habitat” (Danilov *et al.* 2011).

The other important role of beaver is that of a herbivore. Although beaver herbivory may resemble to some extent moose or deer browsing (Donkor and Fryxell 1999), only beavers can harvest mature trees and thus directly affect

forest overstory structure and composition (Donkor 2007). In comparison, moose herbivory only targets young trees, which of course in the long run may also affect overall tree stand structure and tree species composition (Johnston and Naiman 1990a, Persson *et al.* 2005).

Patch-scale effects of beaver

Vegetation

When beavers build their dams, they cause water surface to rise locally so that the vegetation on the shores of the dammed creek or pond is flooded. The dynamics of such flooded beaver patches can vary considerably depending on circumstances; in oligotrophic boreal areas the average occupancy time of a beaver ponds may be less than three years (Hyvönen and Nummi 2008), whereas in more productive areas beavers may inhabit the same patches for several decades (Johnston and Naiman 1990b). Also the pond structure varies a lot depending on habitat. When beavers make a dam in a small stream, most of the beaver pond consists of flooded terrestrial shore (e.g. Naiman *et al.* 1988). But when an already existing pond is dammed, a smaller portion of the beaver pond consists of flooded shores (Nummi and Hahtola 2008).

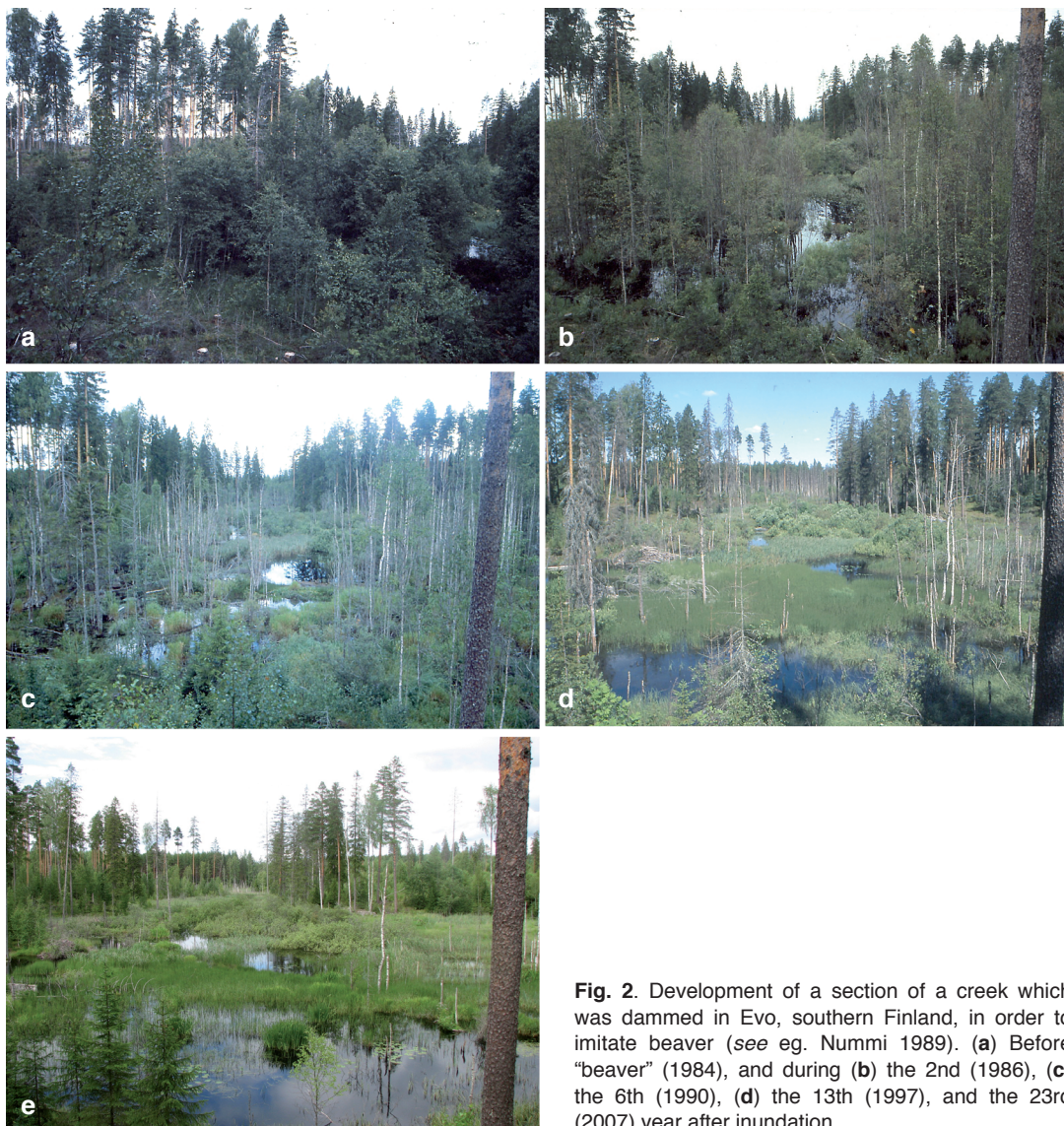


Fig. 2. Development of a section of a creek which was dammed in Evo, southern Finland, in order to imitate beaver (see eg. Nummi 1989). (a) Before “beaver” (1984), and during (b) the 2nd (1986), (c) the 6th (1990), (d) the 13th (1997), and the 23rd (2007) year after inundation.

Coniferous trees are most susceptible to death by flooding (Hyvönen and Nummi 2008), while some deciduous trees can tolerate inundation for some time. Upon flooding, *Betula pubescens* and *Alnus incana* were found to be in good condition for two years, but they died in the third one (Nummi 1989, see Fig. 2a–c). Some *Salix* species can survive inundation for at least a decade with the aid of their adventitious roots (Hyvönen and Nummi 2011, cf. flooded *Salix* bushes seen on the opposite shore in Fig. 2d and e).

Shore flooding will gradually lead to the

death of the less water-tolerant wetland plants, and to the colonization of the pond by water plants. In Finland, it was found that within 1–2 years after flooding, the dominance of *Calamagrostis* and *Carex* species strongly declined (Fig. 2b; Nummi 1989). In early successional ponds (2–5 years), submerged plants such as *Lemna* and *Utricularia*, are common (Ray *et al.* 2001, Hyvönen and Nummi 2011). Later on, also *Ceratophyllum*, *Nymphaea* and *Potamogeton* species colonize the pond (in the center of Fig. 2d). Aquatic vegetation is also affected by

beaver herbivory: plant biomass may be reduced by 60%, and plant species composition can be dramatically affected (Parker *et al.* 2007).

Organic matter and nutrients

During beaver flooding, organic matter rich in nutrients accumulates in pond sediments (Naiman *et al.* 1986, 1994). When properly positioned, a beaver dam made of 4–18 m³ of wood and clay may retain up to 2000–6500 m³ of sediment (Naiman *et al.* 1986). The amount of nitrogen in beaver pond sediments (per m²) has been found to be 9–44 fold as compared with that in riffle (Francis *et al.* 1985) or may even be 10³ times higher in the pond than in the riffle (Naiman and Melillo 1984). Naiman *et al.* (1986) found that the carbon turnover time was 161 years in the pond as compared with the 24 years in the riffle.

During the two first years of flooding, the input of leaf litter has been reported to remain high (ca. 100 g m⁻² yr⁻¹) (Nummi 1989). At this early phase, these allochthonous inputs of carbon to the pond are clearly higher than in older beaver ponds (Naiman *et al.* 1986). In the beaver pond, the decomposing plant biomass and the subsequent release of nutrients form the basis for the productivity and for the food chain of the pond (Hodkinson 1975).

Naiman *et al.* (1994) list three possible reasons why beaver-created patches may have standing stocks of ions and nutrients greater than that of the original forest soil: (1) the beaver ponds and meadows may have acted as efficient sinks for material eroding from the landscape, (2) the rising water from dam construction may have captured sufficient nutrients and ions contained in the preexisting forest vegetation, and (3) biogeochemical processes may have transformed elements in the habitats themselves. Naiman *et al.* (1994) conclude that in their study area the primary influence of beaver impoundment is on *in situ* biogeochemistry rather than waterborne particles from the surrounding uplands.

Biodiversity

The high amount of decomposing plant matter

forms the basis for abundance of aquatic invertebrates, which contribute to the abundance of e.g. fish, waterfowl broods, bats and otters at higher levels of the food chain (McDowell and Naiman 1986, Schlosser and Kallemayn 2000, Rosell *et al.* 2005, Nummi and Hahtola 2008, Nummi *et al.* 2011).

During the aquatic phase, the patch-level diversity of invertebrates is lower than that in non-beaver patches or before flooding (McDowell and Naiman 1986, Nummi 1989). In an experiment imitating beaver flooding in Finland, Nummi *et al.* (1999) found that the diversity of aquatic invertebrates (Simpson's index at order level) was 6.21 before inundation and ranged between 1.57–4.20 during the nine flood years. The diversity of herbaceous plants has been found to be at the same level on beaver and non-beaver shores (Wright *et al.* 2002), but that of amphibians and waterbirds higher in beaver ponds than in non-beaver ponds or before damming by beavers (Dalbeck *et al.* 2007; P. Nummi unpubl. data). In Canada, it has been noted that by providing open-water areas during dry periods, beavers mitigate the effects of climate warming in boreal wetlands (Hood and Bayley 2008); this is especially important for such species groups as frogs. During the succession of beaver ponds, the diversity of different species groups change: the diversity of herbaceous plants is highest in 11–40-year-old ponds (Ray *et al.* 2001) and that of fishes in 9–17-year-old ponds (Snodgrass and Meffe 1998).

By resetting vegetation succession, beavers can contribute to diversity and composition of plant communities and habitat availability which are important for endangered species. An example is provided by the North American butterfly *Neonympha mitchellii francisci*, which occurs in several small subpopulations in wetland meadows along streams where their presumed larval host plants *Carex* spp. are found. By surveying riparian vegetation communities in all stages of beaver-influenced wetland succession, Bartel *et al.* (2010) showed that beavers created habitats that contained plants not found elsewhere in riparian zones. Beavers also increased plant species diversity across the landscape by creating novel combination of patch types (Bartel *et al.* 2010).

Beaver flooding produces considerable amounts of dead wood (Hyvönen and Nummi 2008) which provides habitat obligatory for e.g. many insects and fungi. These aspects remain largely unstudied, but for example Saarenmaa (1978) found that a beaver-flooded stand of Norway spruce (*Picea abies*) harboured 20 species of beetles. In general, riparian sites harbour more wood-decaying fungi than upland forest sites (Komonen *et al.* 2008). Further on in the food chain, insects provide food for insect-eating birds such as woodpeckers, which have been found to use beaver ponds more than control areas without beavers (Lochmiller 1979).

Forest structure

Because beavers are central place foragers, their herbivory especially affects tree stand structure and composition on the shores and the vicinity of beaver ponds (Jenkins 1980, Johnston and Naiman 1990a, Donkor and Fryxell 1999). In Wisconsin, USA, it was found that the density of trees was low near the shore line and increased with increasing distance from the river bank, whereas no changes were found in sapling densities (Barnes and Dibble 1988). When beaver creates canopy openings in stands of early successional species, the gaps may be quickly colonized by sprouting deciduous species such as aspen and downy birch. Because of the litter quality of these species, this can contribute to increased rates of nitrogen cycling and productivity (Pastor and Naiman 1992).

However, beaver browsing can also decrease the amount of deciduous trees in the pond's vicinity. In Ontario, Canada, beavers selectively fed on a small number of deciduous species and the number of cut stems declined with increasing distance from ponds; this led to conifer dominated forests (Donkor and Fryxell 1999, *see also* Naiman *et al.* 1988). Removal of trees may sometimes lead to formation of open meadows with no forest regrowth (Martell *et al.* 2006; *see also* below, peat formation in moist soils). The case leading to the dominance of conifers resembles the impacts of moose herbivory, which may decrease the availability of nitrogen. This occurs when a high density moose population selec-

tively forages on deciduous trees, which leads to increasing number of conifers with slowly decomposing litter. This again leads to decreased soil nutrient availability (Pastor *et al.* 1988, Pastor and Naiman 1992, Persson *et al.* 2005). In some cases, however, the browsing effect of beavers was found to be clearly weaker than that of ungulates (Hood and Bayley 2009).

The flooding of shores by the beaver causes pronounced changes in nutrient balance that can affect the subsequent forest development (Hyvönen and Nummi 2008, 2011). Under anaerobic conditions during flooding, nitrogen and ammonium accumulate in the bottom of the flooded area. When aerobic conditions return after the flowage is abandoned (especially after a short period of flooding), organic nitrogen mineralization and vegetative uptake proceed rapidly leading to high productivity in the early phase of the terrestrial succession (Naiman *et al.* 1994). For example, in boreal Fennoscandia tree stands may in this stage be dominated by deciduous trees such as downy birch (*Betula pubescens*) (Hyvönen and Nummi 2008).

Beaver flooding may change the tree stand composition towards deciduous trees (Hyvönen and Nummi 2008). This bears some conceptual importance since beaver-forest relationship was earlier considered mostly in the light of selective browsing, which changes the forest composition towards conifers (Naiman *et al.* 1988, Pastor and Naiman 1992). It has even been argued that beavers may not act as keystone species in the boreal via herbivory, because their browsing increase the importance of the already dominant conifers (Donkor and Fryxell 1999). Impact of flooding is the opposite: increasing hardwoods in the early phase of the terrestrial succession, starting when beavers abandon the pond (Hyvönen and Nummi 2008). The increase of deciduous trees is beneficial not only to the beaver itself, when it returns to a recovered patch after some time of abandonment, but also to other mammalian herbivores (Wolfe 1974, Rosell *et al.* 2005).

Succession

After abandonment, a beaver pond often gradually converts to terrestrial habitat again. At this

stage, there are several possible successional pathways depending on circumstances. When a beaver dam rapidly collapses after a relatively short period of beaver occupation, forest succession may start within 2–3 years after beaver abandonment (Hyvönen and Nummi 2008). But in places with low spring and autumn runoffs, a beaver dam and the associated flooding may last long after the site has been abandoned, even until beavers again recolonize the patch. At certain sites with a low topographic gradient, the patch may remain so moist that the site is colonized by peatland vegetation and will finally turn into peatland, an alternative ecosystem stable state (Johnston and Naiman 1990b, Charman 2002). It has also been suggested that the flooding and anaerobic conditions of beaver ponds may kill the ectomycorrhizal fungi necessary for the re-establishment of conifers once the pond shores drain (Wilde *et al.* 1950, Terwilliger and Pastor 1999).

Landscape-scale effects of beaver

Habitat diversity and dynamics

From the landscape point of view, a peculiar

spatial aspect of beaver disturbance is that it is restricted to riparian habitats. Temporally, beaver disturbance is characterized by a relatively low level of stochasticity (Table 1). This is because a beaver population exerts continuously some level of disturbance on the riparian part of the landscape (Johnston and Naiman 1990b, Hyvönen and Nummi 2008).

Although restricted to riparian habitats, the amount and rate of beaver-flooded area can be considerable. For example in Minnesota, USA, the beaver population was low in the first half of the 20th century due to historic over-trapping. In 1940, beaver ponds covered only 1% of the landscape. By 1986, the growing population of beavers had impounded 13% of the landscape. Beavers created new ponds at the rate of 0.42% of the landscape area per year (Johnston and Naiman 1990b, Johnston 1995), and another 13% was affected by beaver herbivory (Naiman *et al.* 1988). In Finland, Hyvönen and Nummi (2008) found out that even in areas with low beaver density almost half of the ponds in the landscape were affected by beaver during an 18-year period. In general, it can be envisaged that the impact of beavers in forest landscapes is very landscape-specific, depending on factors such as topographic features and overall site fertility.

Table 1. A tentative comparison of the main characteristics of beaver disturbance with other main disturbance factors in the boreal forest. Explanation: + low/small, ++ intermediate, +++ high/large

	Frequency (years)	Stochasticity	Extent	Severity ^b	Quality	References
Beaver flood	10–15 ^a	+	+	+++	Terrestrial → aquatic	Hyvönen & Nummi 2008
Beaver herbivory	3–15 ^a	+	+	++	Overstory gaps	Fryxell 2001, Hyvönen & Nummi 2008
Moose	1–2	+	++	+	Top and twig browsing of saplings	Pastor <i>et al.</i> 1988, Persson <i>et al.</i> 2005
Defoliating insects	5–30	++	+	+ to ++	Defoliation, overstory gaps	Kneeshaw <i>et al.</i> 2011
Pathogenic fungi	30–300	++	+	+ to ++	Overstory gaps	Kuuluvainen 1994, Lännenpää <i>et al.</i> 2008
Fire	30–300+	+++	+++	++ to +++	Patch to stand replacement	Niklasson & Granström 2000, Pitkänen <i>et al.</i> 2003, Wallenius <i>et al.</i> 2010
Wind	500–1000+	+++	+ to ++	+ to +++	Patch to stand replacement	Kuuluvainen & Aakala 2011

^a In the riparian area potentially available for beaver. ^b Within disturbed area.

At the landscape scale, beavers increase habitat diversity and create habitats that would otherwise not exist — at least not to a similar extent — in the landscape, including shallow ponds, beaver meadows with sedges and early successional stage forests with abundant deciduous trees (Naiman *et al.* 1988, Hyvönen and Nummi 2008, Bartel *et al.* 2010). From the point of view of organisms dependent on dead wood, such as fungi and insects, it is important that at the landscape level beaver activities create a continuous supply of dying and dead trees (Ehnström 2001). In aquatic systems beavers increase stream-level diversity of fish by creating a spatio-temporal mosaic of habitats with different successional pathways and stages (Snodgrass and Meffe 1998, Schlosser and Kallemeyn 2000). Similarly, the landscape-level diversity of the riparian zones increases because of increased heterogeneity of forest and meadow structure and plant species composition. Scale is important: Wright *et al.* (2002) found no differences in diversity of plant species at the patch scale between beaver-modified and forested sites, but because their community composition was so different, the landscape level species richness was 1.3 times higher than richness estimated when drawing only from forest or beaver-modified plots (*see also* Bartel *et al.* 2010).

Beaver density and the resultant patch dynamics play a fundamental role in how beaver engineering impacts ecosystem processes and biodiversity at landscape scale. At high population densities in productive areas, beavers may occupy most or all available patches in the landscape and stay in one site even for decades (Johnston and Naiman 1990b). In low productivity areas beavers may stay in one place only for a few years, and then recolonize it after 10–12 years, when there is enough regrowth of deciduous trees (Fryxell 2001, Hyvönen and Nummi 2008). In both cases, the beaver-mediated forest disturbance process is quite predictable, i.e. its stochasticity is relatively low (*see* Table 1). The depletion and recolonization processes have successfully been predicted using general patch and population dynamics models for ecosystem engineers (Gurney and Lawton 1996, Wright *et al.* 2004). It should be noted, however, that the models have so far not taken into account the situation where the food resource state of beaver

patches develops to a higher level compared with the situation before beaver occupancy. This can happen when riparian tree stands change from dominance of conifers to that of hardwoods (Hyvönen and Nummi 2008).

The situation in which the landscape consists mostly of old beaver ponds may not be optimal from the biodiversity point of view. For example Snodgrass and Meffe (1998) found that in headwater streams fish species richness per pond increased with pond age up to 9–17 years but decreased in ponds older than 17 years. Unnaturally high population densities of beavers are indeed possible in most areas of the globe, which are currently lacking their native large predators naturally controlling the populations of their prey (Ritchie *et al.* 2012).

Organic matter, nutrients, and hydrology

At the watershed level, beaver dams may significantly contribute to preventing nutrients and carbon from leaching out from the watershed ecosystem. For example, beaver dams have been calculated to retain enough sediment to form an additional 42-cm layer of sediment in small-order streams (Naiman *et al.* 1986). This function of beaver dams could be especially important immediately after large, high severity disturbances, such as severe wildfires or windstorms, which release high amounts of carbon and nutrients. Here beaver ponds function as large-mass slow-turnover components in stream ecosystems which may increase the resistance of streams with beaver ponds to perturbations (Naiman *et al.* 1986). It has even been suggested that such nutrient accumulation process that has continued for thousands of years could have formed the basis for the archaic agriculture in northern Fennoscandia based on utilization of flooded hay-meadows as a source of cattle fodder (Huikari 1998). However, flooding of shores by beaver also causes leaching of nutrients and carbon from the forest to the aquatic system. The balance whether a pond acts as a net sink or source of elements to downstream appears to be equivocal: it depends on factors such as pond age, ecological maturity, and channel morphology (Naiman *et al.* 1994).

Accumulation of carbon and nutrients in beaver ponds creates aquatic and terrestrial hotspots of high productivity and biodiversity in the landscape. However, some part of accumulated nutrients is distributed back to the surrounding terrestrial environment via insect emergence and by terrestrial herbivores and insectivores (Wolfe 1974, Naiman *et al.* 1984, Rosell *et al.* 2005, Nummi *et al.* 2011).

It should be noted that some of the carbon of the beaver ponds is released to the troposphere in the form of methane. Beaver ponds create suitable conditions for methanogenesis since they accumulate large amounts of organic matter providing the necessary anoxic environment (Ford and Naiman 1988). Altogether, beaver ponds constitute a measurable factor in the recent increase in tropospheric methane concentration (Naiman *et al.* 1991).

At the watershed level, beavers also have a pronounced effect on hydrology. At times of low base flows, beaver dams can hold 30%–60% of available water. In systems with seasonal water shortages, this storage and subsequent slow release can be crucial to increasing groundwater retention, maintaining minimum baseflows for downstream habitat, and increasing valuable late season flows (Gurnell 1998, Pollock *et al.* 2003). Furthermore, decreased water velocity and more consistent water volume result in a decrease of peak flows and decreased severity of flooding events as well as increased groundwater recharge in downstream waterways. This flood protection aspect is identified as one of the key ecosystem services that beavers provide (Buckley *et al.* 2011).

Conclusions and implications for forest restoration

The beaver is a unique disturbance agent in the boreal forest, because it acts both as an ecosystem engineer and a herbivore. With its dam building ability, the beaver is able to convert terrestrial habitats into aquatic ones, within and around which beaver acts as a herbivore. This two-folded ecological impact of the beaver is typically highest at moist sheltered sites that are rarely affected by otherwise common distur-

bance factors in a boreal forest, such as wildfires and windstorms. Beaver activity significantly contributes to the landscape-level patch and habitat variability and heterogeneity, and maintenance of biodiversity and ecosystem processes, such as carbon and nutrient cycling (Naiman *et al.* 1986, 1994). Thus beaver plays a specific role in the natural disturbance regime of the boreal forest ecosystem.

However, studying and evaluating the ‘natural’ or historical range of variability of beaver impacts in forest ecosystems is made difficult by the fact that the species has for decades been extinct from much of its previous range of distribution because of over-hunting. As a result of reintroductions, beaver populations have recovered in many areas, but now they are often strongly affected by the surrounding human-dominated landscape, where beaver population dynamics is also influenced by the lack of natural predators, such as the wolf and bear.

In spite of these shortcomings in knowledge basis, beaver is unquestionably an inherent and important part of the natural disturbance regime of the boreal forest. Accordingly, Törnblom *et al.* (2011) suggested that knowledge of the beaver as an ecological engineer could be used as a basis for management of water and riverine landscapes according to the EU Water Framework Directive. They pointed out that the condition of “good ecological status” of small or medium sized streams in many cases would need characteristics created by beavers. Because of the interplay of aquatic and terrestrial habitat within a catchment area, the structure of the riparian zone is of particular importance. Without beavers, streams are also assumed to have low resistance to perturbations (Naiman *et al.* 1986). In conclusion, the beaver as a disturbance factor and ecosystem engineer should be given special consideration in all forest landscape restoration projects (Ebenman and Jonsson, 2005, Byers *et al.* 2006).

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