Changes in Ecosystems of the Middle Taiga due to the Impact of Beaver Activities, Karelia, Russia

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Abstract

Ecological consequences of beaver activity at water-bodies in southern Karelia were assessed. Vegetation succession induced by beaver foraging and construction activity was studied; the effect of long-term forest flooding on invertebrate and small mammal fauna. Beaver foraging activity results in the loss of 23.2 to 92.1% of aspen, 3.0 to 26.5% of birch and nearly all willow from the riparian plant community. Beaver dam construction induces the formation of wetland communities of mixed categories, including Sphagnum communities getting overgrown with birch, sedge-Sphagnum, Sphagnum-cotton grass, and various dwarf shrub-Sphagnum communities dominated by one or another dwarf shrub species. Organic carbon and the total nitrogen content in the soils of former beaver ponds increases, whereas pH decreases (Sidorova and Fyodorov 2007). The abundance and species composition of invertebrate and small mammal fauna also change significantly within the drained pond area. The number of invertebrates at beaver ponds increases 2 – 2½ times. Expansion of the terrestrial invertebrate fauna goes along with increase in its species and age diversity. In some surveys, the abundance of small mammals dropped nearly 10 times – from 7.0 animals per trap-day in reference plots to 0.67 in abandoned beaver sites. In other surveys, the abundance of shrews and voles increased 2-2.5 times.

Key words: Beaver activities, changes of riparian ecosystems, forest vegetation, community, small mammals, invertebrates, plant

Introduction

The beaver is often called a “keystone species”, “edifier species”, or even “ecosystem engineer” (Jones et al. 1994, Baker and Hill 2003, Rosell et al. 2005 etc.). All these titles are due to the beaver’s unique capacity to not just modify the environment to suitable for its own needs, but also to generate the conditions favourable for other species. This pronounced environment-shaping activity makes beaver an attractive study object. Yet the ecosystem response to the arrival of beavers would differ depending on landscape, climatic and ecological conditions. In forest steppe, for instance, fertile meadows would form in place of abandoned beaver ponds, whereas land flooding in Karelia would result in formation of wetland communities. In our region, the response of the ecosystem to the impact of beavers has been insufficiently studied. Partly, the reason is that beavers re-appeared in Karelia only in the mid-20th century, after two centuries of absence. The first researcher to study the role of these animals in Karelia was P. Danilov (1963, 1967, 1970). Latest studies have added a lot to the results of previous research. The present study aimed to comprehensively assess the role of beavers in waterside ecosystems, more specifically – the effect of beaver foraging and engineering activities on the composition and structure of plant communities, invertebrate and small mammal fauna. In this article we overview the results of our studies previously published in different issues.

Materials and methods

This paper is based on ten years (1997 to 2007) of observations of various modifications of boreal ecosystems by beavers in the forests of southern Karelia. The Republic of Karelia is located in the north-western part of Russia and shares a border to the west with Finland. Its area is 18,052 thousand hectares. Karelia is called “the land of thousands lakes and rivers”. There are about 64,000 lakes and more than 27,000 rivers in the region. In addition, a great part of the territory has a dense network of forest and agricultural drainage. Arterial drains alone have a combined length of 13,000 km.

Riparian strips in southern Karelia, which comprised our study area, are covered mainly by secondary forests (forests which have re-grown after a forestry). This is rich herbaceous birch forest, rich herbaceous birch-aspen forest, bilberry spruce-birch forest.

The surveys have been performed at 44 beaver impoundments. Furthermore, in 1997, we have started a continuous monitoring of two abandoned beaver sites. These sites were located on two types of water bodies as a small forested lake and a brook.

The control site was a section of the bank/shore of the same waterbody where the colony was located, but bearing no traces of beaver activity. In the case of small lakes, which were often totally occupied by beavers, the control sites were "non-beaver" lakes with a similar type of forest along the shore.

To assess the impact of beavers on forest stands, we established 4 to 8 sample plots (25 by 25 m) at each beaver pond. We also established an equal number of plots in areas unaffected by beavers ("controls"). The composition and diameter distribution of major stand-forming tree species were determined in each plot. To determine beaver browsing activity and tree regeneration capacity, all damaged trees and shrubs within 50 metres from the shoreline were counted.

For characteristics of the tree layer we made up the formula of stand composition (Tkachenko 1955). The formula shows the share of each of tree species (or percent of the number of trunks of adult trees of a given species), growing on a given site assuming the total number of trees corresponds to 10 points (or 100 %). Names of tree species in the formula are designated as capital first letters (e.g. As – aspen, Al – alder, B – birch etc.). The predominant species is put first in the formula . If the share of abundance of a tree species amounts to 2-5 %, it is marked with a "+" sign in the formula (e.g. 7P3Sp+B). The estimated average age of trees is put as a subscript index.

Mosses and herbaceous vegetation were described using the interrupted transect technique. Five parallel transects were established uniformly across the territory of the abandoned beaver pond with recovering terrestrial vegetation and at control sites. The orientation of transects (parallel, perpendicular or at an angle to the waterbody) depended on the size and outline of the formerly flooded area. Twenty plots (1 m^2 each) spaced 5 m apart were surveyed in each transect.

The soil invertebrate fauna was studied by standard methods of excavations (Fasulaty 1971, Rajkov and Rimsky–Korsakov 1994). The area of excavations was 0.25 by 0.25 m. We studied 10 beaver colonies and 10 control sites on lakes and streams. In every beaver colony, 60 samples were taken including 30 at the non-beaver site and 30 at the abandoned beaver site.

The invertebrates of the herb layer were collected using photoeclector. This method is based on the principle of positive phototaxis of invertebrates (Fasulaty 1971). The photoeclector is a veneer box (50 by 50 by 50 cm), which covers and darkens the studied area. At the top of box there is a glass jar with an insecticide. Invertebrates were collected from the glass jar and the inner wall of the device. We studied 10 beaver colonies and 10 control sites. In every beaver colony 80 samples were taken – 40 at the non-beaver site and 40 at the abandoned beaver site.

To assess the communities similarity for control and beaver-transformed sites we used The Jaccard index (the Jaccard similarity coefficient, K_j) that may range from 0 (absolute dissimilarity of two samples) to 1 (absolute similarity of the samples) (Jaccard 1901).

Changes in the fauna of small mammals induced by beaver construction activity were monitored for five years. Small mammals were captured following a conventional technique (Naumov 1951). Snap traps arranged linearly, 3 metres apart, were used. The bait consisted of pieces of rye bread soaked in sunflower seed oil. The traps were exposed for 3 days. The surveys were conducted at two model water-bodies: 1) a small forest lake (Lake Pertilambi), with deciduous species prevailing in stands along the shore (*Betuletum mixto-herbosum*, *Betuleto-populetum mixto-herbosum*) and 2) Kokkoila Brook, with low banks overgrown with mixed forest (*Picceto-betuletum vacciniosum*, *Piccetum vacciniosum*) (description reconstructed). The control was sites at the same water-bodies, but unaffected by beavers. Beavers settled on Pertilambi in 1985, and on Kokkoila Brook in 1981; the sites were abandoned in 1990 and 1988, respectively.

Results

Impact of feeding activities on vegetation

We determined that beavers utterly change the appearance of riparian vegetation through cutting of herbaceous and woody vegetation, the hydrological regime, bank and shore characteristics, composition and abundance of vertebrates and invertebrates, water and soil chemical composition.

We found a beaver family staying in the same place for a long period of time gnaws down nearly all trees of their preferred species in the area. This impact causes profound transformations in the composition and structure of riparian vegetation. Tree counts around beaver colonies in southern Karelia have shown that 933 out of 3,590 trees and shrubs within a 50-m riparian strip in the beaver feeding range and dwelling area had been felled. Beavers had felled nearly a half (47 %) of aspen, 12.4 % of birch, 27.7% of alder, 22.5 % of rowan, 83.3 % of willow plants (Table 1) (Danilov et al. 2007).

Table 1. Effects of beaver foraging activities on waterside vegetation; I – number of trees that used to grow in the site; II – number of beaver-felled trees

Colony	Tree and shrub species									
	Aspen		Birch		Alder		Rowan		Willows	
	I	II	I	II	I	II	I	II	I	II
1	124	44	110	16	16	12	80	44	6	6
2	180	72	148	4	16	8	7	4	2	2
3	128	118	211	56	3	2	7	3	3	3
4	112	85	114	19	6	3	9	4	-	-
5	276	64	444	20	60	9	462	46	-	-
6	132	50	368	62	-	-	36	30	6	4
7	133	77	252	28	90	19	42	14	7	5
Σ	**1085**	**510**	**1647**	**205**	**191**	**53**	**643**	**145**	**24**	**20**

Thus, beaver feeding activities result in the loss of 23.2 to 92.1 % of aspen, 3.0-26.5 % of birch and nearly all willow plants from the riparian community. On some occasions, beavers fell nearly all aspen trees within a 50-m strip along the waterbody. An example is a waterbody in southern Karelia, where beavers have felled 118 out of 128 aspen trees (92.1%) and only 56 out of 211 birch trees (26.5%) growing in the area. As a result, the ratio of major stand-forming species changed. The first canopy layer structure prior to beaver arrival had been $6B_{80}\,3As_{80}\,1Sp_{70}$, changing to $8B_{80}\,1As_{80}\,1Sp_{70}$ afterwards.

When harvesting forage, beavers cut aspen trees of the greater diameter than birch trees, this being another factor for a change of the main stand-forming tree species. We have estimated that the mean diameter of aspen trees growing along the shore is 22.7 cm (n =1,145; σ = 11.28); that of birch trees was 17.0 cm (n =1,680; σ = 6.22). Assessing the beaver activity around the same waterbodies, the mean diameter of felled aspen was 23.1 cm (σ = 9.05), that of birch – 11.9 cm (σ= 4.04). Over a half (71.2%) of beaver-felled birch trees of various age were up to 12 cm in diameter, whereas aspen trees of this diameter are not so often harvested by beavers – 14.9%. A majority of felled aspen trees (61.7%) were 17 – 40 cm in diameter, whereas felled birch of this diameter were very rare.

The “felling” event is followed by regeneration of trees and shrubs. Firstly it depends on the regeneration capacity of individual species. We have found that aspen growing around beaver lodges has a lower regeneration capacity than birch. Five years after being felled by beavers, 9.4% (48 of 510) aspen and 21.9% (45 of 205) birch trees produced stump sprouts. A strong sprouting capacity is demonstrated by alder, rowan and willows – sprouts were produced by 50.9%, 56.7% and 50% of all plants of the species, respectively.

A most evident example illustrating the above mentioned facts is a colony on Lake Valgoi (southern Karelia). There are the aspen and birch in equal proportions ($5As_{80}\,4B_{80}\,1P_{70}$) while the aspen has been felled 15 times more than birch. Considering that 15% of aspen and 50% of birch trees produced sprouts and suckers, one can predict that in a while aspen will no longer be a stand-forming species. Eventually, the stand composition will look as follows: $5B_{80}\,4As_{80}\,1P_{80}$, and locally even $7B_{80}\,2As_{80}\,1P_{80}$.

Impact of construction activities on vegetation and soil properties

Yet more profound changes in waterside forest associations are induced by beaver construction activities, namely the building dam. As a result of rising of the water level in watercourses the trees and shrubs are eliminated and aquatic and wetland vegetation forms in the flooded riparian areas. After beavers have left the area and the dams gradually fall to ruin a totally different type of plant association forms.

When the beavers have left, riparian areas are no longer inundated and acquire a mire community, which is mixed category comprising sphagnum with birch undergrowth, sedge-sphagnum, sphagnum-cottongrass and various dwarf shrub-sphagnum communities with different dwarf shrubs dominating. Vegetation in an abandoned pond grows against a background of heterogeneous microtopography and hydrological regime, with a mosaic plant association forming as the result.

The species diversity in the community and the prevalence of certain ecological groups of plants within it changed markedly (Table 2). Flooding caused the total number of grass and moss species to increase almost by half in the places of former beaver ponds. The share of wetland plants there increased 5- to 8-fold, while the share of forest plants decreased by a factor of 3 to 3.5. After the beavers had left, there remained 13 to 20 % of the herbaceous plants that had grown on the shores before flooding (the Jaccard index for plant communities located on lakes was equal 0.24 and on the streams was equal 0.16).

Table 2. Vegetation composition at the non-beaver sites and abandoned beaver colonies (Danilov et al. 2007)

Indices	Lakes		Streams	
	non-beaver sites	abandoned beaver sites	non-beaver sites	abandoned beaver sites
Number of species of herbaceous plants, dwarf shrubs and mosses	29	38	33	34
Number and proportion (%) of species common for both sites	13 (19.4)		9 (13.4)	
Proportion of forest plants, %	68.9	23.7	72.7	20.6
Proportion of wetland plants, %	13.8	73.7	9.1	76.5

The flooding of the forest, the accumulation of silt and other sediments that has been continuing for several years later tells on the soil characteristics. The changes in the soil are rather varied. Summing all these changes we can assert the following (Danilov et al. 2007, 2011, Sidorova and Fyodorov 2007, 2008):

1. Soils in areas which inundation ceased upon beaver departure are more acidic;

2. Areas regenerating from inundation upon beaver departure experience also a sharp, nearly ten-fold increase in the soil humus content;

3. A distinct trend in the distribution of acidity, organic carbon and total nitrogen is observed in the flooded site: carbon and nitrogen concentrations grow, whereas acidity decreases somewhat towards the river bank;

4. The accumulation of silt and other sediments during pond maintenance by beavers later results in a notable rise in the content of the main plant nutrients – phosphorus and potassium – in the soil. The concentration of ammonia nitrogen also increases;

5. The range of values increases. In other words, the territory of former beaver ponds is more heterogeneous than non-flooded sites.

Impact of construction activities on invertebrate fauna

Beaver-induced transformations of the environment also entail changes in the faunal composition. In our study area, we observed significant changes in the soil invertebrate fauna in drained habitats, to be more specific in the margins of the beaver pond, which were covered in herbaceous vegetation typical of forest edges and felled sites. Lake areas with abandoned colony demonstrate changes in the species composition and abundance of invertebrates. Therefore, in the surveyed sample plots, four families of phytophagous, three of predaceous and three of saprophagous invertebrates have been found. The species diversity of predaceous invertebrates grew sharply on the area after an inundation. Nine families were represented in addition to *Carabidae* and *Staphylinidae* imagoes and *Tabanidae* larvae; there were also larvae of the families *Dolichopodidae* and *Rhagionidae*, mature representatives of the families *Lycosidae* and *Clubionidae*, orders *Lithobiomorpha, Opiliones,* etc. Their abundance has also increased in these areas. The share of predaceous invertebrates in the control being 10.7% of the total number of invertebrate species, the share in the former beaver pond area reached 44.9%. The number of phytophagous invertebrate families remains the same, but their share increased from 32.2% to 43.5%. The abundance of saprophagous taxa dropped markedly. The total abundance of soil invertebrates on areas abandoned by beavers doubled from 72 individuals per m^2 (10 families of 5 orders) to 152 individuals per m^2 (15 families of 9 orders) (Table 3).

At lotic waters (rivers, streams), the abundance of invertebrates shows a little change owing to long-term flooding of the banks, and amounts to 112 individuals per m^2. However, the composition of the soil fauna changes considerably such as: the number of families and species of the order *Diptera* grows sharply owing to the coming of the families *Rhagionidae*, *Dolichopodidae*, *Tabanidae*, *Ceratopogonidae*, *Muscidae*. The share of imago stages of the families *Elateridae*, *Staphylinidae*, *Carabidae* and some others decreases with a simultaneous rise in the proportion of their larvae and

Table 3. Soil invertebrate fauna of riparian communities in South Karelia at non-beaver sites and abandoned beaver sites; p. = pupa, l. = larva, im. = imago (Danilov et al. 2007)

Families	Density, individuals per 1 m^2			
	Lakes		Streams	
	non-beaver sites	abandoned beaver sites	non-beaver sites	abandoned beaver sites
Order Coleoptera	-	24		
Family Elateridae (p.)			10	-
Family Elateridae (l.)	8	22	18	12
Family Elateridae (im.)	-	4	2	-
Family Carabidae (p.)	-	-	2	-
Family Carabidae (im.)	2	4	14	10
Family Staphylinidae (l.)	-	-	2	4
Family Staphylinidae (im.)	2	10	10	-
Family Curculionidae (l.)	6	-	-	2
Family Curculionidae (im.)	-	-	2	4
Family Scarabaeidae (l.)	-	-	-	2
Order Hemiptera	-	-		
Family Miridae			2	-
Family Pentatomidae	-	-	-	4
Order Diptera	-	-		
Family Tabanidae (p.)			-	4
Family Tabanidae (l.)	2	10	-	-
Family Tipulidae (l.)	-	-	4	2
Family Dolichopodidae (l.)	-	4	-	2
Family Muscidae (p.)	16	14	-	10
Family Muscidae (l.)	-	8	-	-
Family Bibionidae (l.)	12	-	-	-
Family Rhagionidae (l.)	-	12	-	12
Family Ceratopogonidae (l.)	-	-	-	2
Order Lepidoptera	-	6	8	-
Family Noctuidae (p.)				
Family Noctuidae (l.)	2	2	-	-
Class Oligochaeta	20	6	16	2
Family Lumbricidae				
Class Myriapoda	-	16	8	10
Order Lithobiomorpha				
Order Juliformia	-	2	-	2
Order Hymenoptera	-	2	-	8
Family Formicidae				
Order Aranei	-	2	4	-
Family Lycosidae				
Family Clubionidae	-	2	10	10
Family Thomisidae	-	-	-	6
Order (Opiliones)	-	2	-	4
TOTAL	**72**	**152**	**112**	**112**

pupae, but the number of earthworms drops abruptly. In areas undisturbed by beaver activities, invertebrates are represented by 7 orders and 11 families. Formerly flooded areas closer to the margins of the empty ponds featured 8 orders and 19 families (Table 3). The coefficients of similarity for invertebrate fauna of riparian communities located on the lakes and the streams were 0.32 and 0.30, respectively.

The abundance and species composition of the mesofauna of herbaceous layer within a former pond also change significantly. Invertebrate abundance on both lakes and watercourses increases 2 to 2.5 times. The fauna of terrestrial invertebrates in drained areas expands also through a rise in the species and age diversity (Table 4). The coefficients of similarity were low (Kj = 0.33 for "lakes" and K_j = 0.43 for "streams").

Impact on small mammals

Many researchers have noted that beaver activity, which alters the hydrological regime of water-bodies and riparian plant associations, also changes the communities of vertebrates quite considerably, although indirectly.

The abundance of small mammals dropped ten times at Lake Pertilambi, and their species diversity decreased (Table 5) (Fyodorov and Yakimova 2008), because a beaver pond which is getting overgrown, is poorly suited to small mammals – open water-logged areas, high light (which would repel shrews, in spite of food abundance), and meagre forage resources for rodents. Rodent species preferring open spaces (common vole) may, however, settle in the habitat (Table 5).

In the place of the overgrowing beaver pond at Kokkoila Brook, total abundance of small mammals was, on the contrary, higher than in the control sites, and much higher than the abundances at Lake Pertilambi, whereas the species diversity was comparatively low. The reason for these differences is the specific characteristics and age of the beaver site – beavers had left 15 years before the beginning of the observations. The vegetation is represented by birch and pine understorey at the sapling stage, with a rich herb and dwarf shrub layers. This is the most favourable type of forest community for small mammals.

Considering the gradual succession of vegetation in overgrowing beaver sites and its effect on small mammals, one can distinguish several stages in the change of this group's abundance and species diversity. Beaver-induced forest flooding results in die-back of the stand, which would regenerate only 10-20 years after drawdown. Often, deciduous or mixed stands would form in place of the primary forest. The small mammal fauna in such forest types is more diverse and abundant than in the original forest.

Table 4. Invertebrate fauna of the herb layer of riparian communities in South Karelia at non-beaver sites and abandoned beaver sites (Danilov et al. 2007)

Families	Density, individuals per 1 m^2			
	Lakes		Streams	
	non-beaver sites	abandoned beaver sites	non-beaver sites	abandoned beaver sites
Order Aranei Family Lycosidae	3.6	17.6	1.2	13.2
Family Lycosidae (immature)	-	10.0	-	3.6
Family Linyphiidae	5.2	10.8	7.6	4.4
Family Salticidae	-	-	-	2.0
Family Clubionidae (immature)	1.2	0.8	-	-
Family Araneidae (immature)	0.4	-	-	-
Family Thomisidae	-	1.2	-	-
Order Acarina Family Ixodidae	0.4	-	-	-
Order Opiliones	6.0	-	7.2	2.0
Order Hemiptera Family Miridae	2.8	2.0	7.6	2.4
Family Pentatomidae	-	-	1.2	1.2
Family Reduviidae	-	1.6	-	-
Family Tingitidae	-	0.4	-	-
Order Homoptera	0.4	2.8	-	1.6
Suborder Psyllinea				
Family Aphididae	-	8.4	-	24.4
Family Aphrophoridae	-	0.8	-	-
Family Cicadidae	-	2.0	-	0.8
Order Lepidoptera	0.8	2.4	0.4	1.6
Family Geometridae (l.)				
Family Noctuidae (l.)	0.8	1.6	0.8	0.8
Family Nymphalidae (l.)	-	-	-	1.2
Order Coleoptera	-	-	-	0.4
Family Chrysomelidae (im.)				
Family Carabidae (im.)	1.2	2.4	-	-
Family Curculionidae (im.)	0.4	-	-	-
Family Staphylinidae (im.)	0.8	1.2	-	-
Family Dermestidae (im.)	0.4	-	-	-
Family Coccinellidae (im.)	-	0.4	-	0.4
Order Hymenoptera Genus *Formica*	1.2	-	4.4	2.8
Genus *Myrmica*	-	-	-	1.6
Genus *Lasius*	-	-	-	2.4
Family Tenthredinidae (l.)			0.4	-
Order Diptera *(im.)* Family *Rhagionidae*	0.8	-	-	-
Family *Simuliidae*	-	2.4	1.2	1.2
Subclass Entognatha Order *Collembola*	0.4	-	-	-
Order Psocoptera	-	-	0.4	0.4
Order Plecoptera (im.)	-	0.8	-	-
TOTAL	**26.8**	**69.6**	**32.4**	**68.4**

Table 5. Composition and average long-term number of the small mammal fauna (sp. per 100 trap-days) in riparian ecosystems of experimental water-bodies (Fyodorov and Yakimova 2008)

Species	Lake Pertilambi		Kokkoila Brook	
	abandoned ponds	non-beaver territories	abandoned ponds	non-beaver territories
Bank vole (*Myodes glareolus*)	0	2.33	0	0.89
Common vole (*Microtus arvalis*)	0.33	0.33	0	0
Common shrew (*Sorex araneus*)	0.34	3.17	4.44	1.78
Masked shrew (*Sorex caecutiens*)	0	0.33	0	0
Pygmy shrew (*Sorex minutus*)	0	0.84	0	0
Total	**0.67**	**7.0**	**4.44**	**2.67**

Similar processes take place as felling sites get overgrown, but because of heavy, often excessive moisture in former beaver sites at early stages of vegetation regeneration small mammal species that prefer open spaces cannot colonize them. As a result, as in the case of the site on Lake Pertilambi, the abundance and species diversity of small mammals in such sites are low. Later on, as the sapling-stage deciduous and coniferous understorey, and then the deciduous and mixed polewood stand forms, the abundance of forest-dwelling small mammals increases, and the number of species that prefer open spaces decreases. This is the situation at Kokkoila Brook, where the abundance of common shrew in higher than in the reference site, but bank vole has not yet regained its position.

Discussion and conclusion

The appearance of beavers heavily transforms the ecosystem around the waterbody. The starting point of the transformations is the gnawing activity – felling of trees for food (bark and shoots), and for construction of lodges and dams.

Such profound changes in the forest associations along banks and shores as replacement of the main stand-forming tree species or even total loss of deciduous stands are caused by the following:

1) Beaver gnawing may reach an enormous scope, both in terms of the number of felled trees and the area of felled sites. In the central and northern parts of Karelia and Arkhangelsk Region, where aspen is rarely a stand-forming species along rivers and lakes, and the main food is birch, all aspen trees get felled in the very first year of beaver presence in the site, and the birch stock would be 60-70% exhausted within 3-4 years. Such sites may be quite extensive: in Karelia they reached 0.5-0.6 ha with 50-70 m^3 of the timber felled, in Pskov Region they ranged from 0.2 to 0.8 ha with 30 to 100 m^3 of the timber felled (Danilov 1967, Danilov et al. 2007). In River Høgebostad watershed, Norway, beavers have felled around 200 m^3 of commercial deciduous timber (Myrberget 1968). Johnston and Naiman (1990) have estimated that each beaver annually fells an average of 1300 kg of woody vegetation per hectare. As the result, the terrestrial vegetation biomass within the colony drops by 40% within 6 years. Less than a third of the biomass is consumed as food, a minor part is utilized in construction, and the rest is not used.

2) Beavers are rather selective in foraging (Fedyushin 1935, Danilov 1967, Zharkov and Sokolov 1967, D'yakov 1975, Jenkins and Busher 1979, Dyozhkin et al. 1986, Novak 1987, Donkor and Fryxell 2000, et al.). Of the 23 species of trees and shrubs in the north of European Russia, e.g., beaver prefers aspen and willow. It has often been recorded from 6-8-year-old beaver colonies in Karelia that no growing aspen was left in foraging areas. Being most fully consumed, aspen is the first species to disappear from the 1^{st} layer of the tree stand (Danilov et al. 2007). Zav'yalov et al. (2005) reported that due to selective foraging of beavers in Darwin Strict Nature Reserve, where aspen was the first to be consumed, there increased the share of tree species avoided by beavers, which used to occupy a suppressed position in the stand.

3) Another factor for a change in the stand-forming species is the difference in the regeneration capacity of damaged and felled trees. According to Shapovalov (1987), the lowest regeneration capacity in the Karelian Isthmus, Leningrad Region, was demonstrated by aspen – 17.5 % of felled trees produced stump sprouts, the corresponding figure for birch being twice higher – 38.7%. This information is in good agreement with our results reported above.

4) Beavers prefer to cache thinner birch and larger aspen specimens. Many researchers have mentioned this fact (Semyonov-Tyan-Shansky 1938, Kanshiev 1983, Zav'yalov et al. 2005, Danilov et al. 2007, et al.). Computations based on Kanshiev's (1983, 1992) data show that the mean diameter of beaver-felled aspen in the Leningrad Region, his study area, was 12.9 cm (n=129), and that of birch – 8.4 cm (n=61). At the same time, trees of these species growing around the water bodies were nearly equal in mean trunk diameter: 16.7 (n=296) and 15.0 cm (n=197), respectively. A half of felled aspen trees in our study were 25-45 cm in diameter, whereas birch of this size was very rare. Other researchers, on the contrary, noted that the thickness of nearly all felled trees (over 90%) did not exceed 12 cm (Hall 1956, Simonsen 1973, Balodis 1990, Szczepański and Janiszewski 1997, etc.). This fact may be due to higher food capacity of the beaver grounds in the study areas of the above authors, wherefore the animals had access to a wider selection of trees and shrubs (Danilov et al. 2007). Some authors however believe that felling of large trees is not a good strategy, since studies have demonstrated that the greater was the tree diameter the less bark the beavers consumed. It is also inefficient in terms of the ratio between energy loss to felling and energy gain from consumption (Jenkins 1980, Dvornikov and Dvornikova 1986, Zav'yalov et al. 2005).

Another factor significantly and interestingly modifying plant communities is the construction activities of beavers – digging burrows and canals, building lodges and, certainly, dams, which causes flooding of large forest areas and gradual die-back of trees and shrubs with following formation of wetland vegetation. After beavers had left and the dams had degraded, a new type of the plant association, completely different from the "pre-beaver" one is formed. However, the future appearance of the riparian/lakeside plant community depends on quite a number of factors – geographical latitude, climate, type of the original plant association, topography, etc. In Karelia, for instance, mire communities, often with non-uniform vegetation composition, would develop in the now-dry former beaver ponds. Typical mid-taiga and secondary forests had grown in the sites prior to beaver colony.

Observations in the Darwin nature reserve show that black alder stands tend to form in place of abandoned beaver ponds, where associations of the aspen-lime tree type had grown. They develop either in specific edge habitats with the exudative hydrological horizon and enriched soils, or through very gradual overgrowing of sedge mires (Zav'yalov and Bobrov 1997, 1998, Zav'yalov 1999).

As reported by Evstigneev and Belyakov (1999) for the Bryansk Region, meadows formed in most of the former pond after beaver departure. Relatively small (200-600 m^2), easily warmed backwaters with wetland-type communities formed in dam-side depressions where beaver had dug for material for dam construction. Wetland vegetation, mostly represented by the *Spirodello-Potamagetosum* association, developed there. The rest of the territory of abandoned beaver ponds was occupied by meadow communities. Floodplain meadows with long inundation period appeared immediately along the river channel, and shorter inundation meadows – a little further away. Later on, black alder communities formed in the sites. Some authors report that beaver ponds accumulate fertile silt, and extensive, densely vegetated meadows develop there afterwards (Warren 1927, Fedyushin 1935, Dyozhkin and Men'kova 1978, Dyozhkin et al. 1986, Balodis 1990 etc.).

Such change in the environment cannot but entail modifications in the fauna. All taxonomic groups of animals are affected, but in this paper we shall consider the effect of beaver activities on the fauna of invertebrates and small mammals.

Analyzing a variety of studies from different countries, we see that where beaver ponds appeared the taxonomic diversity of lentic-water invertebrates increased, and their abundance, density and biomass rose significantly (2-5 times) (Naiman et al. 1988, Sjöberg 1998, et al.). Dam-induced siltation of the bottom causes a rise in the benthic fauna with the dominance of chironomid larvae (Gard 1958, Keiper 1966, after: Savel'ev 1986, Shapovalov and Sharapova 1989, Nummi 1989, Margolis et al. 2001). At the same time, the numbers of free-swimming invertebrates and species typical of lotic waters drop substantially. Therefore, many authors report a decline or vanishing of the larvae of stoneflies *Plecoptera*, caddisflies *Trichoptera*, alderflies *Sialis,* mayflies *Ephemeroptera* (Sprules 1941, Nummi 1989, Smith et al. 1991, Harthun 1999, Margolis et al. 2001).

After beavers had left and the dam had naturally collapsed, the abundance of benthic insects dropped sharply (by up to 90 %). As soon as 60 days after the water level had fallen however, benthic insect numbers rose to 62 % of the initial abundance in sites with rapids and 8% in impounded sites (Stock and Schlosser 1991).

The impact of beavers on the invertebrate community may also be indirect. E.g., sprouts of beaver-felled trees of some poplar species (*Populus fremontii, P. angustifolia*) contain twice more phenol glycoside and total nitrogen than usual. Phenol glycoside is a chemical that protects poplar against herbivorous mammals. These same substances however attract the leaf beetle *Chrysomela confluence* (Martinsen et al. 1998). Flooding the territory and gnawing on trees beavers promote the numbers of *Drosophila virilis,* since this invertebrate species lays eggs in the decaying bark of some deciduous trees (Spieth 1979, cited after: Rosell et al. 2005).

Beaver colonies often attract also small mammals. In Lithuania, for instance, 11 small mammal species were trapped at beaver lodges, whereas trapping at reference sites in the forest yielded only 5 species (Samas and Ulevičius 2011, Ulevičius 2011). Surveys in Oregon have shown the abundance of 3 *Microtus* species in beaver colonies was higher than along non-beaver rivers. The presumable reason for that is the thicker herbaceous vegetation within the colonies. Beaver-inhabited rivers featured also a higher total abundance of all other small mammals (Suzuki and McComb 2004). In Idaho, the small mammal population density around beaver ponds was 2-3 times that of adjacent habitats (Medin and Clary 1991, after: Baker and Hill 2003). Trees felled but not fully utilized by beavers are also attractive for small rodents. In some colonies the bark from the trees felled by beavers in autumn and snow-covered in winter would have often been nearly totally gnawed away by small rodents by March – early April (D'yakov 1975). In our surveys, small mammals were captured from dry former beaver ponds where terrestrial vegetation was recovering, and from adjacent non-beaver sites. Supposedly, the small mammal abundance in those habitats depends on the vegetation succession sere in the abandoned colony, and on the type of the surrounding forest (or forest type in the "pre-beaver" period).

We have thus demonstrated that beaver activities form the floral, faunal and ecological diversity of riparian habitats and communities. The riparian forest communities are replaced by mire communities constituting a mosaic structure with different types of vegetation, water and nutrient supply, chemical and physical characteristics of the environment. Beaver engineering in Karelia leads to inundation of riparian areas, and gley peaty podzols (Histic Gleyic Podzols) replace gleyic podzols (Endogleyic Podzols) there (Sidorova and Fyodorov 2007). A distinct trend in the distribution of acidity, organic carbon and total nitrogen is observed in the flooded site: carbon and nitrogen concentrations grow, whereas acidity decreases somewhat towards the river bank. This impact leads to changes in the composition of the soil and terrestrial fauna. Thus, beavers are powerful ecosystem engineers and keystone species that can greatly alter biological and physical environments in boreal forests.

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ИЗМЕНЕНИЯ ПРИБРЕЖНЫХ ЭКОСИСТЕМ КАРЕЛИИ В РЕЗУЛЬТАТЕ ЖИЗНЕДЕЯТЕЛЬНОСТИ БОБРОВ

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Резюме

На водоемах южной Карелии проводилась оценка экологических последствий жизнедеятельности бобров. Изучали смену растительности в результате кормодобывающей и строительной деятельности животных; оценивали влияние многолетнего затопления леса на фауну беспозвоночных и мелких млекопитающих, пространственную вариабельность почв и их химические свойства. В результате трофической деятельности бобров из околоводного фитоценоза исключаются от 23,2 до 92,1% осины, 3,0 – 26,5% березы и почти все ивы. Строительство бобрами плотин ведет к формированию болотных сообществ, представляющих собой смешанные категории, в которые входят сфагновые, зарастающие березой, осоково-сфагновые, сфагново-пушицевые и различные кустарничково-сфагновые сообщества с преобладанием того или иного вида кустарничков. На месте брошенных бобровых прудов в почвах увеличивается содержание органического углерода и общего азота и понижается pH (Sidorova and Fyodorov 2007). В пределах спущенного пруда также существенно меняется численность и видовой состав фауны беспозвоночных и мелких млекопитающих. На бобровых водоёмах происходит увеличение количества беспозвоночных в 2 – 2,5 раза. Расширение фауны наземных беспозвоночных сопровождается увеличением видового и возрастного разнообразия. Численность *Micromammalia*, в одних наблюдениях, уменьшилась почти в 10 раз – с 7,0 экз. на контрольных участках до 0,67 экз. ловушко/суток на брошенных бобровых поселениях. В других – численность бурозубки и полёвок увеличилась в 2-2,5 раза.

Ключевые слова: бобры, роль в биоценозах, лесная растительность, сообщества, беспозвоночные, мелкие млекопитающие, почвы, растительность