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Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity

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ABSTRACT

1. Wetlands are rich in biodiversity, but globally threatened. After a long period of regional extirpation, beavers have recently returned to many European areas and are now restoring wetlands. The beaver is remarkable regarding the large impacts it has not only on individual species but on entire communities and ecosystems. In fact, beavers are referred to as 'ecosystem engineers'.

2. The facilitative effect of the beaver *Castor canadensis* on a waterbird community of seven species of waders and ducks in boreal ponds was studied by using the before–after control–impact method (BACI) and analysing the effect of the duration of flooding. The before–after setting could be used since beavers had caused disturbance by flooding several forest ponds during the course of this long-term study (1988–2009). The study took place in southern Finland, where waterbirds were surveyed four times during the breeding season.

3. The number of waterbird species per pond per year was significantly higher during beaver inundation than before beaver activity, as was the waterbird abundance per survey. Changes were negligible in the controls. The numbers of all seven species increased during flooding, although the increase was significant in only three species. Common teal *Anas crecca* and green sandpiper *Tringa ochropus* showed the most positive numerical response to flooding. Mallard *Anas platyrhynchos* and wigeon *Anas penelope* were new species entering the duck guild in the flooded wetlands. The beneficial effect of the flood lasted the whole period of inundation, although the most substantial increase in species number appeared during the first two years of flooding.

4. The beaver acted as a whole-community facilitator for waterbirds. It was inferred from previous studies that this was done by modifying the habitat to make it more productive and structurally favourable. It is concluded that favouring beavers is a worthwhile tool in restoring wetlands to promote waterbird communities.

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KEY WORDS: BACI; *Castor canadensis*; duck; keystone modifier; restoration; wader; waterbirds

INTRODUCTION

Wetlands are globally one of the most valuable resources per unit area, with the added value of harbouring especially high biodiversity (Hansson *et al*., 2005). Wetland destruction by humans started long ago and has accelerated in recent times (Gibbs, 2000; Amezaga *et al*., 2002). Apart from

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direct wetland destruction, climate warming (McMenamin *et al*., 2008) and over-exploitation of beavers (Naiman *et al*., 1988; Nolet and Rosell, 1998) have indirectly affected the amount and distribution of wetlands. Landscapes especially in Europe have been in an unnatural state having very few beaver-created wetlands. Recently beavers have dispersed and been re-introduced to their former range, and as a result have started to restore European wetlands (Sjöberg and Ball, 2011; Halley *et al*., 2012). In North America beavers had returned to most of their original range by the 1950s (Jenkins and Busher 1979). Beavers affect their environment in many ways, an important one being facilitation for other species (Nummi and Hahtola, 2008; Bartel *et al*., 2010).

During recent decades, more and more evidence has accumulated on the importance of positive interactions in natural communities (Hacker and Gaines, 1997; Stachowicz, 2001). These positive interactions include facilitation and mutualism (Stachowicz, 2001), and they may be mediated through, for instance, ecosystem engineering (Jones *et al*., 1994).

Facilitation takes place when one species has a beneficial effect on another species (van der Wal *et al*., 2000; Machicote *et al*., 2004). Sometimes a single species can have a substantial impact on a whole community, for example on higher plants (Bruno, 2000; Stachowicz, 2001). One such process is facilitation through habitat modification (Power *et al*., 1996), as many organisms modify the environment to make conditions more suitable for themselves. This habitat modification may facilitate other species by reducing environmental stress, by promoting resource renewal, or by modifying foraging substrates and habitat structure (Dickman, 1992; Bruno *et al*., 2003). Facilitation may operate through ecosystem engineering, which implies that the engineers control the 'availability of resources to other organisms by causing physical state changes in biotic or abiotic materials' (Jones *et al*., 1997). Ecosystem engineers that have a whole-community impact on other species have so far been described mostly among plants (Irlandi and Peterson, 1991), herbivores (Wright and Jones, 2004), and marine invertebrates (Bruno and Bertness, 2001), especially intertidal communities (Bertness and Leonard, 1997). There are only a few studies where a vertebrate species facilitates a whole community of other vertebrates. Some studies have been made on the effects of beavers and hippopotamuses on fish, but in these the possible increase in species number is usually seen at a stream level; at a patch or reach level the effect on species richness can be either positive or negative (Snodgrass and Meffe, 1998; Collen and Gibson, 2001; Mosepele *et al*., 2009). Apart from anecdotal reports – for instance, on alligators (Finlayson and Moser, 1991) – we know of only two studies in which a vertebrate species appeared to be beneficial for a whole community of others at a patch scale: beavers affecting amphibians (Dalbeck *et al*., 2007) and elephants affecting other herbivores (Valeix *et al*., 2011).

In general, ecosystem engineers are predicted to increase species richness if they increase the productivity of a low productivity patch or if they decrease the productivity of a high productivity patch (Wright and Jones, 2004, Figure 1). Ecosystem engineering by beavers leads to alteration in hydrology and riparian zone structure of ponds or streams, which then influences plant and animal community composition and diversity (Naiman *et al*., 1988; Bartel *et al*., 2010).

Beavers affect many animals, from invertebrates (McDowell and Naiman, 1986) to fish (Collen and Gibson, 2001), and from amphibians and reptiles

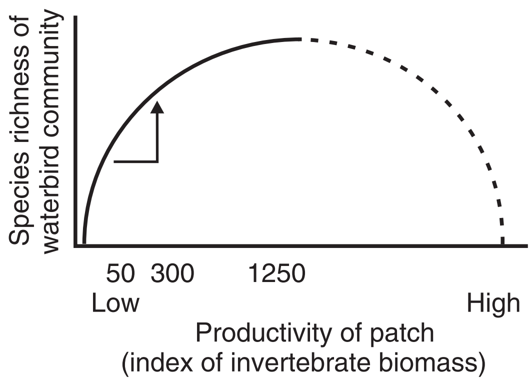

Figure 1. Conceptual model illustrating the effect of ecosystem engineering on species richness at the patch scale along a gradient of productivity, in this case expressed as an invertebrate biomass index. The focus of this study is on the low productivity end of the gradient (see Introduction). The model is modified from Wright and Jones (2004). Invertebrate abundance index 40 is an average of non-beaver ponds and value 280 is an average of beaver ponds in the Evo study area (Nummi and Hahtola, 2008), and as a reference, index 1250 is from eutrophic lakes in eastern Finland (Nummi and Väänänen, 2001).

(Metts *et al*., 2001) to birds and mammals (Aznar and Desrochers, 2008; Nummi *et al*., 2011). Some general descriptions have been made of bird communities in beaver ponds (Grover and Baldassarre, 1995; Brown *et al*., 1996; Edwards and Otis, 1999), and some investigations have compared bird diversity in active and abandoned beaver ponds with non-flooded wetlands (Longcore *et al*., 2006; Aznar and Desrochers, 2008). However, it is rarely possible to compare the same patches between 'before beaver' and 'during beaver' states (Nummi and Pöysä, 1997; Nummi and Hahtola, 2008).

The objective of this investigation was to study an assemblage of seven species of boreal waterbirds comprising ducks (four species) and waders (three species), all of which use invertebrates intensively as food during the breeding season (Batt *et al*., 1992; Colwell, 2010). These duck and wader species constitute the whole community of invertebrate-consuming waterbirds of the study area. An earlier study of three *Anas* species found some indication of increases in species number (Nummi and Pöysä, 1997), and single species, especially the common teal *Anas crecca*, are known to benefit rapidly from beaver inundation (Nummi and Hahtola, 2008).

Previous studies have shown that beaver flooding increases the invertebrate production of boreal wetland patches (Longcore *et al*., 2006; Nummi and Hahtola, 2008). Thus, the above-mentioned model of ecosystem engineering by Wright and Jones (2004) predicted that in an area with limited food, the resource amelioration in beaver ponds will lead to an increased number of invertebrate-eating waterbird species, i.e. to facilitation of the whole community (Figure 1); and, that the greatest difference can be found between the non-flooded situation and the beginning of the flood.

MATERIALS AND METHODS

Site description

The Evo study area consists of a system of 51 lakes and ponds in a 39 km^2 boreal catchment in southern Finland (61°12'N, 25°07'E). All lakes and small ponds within the area containing water throughout the summer were included. The shore types of the lakes range from oligotrophic bog and forest without emergent plants in the water to more eutrophic types with lush stands of *Equisetum fluviatile* and *Typha* spp. Apart from beaver disturbance, the water conditions have only minor year-to-year variation (Nummi and Pöysä, 1993). The boreal study area contains oligotrophic waters in which ducks face resource limitation, i.e. lack of invertebrate food, and which therefore harbour very few duck broods (Sjöberg *et al*., 2000; Gunnarsson *et al*., 2004). The waders are assumed to be in the same situation since aquatic invertebrates also form an integral part of their diet (Colwell, 2010).

The beaver species in the area is the introduced North American beaver (*Castor canadensis* Kuhl.). As has happened in many countries, the European beaver (*Castor fiber* L.) was extirpated from Finland in 1868. When re-introducing the beaver in the 1930s, North American beavers were also brought in, and they now occupy wider areas in Finland (Parker *et al*. 2012). According to recent findings by Danilov *et al*. (2011), both beaver species play a similar ecological role along the waterways; both species have, for example, similar construction activities such as dam building. Thus, they should also affect other species similarly. Beaver ponds in the area are usually formed by a dam built at the outlet of a natural pond.

Waterbird surveys

As part of a long-term population ecology project (Nummi and Pöysä, 1993; Suhonen *et al*., 2011), all four duck species (dabbling ducks: common teal (hereafter 'teal'), mallard (*Anas platyrhynchos* L.), wigeon (*Anas. penelope* L.), and a diving duck: common goldeneye (hereafter 'goldeneye', (*Bucephala clangula* L.)), as well as the three waders (green sandpiper (*Tringa ochropus* L.), common sandpiper (*Actitis hypoleuca* L.), and common snipe (*Gallinago gallinago* L.)) consistently breeding in the area were surveyed from 1988 to 2009. This study took into account four surveys that were relevant for all the species: in early May, early June, late June, and early July all the species are present either as pairs or broods. In 2009, when only two brood surveys were made, only one survey was made in June; in 1988 the early May data were not available, and the mid-July data were included instead. During each survey, a point count was first conducted from the shore and after that a round count was carried out in which the lake was circled by foot or boat (Nummi and Pöysä, 1993). The method was chosen based on the lake size and shoreline structure, i.e. visibility to the lake was optimized (e.g. large lake areas can be viewed better from a boat, whereas in small lakes good views can be obtained also from the shore). In the most densely vegetated beaver ponds all three methods (point count, circling by foot, and boat) were combined to provide visibility of the whole pond area.

Before–after setting created by beavers

Beaver activity formed a natural experiment-like setting, where 'before beaver flood' and 'during beaver flood' situations could be compared and a before–after control–impact assessment (BACI) conducted (Stewart-Oaten *et al.*, 1986; Smith, 2002). The aim was to assess whether or not beaver affects the waterbird community and estimate the magnitude of the beaver effect (Smith, 2002). The duration of the effect was analysed separately and concerned only the flooded lakes.

During the 22 study years, 18 ponds out of the 51 were dammed by the beaver, and 14 of them provided valid before–after data. Some ponds were flooded several times, but only the first flood of the study period was taken into account in this analysis. The averages of bird numbers and number of species per pond over a period of two years before beaver occupation were compared with the corresponding numbers during the first two years of beaver inundation. Two years were chosen for this approach because most of the beaver ponds were flooded for at least that period. In a few cases, data from only one 'before' or 'during' year were available. Therefore the results are expressed as number of species per pond per year, and number (i.e. abundance) of birds of different species per pond per survey. For ducks one observation equals one indicated pair or one brood, and for waders one observation equals one indicated pair or warning individual later in the season (no chicks observed).

One control pond of a similar habitat was established for each of the 14 beaver ponds, which brings the number of ponds used in this BACI study to 28. After choosing one control pond for every beaver-flooded pond, changes in bird numbers in each of the control ponds were studied using exactly the same years that were used in the appropriate beaver ponds. The controls were the nearest neighbours of the beaver ponds in a habitat description gradient made in earlier studies (Nummi and Pöysä, 1997, Suhonen *et al.*, 2011). The gradient was defined by a principal component analysis (PCA) based on habitat descriptions (size, depth and vegetation) of all the water bodies in the area ($n = 51$). Habitat descriptions were made for two years, 1989 and 2009 (Suhonen *et al.*, 2011). Hence, two gradient values existed for every pond. For this analysis the average of these values was used to describe the ponds, but if a pond was dammed in either of the years, only the value from the year without flood was used. This was because of the control–impact setting: control ponds were not allowed to be flooded during the time they acted as control ponds; therefore the gradient values of the control ponds were from their basic, non-flooded state. Beaver flooding increases the productivity of the lake, which in turn is seen as an increase in the gradient value (Suhonen *et al.*, 2011). The pond sizes of the study varied between 0.3 and 37.1 ha. Mean size difference between beaver ponds and their controls was 5.4 ha (ranging from -1.6 ha to 30.6 ha, where negative values indicate that the beaver pond is larger than its control, and vice versa).

The development over time of waterbird species in all of the 18 beaver-flooded ponds was also studied. For that purpose the yearly flood situation of every pond between 1988 and 2008 was categorized: (0) no beaver flood, (1) first and second year flood, (2) third and fourth year flood, and (3) fifth year or older flood. The year 2009 was dropped from the analysis, because unlike in the BACI analysis, the uneven number of counting rounds might have biased the results. Category 1 is based on earlier results, which show that the first two years represent the largest increase in the number of invertebrates (emerging insects and aquatic invertebrates; Nummi, 1992). The length of the second flood category is artificial, and was assigned to be of equal length to the first one, i.e. two years. The mean occupation time of a beaver colony site at Evo has been found to be 2.6 years (Hyvönen and Nummi, 2008), which shows that usually the intensive beaver-affected time is short. Because of the small sample size, the rest of the years were placed in category 3: only four ponds were flooded for five or more years. The average age of the flood in category 3 was 12 years.

Statistical analyses

In the BACI analysis the changes in abundance of birds in different species and number of species were both analysed by comparing the data from ponds before and during beaver occupation. Flooded ponds constituted one group and their control ponds another group in an analysis using the Wilcoxon matched pairs signed ranks test for related samples. In addition, the species-specific waterbird abundances in the beaver ponds were also analysed with the Wilcoxon test for related samples. Analyses were made with PASW Statistics 18 (SPSS Inc, 2009).

The effect of the duration of the flood was analysed with generalized linear mixed modeling (Bolker *et al.*, 2009, Zuur *et al.*, 2009) by using the nlme library (Pinheiro *et al.*, 2013) in R 3.0.0 (R Development Core Team, 2013). Yearly number of species in all of the 18 flooded lakes was explained by the flood duration classification. The data have a nested structure, and data exploration (Zuur *et al.*, 2009) exposed a strong lake effect, but a rather weak year effect. A random part was therefore included in the model, and different random effect scenarios were fitted. The scenarios were: (1) an ordinary linear regression model refitted using the gls function without random intercept; (2) a categorical random factor for the lake effect, and (3) a random intercept and slope model for the year effect (a continuous covariate) per lake (a categorical variable). The comparison of AICs of these three scenarios was made with the Anova function. Based on the AICs scenario (2) was the best fit. Because data exploration also exposed different variances between the flood duration categories, the random part of the preferred model (2) was extended by another scenario: (4) different variances per flood duration category (the VarIdent variance structure function). This extension gave no improvement based on the AIC values, and therefore scenario (2) was used in the analysis. The model of the flood duration effect on the species number is as follows:

$$\text{Species\_number}_{ij} = \alpha + \beta \times \text{Flood\_category}_{ij} + a_i + \varepsilon_{ij} \quad (1)$$

where species_number$_{ij}$ is the number of waterbird species in lake i in year j, where i = 1, . . . 18, and j = 1988, . . . , 2008. α is the intercept and β the coefficient of the flood category. The term a_i is the random effect that indicates the between-lake variation and is assumed to be normally distributed with mean 0 and variance σ_a^2. Term ε_{ij} is the unexplained error and represents the within-lake variation. It is assumed to be normally distributed with mean 0 and variance σ^2.

RESULTS

The BACI analysis showed that the mean number of waterbird species per pond was higher during beaver flooding than before beaver occurrence (average 1.48 vs. 0.43 species per pond per year; Figure 2(A), $N = 12$ (lake pairs with the same result were omitted), $W = 0$, SE = 12.67, $P = 0.002$, Wilcoxon matched pairs signed ranks test), as was their abundance per survey (0.80 vs. 0.14 observations per pond per survey, Figure 3(A) and 3(B), $N = 13$, $W = 1$, SE = 14.31, $P = 0.002$). No change was found in the control ponds in either the number of waterbird species (0.70 vs. 0.54, Figure 2(B), $N = 11$, $W = 27$, SE = 11.18, $P = 0.592$) or the number of observations (0.30 vs. 0.20, $N = 11$, $W = 21$, SE = 11.24, $P = 0.286$).

All seven species of the study seemed to increase during flooding. Teal and green sandpiper showed numerically the most positive response to beaver flooding, but mallard and wigeon were totally new species entering the duck guild in the beaver-affected wetland patches (Figure 3(A) and 3(B)). The increases in the number of teals, green sandpipers and mallards were significant (Table 1). However, wigeon, common sandpiper and common

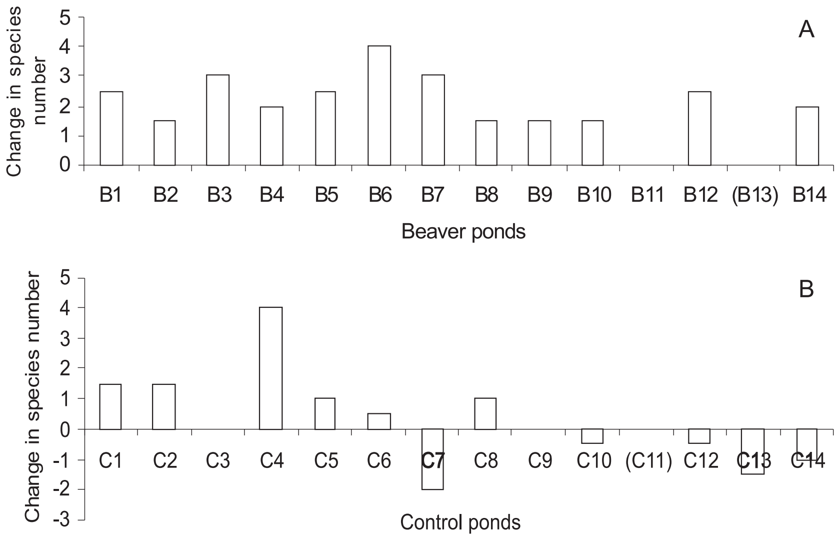

Figure 2. Change in the number of waterbird species in 14 beaver ponds (A) and in their 14 control ponds (B), expressed as number of species per year during the first two beaver occupancy years minus number of species per year during the two years before occupancy. Positive bars indicate an increase in the number of species, and negative bars a decrease. In ponds where flooding lasted for two years, the results are averages for those years and for the two years before the flood. Parentheses around the ponds indicate situations where there were no waterbird observations before or during the flood.

snipe were observed only rarely and therefore their results are uncertain.

The flood duration analysis showed that the number of waterbird species already increased during the first two years of inundation (Table 2, Figure 4). Moreover, it showed that this increase continued during the next phases, even though category 2 (third and fourth year flood) showed large variation. All the categories of flooding (1–3) differed significantly from the non-flooded category which was the baseline (category 0, Table 2), indicating that the number of waterbird species in the ponds was higher during the flooded years than in the non-flooded years, and that the duration of the flood did not change the basic pattern (Table 2).

DISCUSSION

This study showed that the disturbance caused by beavers led to increased abundance and richness of a waterbird community within a wetland patch; this was predicted in a model by Wright and Jones (2004) for ecosystem engineering that increases productivity in low productivity areas (Figure 1). In the case of ecosystem engineering by beavers the previous community is disturbed, and considerable amounts of nutrients are released for the use of invertebrates, which then serve as food for bird species of the newly formed species assemblage (Naiman *et al.*, 1988; Nummi, 1989; Wright *et al.*, 2002). The increase in waterbird diversity is linked to the general relationship between species number and productivity. At low productivity, species richness is limited by stress and resource availability, and resource amelioration should increase species richness (Roxburgh *et al.*, 2004).

From the invertebrate-eating waterbird perspective, the beaver acted as a 'whole-community' facilitator, modifying local conditions to create a more favourable environment (for plants, see Bruno, 2000; Stachowicz, 2001). This facilitation led to a higher abundance in this group of seven waterbird species: all seemed to benefit from beaver although in only three species was the increase significant. In the one previous study showing that beaver was beneficial for a whole community of other species, the European beaver facilitated amphibians in central Europe (Dalbeck *et al.*, 2007). Since that study did not measure species abundances, the only result was that all species of the area were present in beaver ponds, and some only in those ponds. In the before–after investigation of the 14 beaver ponds in this study, teal and green sandpiper showed the most positive numerical response to beaver flooding. However, mallard and wigeon were interesting in that they were totally new species

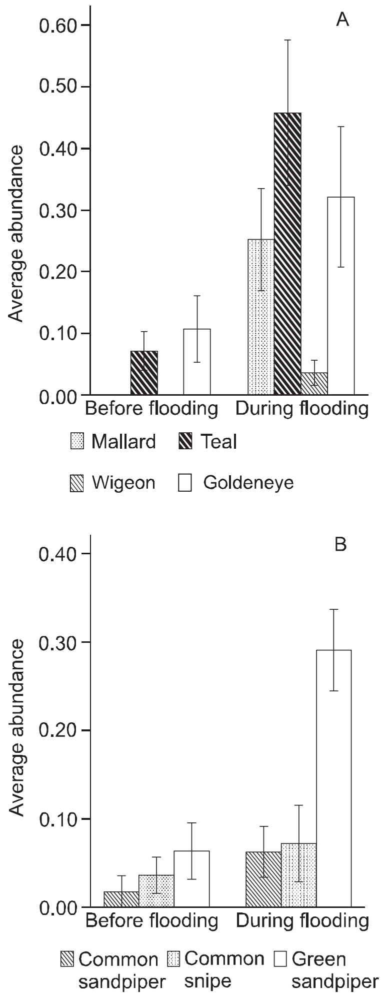

Figure 3. Average abundance of (A) ducks and (B) waders per survey for 14 beaver ponds before and during beaver occupancy. Error bars represent ± SE.

Table 1. Test statistics for the change of the abundance of different waterbird species in the 14 beaver ponds from before the flood to flood. Wilcoxon matched pairs signed ranks tests was used. *N* represents that number of lake pairs that had a different number of birds, *W* is the Wilcoxon test statistic, SE is standard error and *P* value is statistical significance

Species	*N*	*W*	SE	*P*
Mallard	7	0	5.91	0.018
Teal	12	4.5	12.70	0.007
Wigeon	3	0	1.84	0.102
Goldeneye	9	10.5	8.28	0.103
Common sandpiper	4	1.5	2.69	0.194
Common snipe	3	0	1.84	0.102
Green sandpiper	13	4	14.15	0.003

Table 2. Estimated parameters of the effect of flood duration on the number of waterbird species. Flood categories are nominal variables and represent: 0 – no beaver flood (intercept); 1 – first and second year flood; 2 – third and fourth year flood; and 3 – fifth year or older flood. The random effect a_i representing the between-lake variation is $N(0, 1.08^2)$

	Value	SE	*t*-value	*P*
Intercept	2.01	0.26	7.61	$P < 0.001$
Flood category 1	0.97	0.17	5.59	$P < 0.001$
Flood category 2	1.32	0.37	3.59	$P < 0.001$
Flood category 3	1.51	0.34	4.49	$P < 0.001$

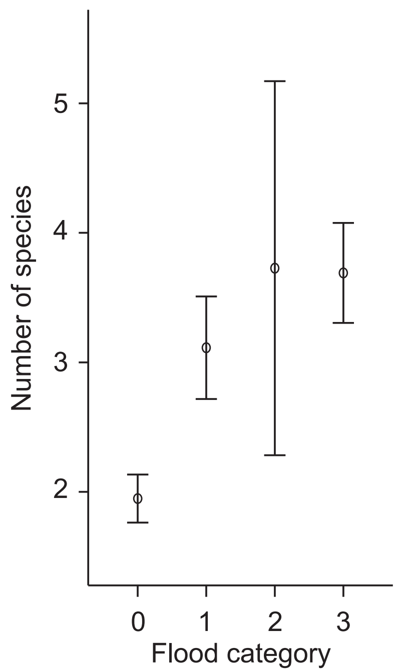

Figure 4. The effect of duration of the beaver flood on the annual number of waterbird species at 18 beaver ponds during the study period of 20 years. Categories represent: 0 – years with no beaver flood (N = 272); 1 – first and second year flood (N = 53); 3 – third and fourth year flood (N = 11); and 4 – fifth year or older flood (N = 42) in those 18 lakes that were flooded at some point. Circles indicate the mean and whiskers 95% confidence intervals.

entering the duck guild in the 14 beaver-affected wetland patches. They are not new species for the area, but are usually found at the more eutrophic end of the gradient of lakes in the area; this finding is especially true for wigeon (Nummi and Pöysä, 1993). Within the boreal ponds of the study area, the frog *Rana arvalis* was present only in beaver ponds (Vehkaoja and Nummi, unpublished data). Beaver flooding typically increased lake vegetation richness in the area, and elevated the position of the flooded lake in the habitat gradient (Suhonen *et al.*, 2011).

In general, the composition of the regional species pool is likely to have a large effect on the composition and richness of modified patches (Wright and Jones, 2004). In some studies in North America, 15 species of waterbirds, and eight waterfowl species alone, have been found in beaver-influenced waters (Beard, 1953; Longcore *et al.*, 2006). In this study, all seven species of the regional species pool were present also in the beaver pond species pool.

When the goal of an ecological study is to determine the factors restricting the distribution of a species, identifying the limiting life history stage is often crucial (Bruno, 2000). In this study, distribution of birds was observed at the local/patch scale at a critical stage of a species' life cycle, the breeding period. In this boreal setting, the patterns at patch scale may be observed also at a landscape level; for example, for teal the landscape-level brood production is concentrated on the beaver ponds (Nummi and Pöysä, 1995; Suhonen *et al.*, 2011). It is likely that the duckling or chick stage limits the occurrence of waterbirds in boreal wetlands, as suggested by the higher survival of teal broods in beaver ponds (Nummi and Hahtola, 2008) and the increased survival of mallard ducklings in boreal ponds where food was added (Gunnarsson *et al.*, 2004). Experimental studies strongly suggest that duck broods are resource limited in boreal lakes (Nummi *et al.*, 2000; Sjöberg *et al.*, 2000), and growth of wader chicks has also been linked to the high invertebrate abundance along the edges of wet features (Eglington *et al.*, 2010). The increase of invertebrate food in beaver ponds is probably an important factor in the increase of all the species in the study. In the study area, the invertebrate abundance index in beaver ponds is about seven-fold compared with that of non-beaver ponds (280 vs. 40, Nummi and Hahtola, 2008, see also Figure 1). Most of the species certainly benefited, too, from the change in habitat structure, i.e. from the increase of shallow water in beaver ponds, which ameliorates foraging possibilities for birds (Beard, 1953; Longcore *et al.*, 2006). In the study area the average water depth measured from the shore is 23 cm in beaver ponds and 64 cm in non-beaver ponds (Nummi and Hahtola, 2008). Thus, with reference to the conceptual model of facilitation by Bruno *et al.* (2003), we think that at least resource enhancement and habitat amelioration took place when beavers modified waterbird habitats.

Wright and Jones (2004) stated that their engineering model would be more likely to give successful predictions of species richness if the resources modified by an ecosystem engineer had similar effects on the species comprising the assemblage studied, e.g. the effect on birds of an invertebrate increase. Of the species studied here, teal and green sandpiper could be seen as disturbance species that readily colonize newly formed beaver ponds (Nummi and Pöysä, 1997). For teal this has been closely linked to its diet, which includes cladocerans, the first invertebrates to bloom in the ponds (Nummi, 1993). Likewise, mallard is found in high densities in flooded temporal and seasonal wetlands of North American prairies (Kantrud and Stewart, 1977). Goldeneye adults and older ducklings, on the other hand, typically thrive in stable ponds and dive for their food (Cramp *et al.*, 1986); their numbers, too, were found to increase upon flooding. Studies also show that invertebrate density increases in the deeper parts of beaver ponds after flooding (Nummi, 1989).

There is little information on habitat use and diet in the breeding grounds of the waders in this study, but they are known to use a wide variety of aquatic and terrestrial insects, including chironomids, which are numerous in beaver ponds (Nummi, 1989). Waders forage in shallow water (Isola *et al.*, 2000; Eske Holm and Clausen, 2006), and probably benefit, as mallards do, from drowning terrestrial invertebrates in the early phases of flooding (Swanson *et al.*, 1985). The shallow shores of beaver ponds in the study area provided the waders as well as duck broods with a more suitable foraging habitat than that of more than 60 cm in undisturbed lakes (Isola *et al.*, 2000; Nummi and Hahtola, 2008). On wintering grounds, waders usually feed in water less than 20 cm deep (Rehfisch, 1994). Common snipe prefers open marsh habitat (Cramp *et al.*, 1985), which was not present in most of the beaver ponds in this study; that is probably why, unlike in North America (Longcore *et al.*, 2006), the increase of this species after beaver flooding was not more distinctive.

From the viewpoint of biodiversity management it is interesting that the number of waterbird species still increased after the two first years of flooding. After three to four years of flooding, diversity remained more or less at the same relatively high level. This pattern is rather different from that found in some other groups: the diversity of herbaceous plants is highest in ponds 11 to 40 years old (Ray *et al*., 2001), and that of fishes in ponds 9 to 17 years old (Snodgrass and Meffe, 1998). For invertebrate-eating waterbirds beaver-flooded ponds offer beneficial circumstances (i.e. abundant food), and as mobile animals birds find them quickly (Nummi and Pöysä, 1997). There were only seven species of invertebrate-eating waterbird species in this study, all of which found the beaver ponds relatively quickly. Community-level benefit is then maintained for the whole period of flooding, at least when flooding is brief as it often is in the Evo study area.

Wetlands and their associated species, such as amphibians and bats, have been in drastic decline (Amezaga *et al*., 2002), even in protected areas (McMenamin *et al*., 2008). This is true also for waders (Colwell, 2010). It is therefore worthwhile considering the promotion of beavers in wetland restoration and to reintroduce them to areas where they have been extirpated in the past (Nolet and Rosell, 1998; Jones *et al*., 2009). Much of wetland management has been motivated by an interest in improving the habitats of hunted waterfowl (Colwell, 2010), but for conservation it is essential that apart from waterfowl beavers also benefit waders. When considering beavers as restoration agents it is important to notice that patch modification by beaver is less stochastic compared with abiotic disturbances. When beavers are present, new ponds are created from time to time, the rate depending on the population dynamics of the animal (Johnston, 1995; Wright *et al*., 2004; Nummi and Kuuluvainen, 2013). It should be noted, however, that when large predators are absent beaver densities might become too high to benefit biodiversity (Ritchie *et al*., 2012).

In conclusion, the findings of this study emphasize the key role of beavers in facilitating individual waterbird species and waterbird communities in boreal wetlands. In habitat conservation and restoration, it is sometimes wise to identify probable keystone species or ecosystem engineers and focus on their management (Ebenman and Jonsson, 2005; Byers *et al*., 2006). In areas where beavers are difficult to manage it is feasible to imitate their flooding with man-made actions, as has been done in many restoration and conservation programmes (Danell and Sjöberg, 1982; Chovanev, 1994; Mazerolle *et al*., 2006; Eglington *et al*., 2010). However, man-made wetlands are more costly to manage than dam-building beavers (Brown and Parsons, 1979).

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REFERENCES

Amezaga JM, Santamaria L, Green AJ. 2002. Biotic wetland connectivity – supporting a new approach for wetland policy. *Acta Oecologia* **23**: 213–222.

Aznar J, Desrochers A. 2008. Building for the future: abandoned beaver ponds promote bird diversity. *Ecoscience* **15**: 250–257.

Bartel RA, Haddad NM, Wright JP. 2010. Ecosystem engineers maintain a rare species of butterfly and increase plant diversity. *Oikos* **119**: 883–890.

Batt BDJ, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds). 1992. *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press: Minneapolis.

Beard EB. 1953. The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. *Journal of Wildlife Management* **17**: 398–436.

Bertness MD, Leonard GH. 1997. The role of positive interactions in communities: lessons from intertidal environments. *Ecology* **78**: 1976–1989.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHS, White J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* **24**: 127–135.

Brown MK, Parsons GR. 1979. Waterfowl production on beaver flowages in a part of New York. *New York Fish and Game Journal* **26**: 142–153.

Brown DJ, Hubert WA, Anderson SA. 1996. Beaver ponds create wetland habitat for birds in mountains of southeastern Wyoming. *Wetlands* **16**: 127–133.

Bruno JF. 2000. Whole-community facilitation through substrate stabilization by the intertidal grass *Spartina alterniflora*. *Ecology* **81**: 1179–1192.

Bruno JF, Bertness MD. 2001. Habitat modification and facilitation in benthic marine communities. In *Marine Community Ecology*, Bertness MD, Gaines SD, Hay ME (eds). Sinauer Associates: Sunderland, MA; 201–218.

Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**: 119–125.

Byers JE, Cuddington K, Jones CG, Talley TS, Hastings A, Lambrinos JG, Crooks JA, Wilson WG. 2006. Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution* **21**: 493–500.

Chovanev A. 1994. Man-made wetlands in urban recreational areas – a habitat for endangered species. *Landscape and Urban Planning* **29**: 43–54.

Collen P, Gibson RJ. 2001. The general ecology of beavers (*Castor* spp) as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. *Reviews in Fish Biology and Fisheries* **10**: 439–461.

Colwell MA. 2010. *Shorebird Ecology, Conservation, and Management*. University of California Press: Berkeley, Los Angeles, London.

Cramp S, Simmons KEL, Ferguson-Lees IJ, Gilmore R. 1985. *Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Vol 3 Waders to Gulls*. Oxford University Press: Oxford; 409–605.

Cramp S, Simmons KEL, Ferguson-Lees IJ, Gilmore R. 1986. *Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Vol 1 Ostrich to Ducks*. Oxford University Press: Oxford; 471–665.

Dalbeck L, Lüsher B, Ohlhoff D. 2007. Beaver ponds as habitats of amphibian communities in a central European highland. *Amphibia–Reptilia* **28**: 493–501.

Danell K, Sjöberg K. 1982. Successional patterns of plants, invertebrates and ducks in a man-made lake. *Journal of Applied Ecology* **19**: 395–409.

Danilov P, Kanshiev V, Fyodorov F. 2011. Characteristics of North American and Eurasian beaver ecology in Karelia. In *Restoring the European Beaver: 50 Years of Experience*, Sjöberg G, Ball JP (eds). Pensoft Publishers: Sofia; 55–72.

Dickman CR. 1992. Commensal and mutualistic interactions among terrestrial vertebrates. *Trends in Ecology and Evolution* **7**: 194–197.

Ebenman B, Jonsson T. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution* **20**: 568–575.

Edwards NT, Otis DL. 1999. Avian communities and habitat relationships in South Carolina Piedmont beaver ponds. *American Midland Naturalist* **141**: 158–171.

Eglington SM, Bolton M, Smart MA, Sutherland WJ, Watkinson AR, Gill JA. 2010. Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology* **47**: 451–458.

Eske Holm T, Clausen P. 2006. Effects of water level management on autumn staging waterbird and macrophyte diversity in three Danish coastal lagoons. *Biodiversity and Conservation* **15**: 4399–4423.

Finlayson M, Moser M (eds). 1991. *Wetlands Facts on File*. Waterfowl and Wetlands Research Bureau: Oxford.

Gibbs JP. 2000. Wetland loss and biodiversity conservation. *Conservation Biology* **14**: 314–317.

Grover AM, Baldassarre GA. 1995. Bird species richness within beaver ponds in South-central New York. *Wetlands* **15**: 108–118.

Gunnarsson G, Elmberg J, Sjöberg K, Pöysä H, Nummi P. 2004. Why are there so many empty lakes? Food limits survival of mallard ducklings. *Canadian Journal of Zoology* **82**:1698–1703.

Hacker SD, Gaines SD. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* **78**: 1990–2003.

Halley D, Rosell F, Saveljev A. 2012. Population and distribution of Eurasian beaver (*Castor fiber*). *Baltic Forestry* **18**: 168–175.

Hansson L-A, Brönmark C, Nilsson A, Åbjörnsson K. 2005. Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both? *Freshwater Biology* **50**: 705–714.

Hyvönen T, Nummi P. 2008. Habitat dynamics of beaver *Castor canadensis* at two spatial scales. *Wildlife Biology* **14**: 302–308.

Irlandi EA, Peterson CH. 1991. Modification of an animal by large plants: mechanisms by which seagrasses influence clam growth. *Oecologia* **87**: 307–318.

Isola CR, Colwell MA, Taft OW, Safran RJ. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. *Waterbirds* **23**: 196–203.

Jenkins SH, Busher PE. 1979. *Castor canadensis. Mammalian Species 120: 1–8.*

Johnston CA. 1995. Effects of animals on landscape patterns. In *Mosaic Landscapes and Ecological Processes*, Hansson L, Fahrig L, Merriam G (eds). Chapman and Hall: London; 57–80.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.

Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946–1957.

Jones K, Gilvear D, Willby N, Gaywood M. 2009. Willow (*Salix* spp.) and aspen (*Populus tremula*) regrowth after felling by the Eurasian beaver (*Castor fiber*): implications for riparian woodland conservation in Scotland. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 75–87.

Kantrud HA, Stewart RE. 1977. Use of natural basin wetlands by breeding waterfowl in North Dakota. *Journal of Wildlife Management* **41**: 243–253.

Longcore JR, McAuley DG, Pendelton GW, Bennatti CR, Mingo TM, Stromborg KL. 2006. Macroinvertebrate abundance, water chemistry, and wetland characteristics

affect use of wetlands by avian species in Maine. *Hydrobiologia* **567**:143–167.
Machicote ML, Branch C, Villareal D. 2004. Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* **106**: 527–535.
Mazerolle MJ, Poulin M, Lavoie C, Rochefort L, Desrochers A, Drolet B. 2006. Animal and vegetation patterns in natural and man-made bog pools: implications for restoration. *Freshwater Biology* **51**: 333–350.
McDowell DM, Naiman RJ. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* **68**: 481–489.
McMenamin SK, Hadly EA, Wright CK. 2008. Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *PNAS* **105**: 16988–16993.
Metts BS, Lanham JD, Russell KR. 2001. Evaluation of herpetofaunal communities on upland streams and beaver-impounded streams in the upper piedmont of South Carolina. *American Midland Naturalist* **145**: 54–65.
Mosepele K, Moyle PB, Merron GS, Purkey DR, Mosepele B. 2009. Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. *BioScience* **59**: 53–64.
Naiman RJ, Johnston CA, Kelley JC. 1988. Alteration of North American streams by beaver. *BioScience* **38**: 753–762.
Nolet B, Rosell F. 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biological Conservation* **83**: 165–173.
Nummi P. 1989. Simulated effects of the beaver on vegetation, invertebrates and ducks *Annales Zoologici Fennici* **26**: 43–52.
Nummi P. 1992. The importance of beaver ponds to waterfowl broods: an experiment and natural tests. *Annales Zoologici Fennici* **29**: 47–55.
Nummi P. 1993. Food niche relationships of sympatric mallard and green-winged teal. *Canadian Journal of Zoology* **71**: 49–55.
Nummi P, Pöysä H. 1993. Habitat associations of ducks during different phases of the breeding season. *Ecography* **16**: 319–328.
Nummi P, Pöysä H. 1995. Habitat use by different-aged duck broods and juvenile ducks. *Wildlife Biology* **1**: 181–187.
Nummi P, Pöysä H. 1997. Population and community level responses in *Anas*-species to patch disturbance caused by an ecosystem engineer, the beaver. *Ecography* **20**: 580–584.
Nummi P, Väänänen V-M. 2001. High overlap in diets of sympatric dabbling ducks – an effect of food abundance? *Annales Zoologici Fennici* **38**: 123–130.
Nummi P, Hahtola A. 2008. The beaver as an ecosystem engineer facilitates teal breeding. *Ecography* **31**: 519–524.
Nummi P, Kuuluvainen T. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. *Boreal Environmental Research* **18** (suppl A): 13–24.
Nummi P, Sjöberg K, Pöysä H, Elmberg J. 2000. Individual foraging behaviour indicates resource limitation: an experiment with mallard ducklings. *Canadian Journal of Zoology* **78**: 1891–1895.
Nummi P, Kattainen S, Ulander P, Hahtola A. 2011. Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. *Biodiversity and Conservation* **20**: 851–859.
Parker H, Nummi P, Hartman G, Rosell F. 2012. Invasive North American beaver *Castor canadensis* in Eurasia: a review of potential consequences and strategy for eradication. *Wildlife Biology* **18**: 354–365.
Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-111.
Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. *BioScience* **46**: 609–620.
R Development Core Team. 2013. *A language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna.
Ray AM, Rebertus AJ, Ray HL. 2001. Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany* **79**: 487–499.
Rehfisch MM. 1994. Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. *Journal of Applied Ecology* **31**: 383–401.
Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA. 2012. Ecosystem restoration with teeth: what role for predators? *Trends in Ecology and Evolution* **27**: 265–271.
Roxburgh SH, Shea K, Wilson JB. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* **85**: 359–371.
Sjöberg G, Ball JP (eds). 2011. *Restoring the European Beaver: 50 Years of Experience*. Pensoft Publishers: Sofia.
Sjöberg K, Pöysä H, Elmberg J, Nummi P. 2000. Response of mallard ducklings to variation in habitat quality: an experiment of food limitation. *Ecology* **81**: 329–335.
Smith EP. 2002. *BACI Design in Encyclopedia of Environmetrics Vol 1*. John Wiley: Chichester; 141–148.
Snodgrass JW, Meffe GK. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology* **79**: 928–942.
SPSS Inc. 2009. PASW Statistics for Windows, Version 18.0. Chicago.
Stachowicz JJ. 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience* **51**: 235–246.
Stewart-Oaten A, Murdoch WW, Parker KR. 1986. Environmental impact assessment: pseudoreplication in time? *Ecology* **67**: 929–940.
Suhonen S, Nummi P, Pöysä H. 2011. Long term stability of habitats and their use by ducks in boreal lakes. *Boreal Environmental Research* **16**(suppl B): 71–80.
Swanson GA, Meyer MI, Adomatis VA 1985. Foods consumed by breeding mallards on wetlands of south-central North Dakota. *Journal of Wildlife Management* **49**: 197–203.
Valeix, M, Fritz, H, Sabatier, R, Murindagomo F, Cumming, D, Duncan, P. 2011. Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation* **144**: 902–912.
van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D. 2000. On facilitation between herbivores: how brent geese profit from brown hares. *Ecology* **81**: 969–980.
Wright JP, Jones CG. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**: 2071–2081.
Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**: 96–101.
Wright JP, Gurney WSC, Jones CG. 2004. Patch dynamics in a landscape modified by ecosystem engineers. *Oikos* **105**: 336–348.
Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed Effects Models and Extension in Ecology with R*. Springer Science + Business Media: New York