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Beaver facilitation in the conservation of boreal anuran communities
(Anura: Bufonidae, Ranidae)

Die Förderung des Bibers und die Erhaltung der borealen Anurengemeinschaften
(Anura: Bufonidae, Ranidae)

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KURZFASSUNG

Artensterben und Habitatverlust verlaufen in Europa und weltweit rasant. Amphibien und Feuchtlebensräume sind ganz wesentlich davon betroffen. Letztere warden in der borealen Zone häufig durch die Dammbau-Tätigkeit des Bibers (*Castor* sp.) bereitgestellt. Die Autoren untersuchten die Anurenfauna in zehn derartigen Biber-Gewässern, zehn nicht vom Biber bewohnten und acht temporären Wasserkörpern in Finland. Alle drei in der Region heimischen Anurenarten (Erdkröte, Moor- und Grasfrosch) besiedelten die Biber-Gewässer, wobei der Moorfrosch in nicht vom Biber bewohnten und temporären Gewässern des Gebietes nicht gefunden wurde. Moorfrösche profitierten offensichtlich vom Teichbaua und dem Fällen von Bäumen durch den Biber und die damit verbundene Schaffung einer Vielzahl von seichten Gewässerabschnitten mit breiten emersen Vegetationsgürteln. Die Ergebnisse zeigen, daß Biber qualitative hochwertige Anurenhabitate schaffen und das Vorkommen des Moorfrosches begünstigen.. Es wird angeregt, Biber als Ingenieure bei der Wiederherstellung von Ökosystemen einzusetzen, um die Ziele des Amphibienschutzes zu unterstützen.

ABSTRACT

A rapid loss of species and habitats is occurring globally. Amphibians and wetlands are important components of this overall decline. Wetlands in the boreal region are frequently constructed by damming activities of an ecosystem engineer, the beaver (*Castor* sp.). The authors investigated the anuran fauna in ten such ‘beaver ponds’, ten ‘non-beaver ponds’ and eight temporary ponds in Finland. All three anuran species present in the region occupied the beaver ponds, including a species absent (the Moor Frog *Rana arvalis* NILSSON, 1842) in natural waters (non-beaver ponds and temporary ponds). Moor Frogs obviously benefitted from pond construction and removal of trees by beavers leading to a plenitude of shallow water and a wide belt of emergent vegetation. The results show that beavers offer high-quality habitats for anurans and facilitate the occurrence of Moor Frogs. It is suggested that these ecosystem engineers could be used in ecosystem restoration. The beaver clearly represents a species that promotes amphibian conservation.

KEY WORDS

Amphibia: Anura: Bufonidae, Ranidae; *Rana arvalis*, *Rana temporaria*, *Bufo bufo*, beaver, *Castor*, beaver pond, ecosystem engineer, draining, boreal amphibian community facilitation, ecology, conservation, Finland

INTRODUCTION

Species and habitat loss at a global scale is occurring at an increasing rate. Amphibians and wetlands compose a considerable proportion of this overall loss, even in areas not under immediate human influence (PETRANKA et al. 2004; GIBBONS et al. 2006; SAYIM et al. 2009; DODD 2010). Since the 1900s, approximately half of the world’s wetlands were destroyed (BARBER 1993), and during this time, at a regional scale, up to two-thirds of European wetlands became lost (AMEZAGA et al. 2002). The fact that 23 % of Europe’s amphibians are threatened reflects this trend (TEMPLE & COX 2009). Pond, wetland protection and restoration are the principle methods for conserving pond-breeding amphibians (STEVENS et al. 2007).

Boreal ecosystems are under considerable stress. The boreal climate is severe and often unpredictable (HANSKI et al. 1998), which creates additional challenges for wetland conservation. Furthermore, nearly 14 million hectares of wetlands have been drained for forestry in northern Europe

(Paavilainen & Päivänen 1995, Suislepp et al. 2011). Most of these wetlands are in the boreal zone. More than 5.5 million hectares of wetlands and forests have been drained in Finland alone (Peltomaa 2007). Ditches drain excess surface water which affects the natural quality and processes of aquatic ecosystems, resulting in reduced wetland diversity (Suislepp et al. 2011). Wetland loss reduces amphibian productivity and abundance via the number and density of breeding sites by changing the natural hydrological regime of an area (Suislepp et al. 2011).

The use of ecosystem engineers in ecosystem restoration has recently received increasing attention (Byers et al. 2006; Bartel et al. 2010). Beavers (*Castor* sp.) act as ecosystem engineers in the Northern Hemisphere (Jones et al. 1994; Wright et al. 2002), and both beaver species play a similar ecological role along the waterways (Danilov et al. 2011). They create and maintain special habitats by constructing dams (Baker & Hill 2003). Damming changes both abiotic and biotic conditions via hydrological changes, which can affect a large number of other species. Beaver modifications create wetland patches varying in successional stage, thereby increasing structural heterogeneity at the landscape scale (Naiman et al. 1988; Snodgrass 1997; Cunningham et al. 2006; Hyvönen & Nummi 2008). Riparian zones along water bodies are especially modified. Tree felling creates openings in the riparian forest, resulting in open and sunny ponds (Pastor & Naiman 1992; Krylov et al. 2007). Belts of emergent vegetation can be wide due to flooding (Nummi 1992), and submerged and floating vegetation dominates in older beaver ponds (Ray et al. 2001; Nummi & Kuuluvainen 2013). Detritivorous invertebrates, e.g., chironomids and *Asellus* are the most abundant benthic invertebrates in boreal beaver ponds (McDowell & Naiman 1986; Nummi 1989).

Beavers dams create warm, shallow water, rich emergent vegetation and large amounts of woody debris, conditions that are favored by many amphibian species during breeding (Cunningham et al. 2006; Dalbeck et al. 2007; Stevens et al. 2007). Beaver ponds are favorable for amphibian larval development because they have a long hydroperiod compared to temporary ponds. Beaver ponds may harbor a relatively rich fish population, but large amount of woody debris and aquatic vegetation protect both the larvae and adult frogs from predators. In addition they provide suitable attachment places for spawn (Porej & Hetherington 2005). The tadpole diet varies widely in the relative amounts of proteins, carbohydrates and lipids. This diet mainly comprises vegetal detritus (Castaneda et al. 2006) such as filamentous green algae and epiphytic diatoms (Kupferberg 1997), but some studies have indicated that all anuran larvae are carnivorous to some degree (Schiesari et al. 2009). The animal component of the tadpole diet includes ciliates, flagellates, amoebae (Baffico & Ubeda 2006) and other zooplankton, which are very abundant in beaver ponds (Bledzki et al. 2011). Beaver ponds also provide overwintering places for adult frogs both in water and on land (Dalbeck et al. 2007).

Only a few studies examined beaver effects on drained landscapes, e.g., Ulevičius et al. (2009) who found that, in Lithuania, beaver activity improved the ecological value of drainage canals. Nonetheless, the influence of beavers on amphibians in boreal forest landscapes remains poorly studied, although wetlands in these landscapes are often significantly affected by damming. Due to the eradication of the beaver in the last centuries, the landscapes persisted in an unnatural state for a long time, especially in Europe, where beaver-created wetlands are currently lacking. However, European beavers have recently begun returning to their former range, often aided by reintroductions (Sjöberg & Ball 2011; Halley et al. 2012). The European beaver (*Castor fiber*) was reintroduced to Finland in 1935. Along with these reintroductions, the American beaver (*Castor canadensis*) was brought to Finland in 1937.

It was the aim of this study to investigate the beaver effect on the Finnish anuran community in a landscape where 100 % of the forests are drained. There are only three native anuran species in Finland: the Common Frog *Rana temporaria* (Linnaeus, 1758), the Moor Frog *Rana arvalis* Nilsson, 1842 and the Common Toad *Bufo bufo* (Linnaeus, 1758).

Table 1: Mean values of descriptive characteristics of the study sites. Numbers in parentheses represent the minimum and maximum numbers of the value. The degree of shallow water was determined by measuring the distance between the shoreline and the point where water depth exceeded 0.6 m. The emergent vegetation coverage was received from the 10 vegetation squares (1 m^2) per water body. The canopy cover was calculated from 10 photograph points per water body with a Canon EOS 550d using a focal length of 25 mm. DOC – Dissolved Oxygen Concentration.

Tab. 1: Mittelwerte beschreibender Merkmale der untersuchten Gewässer. Zahlen in Klammern bezeichnen zugehörige Minima und Maxima. Der Flachwasseranteil ist durch die Breite des Flachwassergürtels (Wassertiefe < 0,6 m) ausgedrückt. Der Deckungsgrad der emersen Vegetation wurde für die einzelnen Gewässer aus je 10 zufällig gewählten Meßfeldern von 1 m^2 Fläche ermittelt. Das Ausmaß des Kronendachschlusses am Ufer wurde für jedes Gewässer aus jeweils 10 senkrecht nach oben gemachten Weitwinkelfotos an zufällig gewählten Uferstandorten berechnet. DOC – Konzentration des im Wasser gelösten Sauerstoffs.

Type of wetland Gewässertyp	*n*	Size (ha) Fläche	Extension of shallow water (m) Breite des Flachwassergürtels (m)	Water temperature (°C) Wassertemperatur (°C)	Emergent vegetation cover (%) Deckungsgrad der emersen Vegetation (%)	Riparian canopy cover (%) Schluß des Kronendaches (%)	pH	DOC (mg/L)
Beaver pond / Biber-Gewässer	10	$\bar{x}$ = 5.0 (0.8-8.0)	13.0 (4.5-31.3)	19.7 (16.6-23.0)	63.4 (24.6-84.6)	38.1 (16.5-68.0)	4.9	7.4 (3.8-8.8)
Non-beaver pond / Nicht vom Biber bewohntes Gewässer	10	$\bar{x}$ = 3.9 (0.8-9.3)	1.7 (0.1-9.1)	18.5 (16.2-20.7)	36.0 (13.0-52.2)	60.1 (0-87.0)	4.9	7.7 (6.8-9.4)
Temporary pond / Temporäres Gewässer	8	$\bar{x}$ = 0.09 (0.003-0.3)	4.0 (2.0-6.2)	17.3 (14.6-19.2)	57.1 (18.0-78.0)	51.9 (0.8-86.2)	5	8.1 (7.2-8.9)

MATERIALS AND METHODS

The study area (6,650 ha) was situated in Evo in southern Finland (61°10'N, 25°05'S), which belongs to the southern boreal vegetation zone (AHTI et al. 1968). The area consists of approximately 100 lakes and ponds (average size circa 4.3 ha) interrelated with brooks. The altitudinal topography of the area varies from 125 m to 185 m a.s.l. The soil in Evo is low in nutrients. Forestry has molded the development of Evo's forests, which are mainly coniferous forest. The most common tree species is pine (*Pinus sylvestris*), which covers over half of the tree stands in the area. Beaver ponds in the study area are most commonly formed by damming an existing pond (NUMMI & HAHTOLA 2008), and currently the area's beaver population (five colonies) consists solely of American beavers which were introduced to Evo in 1957.

Data was collected at three different site types (Table 1). The first site type consists of beaver-flooded ponds (n = 10) with relatively stable water levels and substantially shallower slopes than non-beaver ponds (NUMMI & HAHTOLA 2008). The shallow-water section (< 0.6 m) in the beaver ponds extends up to 100 m from the shoreline. The majority of trees in the flooded area die because of inundation, or are felled by beavers (HYVÖNEN & NUMMI 2008). Beaver ponds are consequently open and sunny, with shallow shores rich in emergent vegetation, dead trunks and high amounts of coarse woody debris (CWD). The beaver ponds in the study comprised both newly established and older ponds. The second site type consists of ponds (n = 10) without beaver influence (hereafter termed non-beaver pond). A typical non-beaver pond is shady because of large trees growing near the shore line, and has less emergent vegetation than beaver ponds due to the precipitous configuration of the shoreline. The slopes of the pond shores in this study are normally very steep. The third site type consists of temporary ponds (or vernal pools) (n = 8) that hold water for a few months and run dry by August at the latest. During the study year, the majority of the temporary ponds ran dry by the middle of June. Temporary ponds are small, less than 0.3 ha, shady and have emergent vegetation similar to beaver ponds. All temporary ponds are absent of fishes due to the dry conditions at the end of summer and to the pond freezing all the way to the bottom.

All study sites are close to one another at the landscape scale. The mean distance to the nearest study site is 275 m. Distances between the nearest study sites vary between 20 m and 1000 m. An isolation index (I) was calculated for every study site using the algorithm by KRAUSS et al. (2003), which is computed by adding up the areas and distances of all the water systems within one kilometer of the study sites:

$$I = \sum \exp(-a * d_{ij}) * A^{b}_{j}$$

where a = the effect of distance on isolation, d_{ij} = the distance from the neighboring wetland j to the study site I, A_j = the size (in m^2) of neighboring wetlands and b = migration. The simplified formula was applied where a = 1 and b = 1.

The data was collected between May 5 and 31, 2010, the main calling season for anurans in Finland, which usually lasts for two to three weeks. Each study site was surveyed on five nights to detect anuran calls. The environmental variables were measured during the daytime. The anuran chorus surveys were conducted in a 5-minute time frame at each site and identified all three species (*B. bufo*, *R. temporaria* and *R. arvalis*) using the NAAMP protocol (North American Amphibian Monitoring Program < https://www.pwrc.usgs.gov/naamp/index.cfm?fuseaction= app.protocol >). The environmental variables measured for all study sites were the extent of shallow water (< 0.6 m), water temperature (accuracy: 0.1 °C), pH, dissolved oxygen concentration (DOC) (accuracy: 0.01 mg/L), riparian canopy cover, and emergent vegetation coverage. The extent of shallow water was determined by measuring the distance between the shoreline and the point where water depth exceeded 0.6 m. Temperature and DOC were gauged at the same time using Marvet Junior 2000 (Elke Sensor, MJ 2000, GWM-Engineering Ltd., Kuopio, Finland) and pH using Merck's pH test strips (Merck KGaA, 64271 Darmstadt, Germany). The average coverage of 10 randomly defined squares (1 m^2 each) was calculated for each study site to determine its emergent vegetation coverage. The authors photographed the canopy cover using a Canon EOS 550d with a focal length of 25 mm. Canopy cover was photographed by perpendicularly facing the sky while standing on the shoreline. The photographs were divided into 3,700 small squares per picture and the proportion of squares with canopy coverage was calculated from these squares. Average canopy coverage for each study site was calculated from 10 photograph stations each that were located in the same places as the vegetation squares.

Abundance and species richness.- The amphibian calling index (ACI) was used to estimate species abundance in vocalizing anurans. The amphibian calling index (NAAMP protocol) ranged from zero to three (0 - no calls, 1 - non-overlapping calls, 2 - distinguishable calls with some overlapping and 3 - full chorus with individual calls indistinguishable). ACI surveys consisted of five visits per water body made over the breeding period of all three indigenous anuran species. The calling surveys were performed observing the following standards: tolerated wind speed maximum was 3 m/s; the surveys were not carried out under heavy rain conditions (DORCAS et al. 2010); the ACI surveys were conducted at night between 21:30 and 01:00, thereby including the calling peak of most anuran species in temperate regions (DORCAS et al. 2010); these surveys lasted five minutes at each site, and began after one minute of silence.

The data generated from the calling surveys consisted of site-specific 5-minutes index histories. From these the maximum index value for each species was used from each study site. As surveys were abandoned once no calls were detected, the authors are confident that the maximum index observed represents the real maximum index of the site. Despite no precise relations between population size and calling index values existing, the calling index values give useful information of anuran abundance. As not detecting species or calls is always a possibility, the minimum number of visits (N_{min}) necessary to achieve 95 % probability that the species is absent was calculated using the formula in PELLET & SCHMIDT (2005)

$$N_{\min} = \log (0.05) / \log (1-p),$$

where p is the detection probability.

The abundance index (N) for each site is interpreted as the maximum possible index value (N) of each site. Using variables p and N, the probabilities of calling index distributions for all the studied species were calculated based on the algorithm by ROYLE (2004)

$$(N! / (j!\cdot(N-j)!)\cdot p^j\cdot(1-p)^{N-j}$$

where $j = 0, 1, \ldots, N$.

Species richness was calculated from the anuran calling data. Each anuran species present in the study area has a unique, identifiable call. The study site type effect (beaver, non-beaver and temporary pond) on the abundance of each anuran species, as well as on species richness was analyzed with generalized linear mixed modelling (BOLKER et al. 2009; ZUUR et al. 2009) by using the glmer function in the lme4 library (BATES & MAECHLER 2009) in R 2.15.0 (R Development Core Team 2013). Abundance of each anuran species and species richness in the 28 study sites were explained by the wetland type of the sites. Data exploration exposed the wetland type effect. Wetland type was used as a categorical parameter. Formulation of the equation is as follows:

$$\text{Arvalis/Temporaria/Bufo\_abundance}_i = \alpha + \beta \times \text{Wetland\_type}$$

$$\text{Species\_richness}_i = \alpha + \beta \times \text{Wetland\_type},$$

where Arvalis/Temporaria/Bufo_abundance $_i$ is the index value of the species of site i and Species_richness $_i$ is the number of species at site i, where i = 1, . . . 28; α is the intercept and β the coefficient of the wetland type.

Principal component analysis (PCA).- The six environmental variables were analyzed using principal component analysis (PCA, see e.g., PIMENTAL 1979; GAUCH 1982), to investigate the main environmental factors defining the study site groups. The first and second PCA components explained 30 % and 20.3 % of the total variation in the habitat data, so combined these two components explained 50 % of the variation. The score values of the first component organized the wetlands on a shoreline configuration gradient: habitats with shallow shores, rich emergent vegetation and warm water temperature were located at the positive end of the gradient, while habitats with deep shores and heavy riparian canopy cover were at the negative end (see also NUMMI & PÖYSÄ 1997; SUHONEN et al. 2011). Shoreline configuration scores were normally distributed. The GLM (Generalized Linear Models) univariate analysis of variance was used to test the shoreline configuration score and the isolation index differences between study site types.

Both species richness and abundance of each species were correlated with the shoreline configuration score and the isolation index of the study site types using the Pearson product-moment correlation coefficient, to determine whether these two variables were dependent on the shoreline configuration score or the isolation index of the study site type.

RESULTS

Presence and abundance.- Common Toads were heard at 16 out of 28 sites, so the naive proportion of sites occupied by this species is 16/28 = 0.57. The sites were visited five times, which was enough (minimum 4.48) to be 95 % certain that the species was absent from sites where it was not heard. The Moor Frog was heard at seven out of 28 sites, so the naive proportion of sites occupied by this species is 7/28 = 0.25. The sites were visited five times, which was enough (minimum 3.54) to be 95 % certain that the species was absent from sites where it was not heard. The Common Frog was heard at 20 out of 28 sites, so the naive proportion of sites occupied by this species is 20/28 = 0.714. The sites were visited five times, which was enough (minimum 3.75) to be 95 % certain that the species was absent from sites where it was not heard. The detection probabilities for each anuran species were quite similar: Moor Frog 0.57, Common Frog 0.55 and Common Toad 0.49.

Table 2: Mean species richness and anuran abundance in different wetland types. Anuran abundance was measured according to the amphibian calling index (ACI) using the NAAMP protocol. ACI scores can vary between 0 and 3. Species richness was taken from the ACI. From three different wetland types (beaver ponds, non-beaver ponds, and temporary ponds) the non-beaver ponds were set as a baseline (Intercept), and the other two are compared whether or not they differ from the baseline ponds. In beaver ponds species richness and abundance of *R. arvalis* and *R. temporaria* were significantly different from non-beaver ponds (*p*-values in bold). Value - Species richness and abundance values, SE - standard error, *t* - *t*-test value, *p* - statistical significance.

Tab. 2: Mittlerer Artenreichtum und mittlere Häufigkeit der Anuren in unterschiedlichen Feuchtbiotop-Typen. Abundanzen wurden mittels Rufindex (amphibian calling index - ACI) unter Verwendung der NAAMP-Protokolls erhoben. ACI-Werte konnten zwischen 0 and 3 liegen. Der Artenreichtum wurde aus den ACI-Aufzeichnungen entnommen. Von den drei unterschiedenen Feuchtbiotop-Typen (Biber-Gewässer, nicht vom Biber bewohntes Gewässer, temporäres Gewässer) dienten die nicht vom Biber bewohnten Gewässer als Meßbasis (Intercept), mit der die anderen beiden verglichen wurden. In Biber-Gewässern waren Artenreichtum und Abundanz von *R. arvalis* and *R. temporaria* signifikant verschieden von den Werten der Vergleichsgewässer (*p*-Werte in Fettschrift). Wert - Artenreichtums- und Abundanzwerte, SE - Standardfehler, *t* - *t*-Test-Wert, *p* - Signifikanz.

	Value / Wert	SE	*t*	*p*
Species richness / Artenreichtum				
(Intercept)	1.2000	0.2200	5.4600	0.0000
Beaver pond / Biber-Gewässer	1.0000	0.3110	3.2170	**0.0040**
Temporary pond / Temporäres Gewässer	-0.0750	0.3300	-0.2170	0.8220
Abundance / Abundanz				
Rana arvalis				
(Intercept)	0.0000	0.2691	0.0000	1.0000
Beaver pond / Biber-Gewässer	1.7000	0.3805	4.4675	**0.0001**
Temporary pond / Temporäres Gewässer	0.0000	0.4036	0.0000	1.0000
Rana temporaria				
(Intercept)	1.3000	0.3821	3.4023	0.0023
Beaver pond / Biber-Gewässer	1.6000	0.5404	2.9609	**0.0066**
Temporary pond / Temporäres Gewässer	0.4500	0.5732	0.7851	0.4398
Bufo bufo				
(Intercept)	1.3000	0.2862	4.5426	0.0001
Beaver pond / Biber-Gewässer	-0.8000	0.4047	-1.9767	0.0592
Temporary pond / Temporäres Gewässer	-0.6750	0.4293	-1.5724	0.1284

Table 3: Association of wetland type to shoreline configuration and isolation index. The GLM ANOVA test was used with Gaussian distribution. Shoreline configuration was received from principal component analysis. From three different wetland types studied (beaver ponds, non-beaver ponds, and temporary ponds) the non-beaver ponds were set as a baseline (Intercept), compared whether or not they differ from the baseline ponds. Value - Shoreline configuration and isolation index values, SE - standard error, *t* - *t*-test value, *p* - statistical significance.

Tab. 3: Der Zusammenhang zwischen Feuchtlebensraum-Typ, Uferbeschaffenheit und Isolationsindex wurde mittels GLM (Generalized Linear Models) ANOVA Test bei Normalverteilung untersucht. Die Uferbeschaffenheitsdaten entstammen einer Hauptkomponentenanalyse. Von den drei unterschiedenen Feuchtbiotop-Typen (Biber-Gewässer, nicht vom Biber bewohntes Gewässer, temporäres Gewässer) dienten die nicht vom Biber bewohnten Gewässer als Meßbasis (Intercept), mit der die anderen beiden verglichen wurden. Wert - Uferbeschaffenheits- und Isolationsindex-Werte, SE - Standardfehler, *t* - *t*-Test-Wert, *p* - Signifikanz.

	Value / Wert	SE	*t*	*p*
Shoreline configuration / Uferbeschaffenheit				
Intercept	-0.5020	0.1671	-3.0040	0.0060
Beaver pond / Biber-Gewässer	1.6270	0.2364	6.8840	0.0000
Temporary pond / Temporäres Gewässer	-0.2768	0.2507	-1.1040	0.2801
Isolation index / Isolationsindex				
Intercept	85646	20106	4.2600	0.0003
Beaver pond / Biber-Gewässer	-31623	28434	-1.1120	0.2767
Temporary pond / Temporäres Gewässer	-36454	30159	-1.2090	0.2381

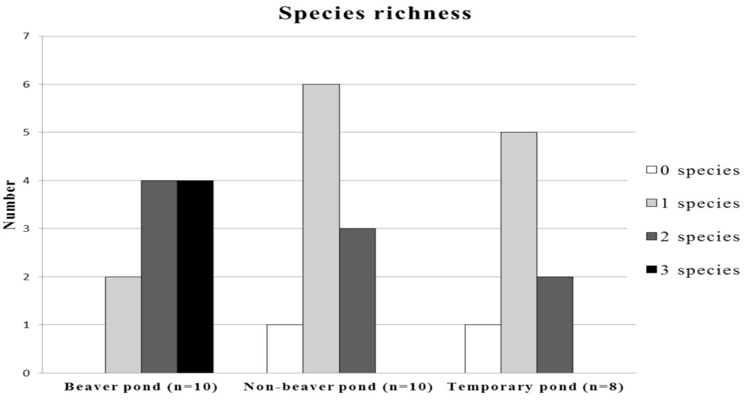

Fig. 1: Anuran species richness at beaver ponds (2.2), non-beaver ponds (1.2) and temporary ponds (1.1) of the Finnish study area (mean numbers in parentheses). No frogs were detected at two study sites: one non-beaver pond and one temporary pond.
Abb. 1: Artenzahl der Anuren in Biber-Gewässern (2,2), nicht vom Biber bewohnten Gewässern (1,2) und temporären Gewässern (1,1) des finnischen Untersuchungsgebietes (Mittelwerte in Klammern). An zwei Untersuchungsgewässern wurden keine Froschlurche gefunden, einem nicht vom Biber bewohnten und einem temporären Gewässer.

Study site type influenced the calling index value of all the anuran species (Table 2). The abundance of Moor and Common Frogs differed between beaver ponds and non-beaver ponds, as well as between beaver ponds and temporary ponds. The calling indexes of Moor and Common Frogs were significantly higher at beaver ponds. However, the abundance of the Common Toad was not affected by beaver ponds. The Common Toad received lower calling index values at beaver ponds, and its abundance was higher at non-beaver ponds.

Species richness.- Anuran species richness differed in the three different aquatic habitats. The number of species per site was higher at beaver ponds compared to the two other habitat types in the study area (Table 2, Fig. 1). The mean number of species was 2.2, 1.2 and 1.1 in beaver ponds, non-beaver ponds and temporary ponds. All three anuran species in the region occupied beaver ponds, including the Moor Frog, which was absent from non-beaver ponds and temporary ponds. Also, each beaver pond had at least one anuran species occupying the site. No frogs were recorded from one of ten non-beaver ponds and one of eight temporary ponds.

All the beaver ponds received positive scores in the PCA shoreline configuration gradient, whereas all temporary ponds and nine out of ten non-beaver ponds had negative scores. Beaver pond shoreline configuration scores thus differed significantly from the non-beaver pond and temporary pond scores (Table 3, Fig. 2).

Species richness correlated with the habitat's shoreline configuration score (Pearson correlation r = 0.468, P = 0.012, Table 4). The higher the shoreline configuration score, the more species were observed. There was a significant correlation between shoreline configuration scores and the abundance of anurans. The correlation was positive in Common and Moor Frogs but negative in Common Toads.

Only large values were obtained from the isolation index, which indicates low isolation and good connectivity within the studied wetlands. The isolation index did not differ between the study site types (Table 4), indicating that all study sites were equally reachable. The isolation index did not correlate with the species richness or the abundance of different frog species (Table 4).

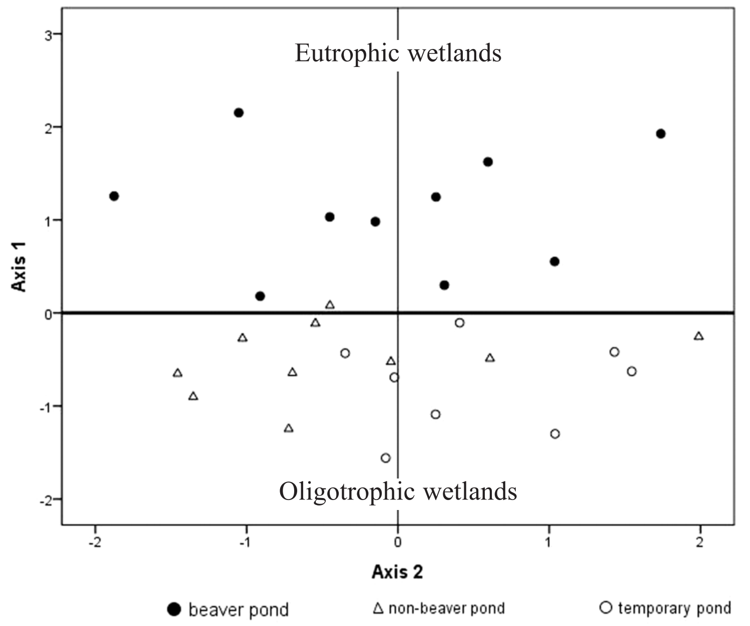

Fig. 2: The position of the 28 studied water bodies in the graphic representation of the Principal Component Analysis. Filled circles – Beaver ponds, triangles – non-beaver ponds, empty circles – temporary ponds. The scores for axis 1 are explained by the variables "emergent vegetation", "water temperature" and " extent of shallow water". Positive values of axis 1 could therefore classify sites as eutrophic and negative values as oligotrophic wetland. The scores for axis 2 are explained by the variables "emergent vegetation", "extent of shallow water" and "concentration of dissolved oxygen".

Abb. 2: Die Lage der 28 Untersuchungsgewässer in der graphischen Darstellung der Hauptkomponentenanalyse. Gefüllte Kreise – Biber-Gewässer, Dreiecke – nicht vom Biber bewohnte Gewässer, leere Kreise – temporäre Gewässer. Die Ladungen der ersten Achse sind durch die Werte der Variablen "emerse Vegetation", "Wassertemperatur" und "Breite der Seichtwasserzone" erklärt, die Ladungen der zweiten Achse durch die Werte der Variablen "emerse Vegetation", "Breite der Seichtwasserzone" und Konzentration des im Wasser gelösten Sauerstoffs. Positivwerte entlang der ersten Achse würden Gewässer somit als eher eutroph, Negativwerte als eher oligotroph einstufen.

DISCUSSION

All three anuran species naturally occurring in Finland were found in beaver ponds. The species richness was higher in beaver ponds compared with non-beaver ponds or temporary ponds. A similar increase in patch diversity at beaver ponds is found in anuran communities of Central Europe and in water bird communities in boreal areas (DALBECK et al. 2007; NUMMI & SUHONEN 2014). Ecosystem engineers are generally predicted to increase species richness if they increase the productivity of a low-productivity patch (WRIGHT & JONES 2004), which seems to be the case in low-productivity boreal areas. The special value of beaver ponds in our boreal setting was that they appeared to provide a suitable habitat for the Moor Frog. In this respect the beaver can be seen as a facilitator of Moor Frogs. This is particularly important as the Moor Frog is considered in the EU inland water directive. Beavers have also been shown to facilitate several other vertebrate species, such as fishes, waterfowl and bats (SCHLOSSER & KALLEMEYN 2000; NUMMI & HAHTOLA 2008; NUMMI et al. 2011). Waterfowl facilitation has been shown to be quite similar to that of anurans:

Table 4: Association of shoreline configuration scores and isolation indexes of water bodies with species richness and abundance of different species (n = 28). Shoreline configuration was received from the principal component analysis. The Pearson correlation (*r*) was used for all correlation analyses. *t* - *t*-test value, *p* - statistical significance.

Tab. 4: Der Zusammenhang zwischen Uferbeschaffenheit und Gewässer-Isolationsindex einerseits sowie Artenzahl und Individuenhäufigkeit der untersuchten Anurenarten andererseits (n = 28). Die Uferbeschaffenheitsdaten entstammen einer Hauptkomponentenanalyse, für die Korrelationsanalysen wurde Pearsons Korrelationskoeffizient (*r*) verwendet. *t* - *t*-Test-Wert, *p* - Signifikanz.

Dependent variable / Abhängige Variable		*r*	*t*	*p*
Species richness / Artenreichtum	Shoreline configuration / Uferbeschaffenheit	0.468	2.703	**0.012**
	Isolation index / Isolationsindex	-0.213	-1.112	0.276
Abundance / Abundanz				
R. arvalis	Shoreline configuration / Uferbeschaffenheit	0.709	5.124	**< 0.001**
	Isolation index / Isolationsindex	-0.008	-0.043	0.966
R. temporaria	Shoreline configuration / Uferbeschaffenheit	0.477	2.767	**0.010**
	Isolation index / Isolationsindex	-0.169	-0.877	0.387
B. bufo	Shoreline configuration / Uferbeschaffenheit	-0.395	-2.195	**0.037**
	Isolation index / Isolationsindex	-0.034	-0.175	0.862

some ducks (e.g., Wigeon, *Anas penelope*) in oligotrophic boreal ponds are only found in beaver ponds (Nummi & Suhonen 2014).

The species richness and abundance of frogs correlated positively with the luxuriance (i. e., infrastructural diversity) score of the study sites. The three main factors influencing the luxuriance score were emergent vegetation, water temperature and the proportion of shallow water. Emergent vegetation protects both larvae and adult frogs from predators and acts as an attachment surface for spawn (Babbit & Tanner 1998; Porej & Hetherington 2005). All the beaver ponds in this study existed prior to the beaver's reintroduction and harbor fish populations. Pike (*Esox lucius*) and European perch (*Perca fluviatilis*) are the main fish species found in the study sites (Väänänen et al. 2012), and both feed on anuran eggs, larvae and adults (Koli et al. 1988; Koli 1989a, 1989b; Wang & Appenzeller 1998). Both Common and Moor Frogs were more abundant in beaver ponds than in non-beaver ponds, so predatory fish did not strongly affect their presence. This may indicate that the rich vegetation of beaver ponds ameliorates habitat structure into a more favorable state for anurans.

Beaver activity usually leads to increased organic material and sediment accumulation (Rosell et al. 2005) increasing the density of algae and detritus in beaver ponds, which enhance the abundance of predatory zooplankton (Bledzki et al. 2011). Anuran larvae have traditionally been considered microphagous, suspension-feeding herbivores and detrivores, but studies suggest that tadpoles also feed on animal components, such as ciliates, flagellates and amoebae (Kupferberg 1997; Baffico & Ubeda 2006; Castaneda et al. 2006; Schiesari et al. 2009). Beaver ponds are also suitable feeding habitats for metamorphs, as several groups of emerging insects, e.g., chironomids and mayflies, are abundant in these habitats (McDowell & Naiman 1986; Nummi 1989; Rosell et al. 2005). Since insects are the main diet of most post-metamorph anurans (Arnold & Ovenden 2002), the beaver's facilitation of anurans does not just include habitat amelioration, but also enhances resource availability.

The warmer water temperature in beaver ponds is beneficial for anurans, as higher water temperature accelerates hatching and tadpole growth (Arendt & Hoang 2005; Stevens et al. 2006; Dahl et al. 2012). Temperature is the main factor influencing and promoting the speed of larval development and time of metamorphosis (Castaneda et al. 2006). Accelerated growth is advantageous for anuran larvae in avoiding predation (Kupferberg 1997;

KNIGHT et al. 2009). In addition to water temperature, food quality can influence tadpole growth rates and time of metamorphosis (KUPFERBERG 1997; RICHTER-BOIX et al. 2007). The high densities of phyto- and zooplankton, as well as the higher water temperature, foster anuran larvae in beaver ponds. The advantage of beaver ponds over ponds without beavers is a result of higher water temperature, more abundant vegetation and a wider section of shallow water.

Beaver ponds also create habitats for anurans. Dams and lodges are suitable overwintering habitats for anurans (STEVENS et al. 2006; DALBECK et al. 2007). In addition to building activities, beavers also dig foraging channels and increase pond depth (NAIMAN et al. 1986; WESTBROOK et al. 2006; HOOD & BAILEY 2008). All three anuran species studied hibernate under water (KOSKELA 1989; ARNOLD & OVENDEN 2002; LAPPALAINEN & SIRKIÄ 2010). The benefit of a deeper lakebed is the reduced probability of the pond or lake freezing down to the bottom. Deeper lakebeds in beaver ponds therefore enhance the over-wintering survival of anurans.

The Common Toad prefers habitats with deeper water, whereas Common Frogs value habitats with shallow water and Moor Frogs prefer rich aquatic vegetation environments as breeding habitats (KOSKELA 1989; ARNOLD & OVENDEN 2002; LAPPALAINEN & SIRKIÄ 2010). Beaver ponds are very heterogeneous environments when compared to non-beaver ponds and temporary ponds, with both shallow and deeper parts (HODKINSON 1975; NUMMI 1989). Shallow shores are restricted to a narrow strip in most boreal ponds and lakes (NUMMI & HAHTOLA 2008), whereas temporary ponds are shallow throughout. The heterogeneity of beaver ponds may be one factor explaining anuran species richness.

Some beaver ponds studied were recently constructed, their fast colonization by *R. arvalis* was remarkable. *Rana arvalis* dispersal distances vary between one to three kilometers per year (HARTUNG & GLANDT 2008; VOSS & CHARDON 1998) and many individuals return to their birth pond for reproduction (ELMBERG 2008). For dispersal, Moor Frogs prefer landscapes with ditches and hedgerows and avoid dry and open areas (HARTUNG & GLANDT 2008). Nearly all beaver ponds in Evo are connected to each other by a network of ditches and other water bodies. This would explain how the Moor Frog can find hospitable habitats so quickly. The distance between water sites at Evo cannot be a dispersal barrier for anurans, as the mean distance is 275 m between water sites and 648 m between beaver ponds.

Complete drainage of the forests in the study area had dramatically reduced the wetland diversity of Evo already before the introduction of the beaver in 1935. Man-made ditches lead excess surface water away and impair the quality and processes of aquatic ecosystems (SUISLEPP et al. 2011). Wetland loss decreases amphibian productivity and abundance via the number and density of breeding sites. Beaver actions reduce the effects of draining, because beaver dams increase both surface and groundwater and are able to attenuate declines in the water table (WESTBROOK et al. 2006; BROMLEY & HOOD 2013). Wetland diversity and anuran richness at Evo would be more restricted without the presence of beavers. Beaver facilitation of anurans is an important factor to keep in mind when planning anuran conservation management.

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