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Abundance and diversity of small mammals in Swedish beaver systems

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Abstract

Through their ecosystem engineering activities, beavers (*Castor fiber*) create ponds and riparian zones littered with deadwood, providing heterogeneous micro-habitats for a variety of small mammal species. In this study small mammals were snap-trapped in nine beaver systems and four reference wetland systems that were not created by beavers in southern and central Sweden to compare abundance and diversity of voles, shrews and mice. In addition, structural habitat factors were recorded at the study sites. Beaver sites had high amounts of coarse and fine woody debris and standing deadwood. A principal component analysis of the structural habitat factors showed that over a third of the variation in the data can be explained by the degree of influence that *C. fiber* has on the system. Abundance and true diversity ($\exp H'$) of small mammals were positively correlated with the amount of deadwood in the systems. Bank voles (*Myodes glareolus*) were shown to have no preference for either beaver or non-beaver wetlands, but subadult bank voles had higher mean weights in newly colonized beaver systems with extensive grass layers than in recolonized systems. It has been concluded that beavers are indeed creating habitat conditions that are favourable for small mammal diversity and abundance, especially as far as shrews and mice are concerned.

Zusammenfassung

In seiner Funktion als Ökosystemgestalter bewirkt der Biber (*Castor fiber*) die Entstehung von totholzreichen Teichen und Uferzonen, und schafft dadurch heterogene Mikrohabitate für eine Vielzahl von Kleinsäugerarten. Für diese Arbeit wurden in Süd- und Mittelschweden in neun Biberhabitaten und vier Referenzfeuchtgebieten die nicht von Bibern geschaffen wurden Kleinsäuger gefangen, und die Biodiversität und Abundanz von Kleinsäufern in den beiden Habitattypen verglichen. Zusätzlich wurden in den untersuchten Systemen strukturelle Habitatfaktoren aufgenommen. Bibersysteme wiesen hohe Anteile an liegendem und stehendem Totholz auf. Eine Hauptkomponentenanalyse der strukturellen Habitatfaktoren zeigte, dass über ein Drittel der Varianz in den Daten durch den Grad des Einflusses von Bibern auf das System erklärt werden können. Abundanz und echte Diversität ($\exp H'$) von Kleinsäufern korrelierten positiv mit der Totholzmenge im System. Rötelmäuse schienen weder Biberhabitate noch Referenzhabitate zu präferieren, Jungtiere in neukolonisierten Bibersystemen mit ausgeprägter Grasschicht wiesen jedoch durchschnittlich ein höheres Körpergewicht auf, als in wiederbesiedelten Gebieten. Daraus kann geschlossen werden, dass Biber in der Tat Lebensraumbedingungen schaffen, die sich positiv auf die Abundanz und Diversität von Kleinsäufern, insbesondere von Spitzmäusen und Echten Mäusen, auswirken.

Popular Science Summary

By felling trees and building dams, beavers change the ecosystems they live in. They alter water flow conditions, create ponds, and generally increase the amount of lying and standing deadwood, because they feed on trees and shrubs. While this has made them unpopular with farmers and foresters, it has drawn the interest of ecologists. At least by the latter, beavers are increasingly seen as an asset rather than a nuisance because they are able to diversify landscape structures, and to provide habitats for a variety of plants and animals.

This study investigated the effect that beaver activities have on small mammals, such as voles, shrews and mice. It was assumed that these animals would benefit from a high amount of deadwood in the ecosystem because it provides them with shelter and cover. Also, beaver meadows are rich in grasses and herbs, in contrast to the pine and spruce forests that cover large parts of the Swedish countryside, providing small mammals and their prey with important food sources.

The systems that I investigated were situated in southern and central Sweden. Nine study sites were beaver systems, and four study sites were lakeside systems, which had not been created by beavers. In each system, I snap-trapped for three consecutive nights in autumn, catching over 200 small mammals. The animals caught were mainly field and bank voles, but also included common shrews, least shrews, water shrews and wood mice. In addition to this, I recorded structural habitat factors, such as tree cover, grass cover, amount of deadwood and water area.

I then investigated correlations between the amount of small mammals trapped in the systems, their diversity, and the amount of deadwood found at the respective sites. Indeed, I found that study sites with beavers had higher amounts of deadwood, which in turn led to a higher amount of small mammals and more small mammal species. Shrews and wood mice were absent from the lakeside systems, which shows that for these species beaver systems are more attractive. Bank voles did not show a preference for either beaver or reference systems, but, on average, young bank voles were heavier in new beaver systems with high amounts of grasses and herbs than in re-used systems with a higher amount of shrubs and trees.

This shows, that beaver do have a positive influence on small mammal communities because they create diverse habitat structures and change the vegetation in the areas they inhabit.

Populärwissenschaftliche Zusammenfassung

Durch das Fällen von Bäumen und das Bauen von Dämmen beeinflussen Biber die Ökosysteme, in denen sie leben. Sie verändern Wasserläufe, schaffen Teiche und erhöhen ganz allgemein die Menge von liegendem und stehendem Totholz in ihrem Lebensraum, da sie sich von Bäumen und Büschen ernähren. Während sie sich dadurch bei Bauern und Forstarbeitern unbeliebt gemacht haben, interessieren sich ÖkologInnen für die positiven Auswirkungen, die Biber auf Landschaftsstrukturen haben können. Die Bautätigkeit des Bibers schafft Lebensräume für eine Vielzahl von Pflanzen und Tieren, weil vorhandene Landschaften abwechslungsreicher gestaltet werden.

Diese Arbeit beschäftigte sich mit den Auswirkungen von Bibern auf Kleinsäugetiere wie Wühl-, Spitz- und Echte Mäuse. Es wurde angenommen, dass diese Tiere von Totholz im Ökosystem profitieren, weil es ihnen Unterschlupf und Schutz vor Fressfeinden gewährt. Außerdem sind von Bibern gestaltete Graslandschaften reich an Gräsern und Kräutern, die für viele Kleinsäuger und ihre Beutetiere wichtige Futterquellen darstellen.

Die von mir untersuchten Systeme lagen in Süd- und Mittelschweden. Neun Untersuchungsflächen waren Bibersysteme und vier Untersuchungsflächen waren Seeuferflächen, die nicht von Bibern geschaffen wurden. In jedem System fing ich an drei aufeinanderfolgenden Nächten im Herbst Kleinsäuger, wobei ich auf eine Gesamtzahl von über 200 Tieren kam. Unter den gefangenen Tieren waren hauptsächlich Rötel- und Erdmäuse, aber auch Waldspitzmäuse, Zwergspitzmäuse, Wasserspitzmäuse und Waldmäuse. Zusätzlich nahm ich in den Untersuchungsflächen auch strukturelle Lebensraumfaktoren, wie Baumschichtdeckung, Gras- und Krautdeckung, Totholzmenge und Wasserfläche, auf.

Auf Basis dieser Daten untersuchte ich den Zusammenhang zwischen der Menge der gefangenen Mäuse, ihrer Artenvielfalt, und der Menge an Totholz in den jeweiligen Systemen. In der Tat konnte ich nachweisen, dass Bibersysteme einen höheren Totholzanteil aufweisen, als vergleichbare Seeuferflächen, was wiederum eine größere Anzahl von Kleinsäufern und eine höhere Artenvielfalt bedingt. Spitzmäuse und Echte Mäuse fehlten in den Referenzsystemen völlig, was zeigt, dass Bibersysteme für diese Arten attraktiver sind. Rötelmäuse schienen weder Biber- noch Referenzsysteme vorzuziehen. Allerdings waren junge Rötelmäuse in den neu besiedelten Bibergebieten, mit einem hohen Anteil an Gräsern und Kräutern, im Durchschnitt schwerer als in wiederbesiedelten Gebieten, die höhere Anteile an Bäumen und Sträuchern aufwiesen.

Biber haben also einen positiven Einfluß auf das Vorkommen von Kleinsäufern, weil sie vielfältige Lebensraumstrukturen schaffen und die Vegetation ihrer Lebensräume verändern.

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1 Introduction

More than any other terrestrial animal in Europe and North America, the beaver (*Castor fiber*, L., *Castor canadensis*, Kuhl) is able to shape its environment according to its needs – it is an *ecosystem engineer* (Jones et al. 1994; Johnston & Naiman 1990). By felling trees, building dams and digging holes in bank structures, beavers modify and stabilize water tables and change the composition and succession of plant species in their habitats (Pollock et al. 1995; Rosell et al. 2005). The effects of these activities can be seen in biotic and abiotic characteristics of water bodies. For example, nutrient regimes are altered through a change in flow characteristics, resulting in reduced downstream nitrogen levels (Maret et al. 1987). Naiman et al. (1988) report a generally higher resilience of beaver-affected water bodies against ecologic disturbances. Hood and Bayley (2008) have shown that beavers are able to mitigate the effects of droughts on open wetlands, because their activities increase and maintain water surface areas. These effects are mostly due to the increased input of woody debris (e.g. logs and branches) into the streams (Gurnell 1998). Accumulations of woody debris change the channels' morphology, and lead to the creation of islands and smaller channels (Naiman et al. 1986). Spatial heterogeneity of rivers and streams is thus strongly influenced by the beavers' construction and feeding activities.

As Claudio Saunt (2014) points out in his popular science history of 1776, we cannot know what North America would look like today if the American beaver (*C. canadensis*) had been able to shape the landscape for the past centuries. The same is probably true for European landscapes. The Eurasian and the American beaver were hunted to the brink of extirpation in both North America and Europe towards the end of the 1800s. The animals were killed for their pelts, the perfume aroma castoreum and their meat, which in the winter months is rich in fat and nutritious (Schulz 2012). Beaver meat is described as "very palatable" by one nineteenth century author, who also remarks on the species' dwindling numbers (Wislizenus 1912). In Europe, the Eurasian beaver had almost died out at the beginning of the twentieth century. Although the species was once found almost all over the European and Asian temperate zones, at the turn of the last century only remnant populations were left in Eastern Europe, Germany, France, Norway, Mongolia and China (Nolet & Rosell 1998).

However, like its American cousin, the Eurasian beaver (*C. fiber*, L.) has made a remarkable comeback in the past one hundred years. It has been successfully reintroduced in most European countries, first for economic, then for ecological purposes. In Sweden, the species died out in 1871 and was reintroduced between 1922 and 1939 (Nolet & Rosell 1998). Today, the Swedish beaver population is estimated to comprise about 130,000 individuals (Ogden 2014). They are now often seen as problematic in the agricultural landscape. Their dams cause flooding, destroying forests and agricultural land, their tree felling activities can be a threat to orchards and other plantations, making them a "problem species" (Strandl 2013; Wallén 2015; Marakovits 2015). It has therefore become increasingly important to investigate the positive influence that beavers have on ecosystem

stability. Beavers can fulfil an important ecological function: that of diversifying today's largely industrialized landscapes. The positive effect that beavers have on populations of invertebrates, fish, amphibia and birds has been shown in a variety of studies. The ecosystems they create are refuges for plants and other animals that have come under pressure because of habitat loss (Bailey & Whitham 2006; Meßlinger 2013; Hood & Larson 2014).

Ciechanowski et al. (2011) have shown the positive effects of beaver activities on one group of small mammals, namely vespertilionid bats. According to the authors, small stream riparian zones modified by beavers were passed more frequently by bats than stream sections that were not influenced by beavers. Another study, this time on small mammal abundance and diversity on beaver lodges in Lithuania, indicates that these lodges might be an important overwintering habitat for bank voles (*Myodes glareolus*, Schreber 1780) (Ulevičius & Janulaitis 2007). Small mammals, such as voles, shrews and mice, make up the staple diet of many mammalian and avian predators. The abundance of small mammals therefore has a direct influence on predator survival and breeding success (Erlinge 1974; Korpimäki & Norrdahl 1991; Moss et al. 2012). They are well suited as indicator organisms because they are relatively high up the food chain, ubiquitous, and usually occur in relatively large numbers, compared to larger mammals. They are easy to trap, and, even though they can have home ranges of several hundred square metres, their home ranges are small enough to provide information about the trapping area (Szacki & Liro 1991; Wolff 1999; Resch & Blatt 2015).

Hansson (1978) and Chętnicki & Mazurkiewicz (1994) have shown that habitat factors that increase the availability of shelter from predators and the possibility to burrow are important for the abundance of small mammals. Ecke et al. (2001) have pointed out the positive effects of woody debris on population stability in bank voles. At micro-level, habitat heterogeneity is believed to be positively influenced by structural habitat factors such as grass and herb layer vegetation, boulders, fine woody debris and fallen trees (Stenseth 1977; Ecke et al. 2001, 2002). In beaver meadows, fallen branches and logs lead to a lateral and vertical stratification of the habitat and thus increases heterogeneity (Wright et al. 2002; Naiman et al. 1986). This might lead to a higher abundance of small mammals.

Density of small mammals is, however, not sufficient for assessing habitat quality if no other factors are taken into account (Van Horne 1983). Kristan (2003) has pointed out that habitats can be attractive to individuals even if their quality is suboptimal. Bank voles, for example, are known to disperse to suboptimal habitats when population density exceeds the carrying capacity of the optimal habitat (Gliwicz 1993). While investigating source-sink dynamics (Kristan 2003; Diffendorfer 1998) would go beyond the scope of the present study, it is possible to make a tentative statement about habitat quality on the basis of the vole population's age structure. Bank voles move over long distances for two reasons: to look for new habitat, and to find mating partners (Kozakiewicz et al.

2007). Studies have found that it is especially young individuals who disperse (Bondrup-Nielsen & Karlsson 1985; Viitala et al. 1994). A low percentage of mature individuals in a habitat could therefore indicate low habitat quality for this species. However, bank vole populations in Sweden show cyclic fluctuations that grow more pronounced with increasing geographical latitude (Hansson 1979). The age structure of cyclic vole populations changes with the phase of the cycle, as Boonstra (1994) and Tkadlec & Zejda (1998) have shown. The authors point out that in peak years, voles-of-the-year do not reach maturity, while they do in other phases of the cycle. Interpretations of age structure in this study can therefore only be tentative and must be seen in the context of studies on cyclicity.

Here, I study small mammal communities in beaver systems. I assume that through their ecosystem engineering activities (mainly tree felling and dam construction) beavers create diverse habitat structures that are favorable for several species of small mammals. My aim is to evaluate if beaver systems are a better habitat for small mammals than lakeside wetlands. If the answer is yes, small mammals in beaver habitats should be more abundant and more diverse than in lakeside habitats. I will assess this on the basis of the following questions:

- Do beavers create riparian zones that are more heterogeneous than lakeside wetlands?
- Is there a difference in species diversity and abundance of small mammals between beaver habitats and lakeside wetlands?
- Does age and weight structure of *M. glareolus* indicate a qualitative difference in the two habitat types?

My first hypothesis is that due to a higher input of deadwood, such as logs and branches, riparian zones created by beavers are more heterogeneous than comparable riparian zones of small lakes that were not created by beavers. As a consequence, small mammals in beaver systems should be more abundant and their species richness and the resulting diversity index higher than in lakeside systems. My second hypothesis is that the relative amount of mature bank voles (*M. glareolus*) and the average weight of bank voles is higher in beaver systems than in the riparian zones of lakesides because for this species the former habitat provides better living conditions in terms of food and shelter.

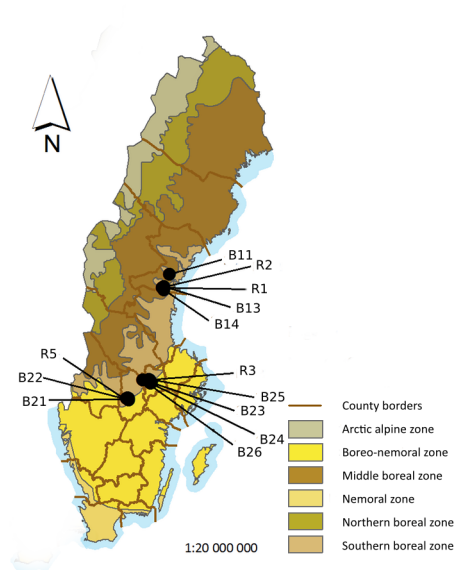


Figure 1: Map of Sweden with vegetation zones and study systems in the counties of Örebro, Västmanland and Västernorrland. Beaver systems are labelled B*x*, reference systems R*x*.

2 Materials and Methods

In the present study, 13 different wetland systems were investigated. Nine of them are wetlands created by beavers. They are part of an ongoing research project of SLU's Department of Aquatic Sciences and Assessment. The other four were reference systems (riparian zones of small lakes) in the vicinity of the beaver systems. I compared these different kinds of habitats (wetlands created by beavers and lakeside wetlands not created by beavers) on the basis of the following variables:

- small mammal abundance;
- species diversity;
- age of *M. glareolus*;
- weight of *M. glareolus*.

In addition, I examined the link between structural habitat factors that dominate these habitats (vegetation, amount of deadwood, etc.) and the other variables I measured.

2.1 Study sites

Sampling was performed in nine different beaver habitats and four reference systems that were located in the same regions as the beaver systems. The study sites were situated in three different counties of Sweden. System B21, B22 and reference system R5 were in the county of Västmanland, and B23, B24, B25, B26 and reference system R3 lie in Örebro county. The systems in Örebro and Västmanland were located on the border between the boreo-nemoral and the Southern boreal zone (fig.1), which coincides with the border between semi-cyclic and cyclic vole populations in Sweden (Hansson 1979). Beaver systems B11, B13, B14 and reference systems R1 and R2 were in Västernorrland. The systems in Västernorrland belong in the Southern boreal zone, bordering the middle boreal zone, where vole populations are strongly cyclic (Hansson & Henttonen 1985). Originally, this study contained six reference systems, two of which (situated in Örebro county) had to be dropped from the analysis because of issues with the trapline operation (see Appendix A).

A distinction was made between pioneer and recolonized systems on the basis of research carried out by Levanoni et al. (Just Accepted Manuscript). According to this classification, systems B23, B24 and B26 are pioneer systems, having been newly colonized by beavers after their re-introduction to Sweden in the twentieth century. The rest of the beaver systems are recolonized systems that have been active before the beaver's extirpation at the end of the nineteenth century.

Reference systems represented wetlands that were not created by beavers, and were selected by screening orthophotos on the webservice kartor.eniro.se. In order to allow for comparison with beaver systems, the reference systems had to fulfil five main criteria:

- geographical vicinity to the beaver systems;
- no impact of beavers on the system's hydrology and vegetation;
- not part of the same catchment as the beaver systems;
- size no larger than that of the largest beaver system in the study;
- lake shore vegetation predominantly herbal, grassy or mossy.

The linear distance was measured between the studied beaver and reference systems, and was between 1000 m to 7500 m. Beavers are abundant in the Swedish countryside and lodges were spotted in closer vicinity to the reference systems. However, as far as we could determine, the hydrology and vegetation of the reference systems was not influenced by the beaver activities in these areas, i.e. there were no trees felled by beavers and no beaver constructions in these systems. Otherwise, reference systems were chosen for their similarity with the beaver systems. Both types of systems were surrounded by managed forest (mostly *Picea abies* and *Pinus sylvestris*) but for the most part had little tree cover themselves. Plant species found in the two system types were similar with different species abundances.

The map was created in ArcGIS (ESRI 2010), and edited in Gimp and Inkscape (both licenced under GNU). It is based on maps provided by Lantmäteriet. For system coordinates, see Appendix A.

2.2 Small Mammal Sampling

The small mammal species this study focused on, were primarily herbivorous and folivorous voles and mice as well as insectivores, such as shrews. Based on the placement and size of traps, the bait, and habitat preferences, species that we expected to be able to trap were bank voles (*M. glareolus*), grey-sided voles (*Myodes rufocanus*, Sundevall 1846), field voles (*Microtus agrestis*, L.), water voles (*Arvicola amphibius*, L.), common shrews (*Sorex araneus* L.), pygmy shrews (*Sorex minutus* L.), Eurasian water shrews (*Neomys fodiens*, Pennant 1771), wood mice (*Apodemus sylvaticus* L.), yellow-necked mice (*Apodemus flavicollis*, Melchior 1834), Eurasian harvest mice (*Micromys minutus*, Pallas 1771), Northern birch mice (*Sicista betulina*, Pallas 1779) and wood lemmings (*Myopus schisticolor*, Lilljeborg 1844).

To make the results more comparable for further research, I adopted a trapping scheme used in other research projects on small mammals in Sweden (Hörnfeldt 1994). In each system I set up a trapping line of 10 trap stations with five standard all-metal snap traps (100 mm x 50 mm) per station. The trapping lines were each operated for three consecutive nights. The spacing between the stations was roughly ten metres, resulting in either one 90 m or two 40 m trapping lines of 50 traps. The catch was measured in individuals per 100 trapping nights, a unit commonly used by other researchers in small mammal ecology (Cockle & Richardson 2003; Hörnfeldt 2004). Trapnights were calculated as number of traps multiplied by the number of nights they were active, e.g. 50 traps that were active for three nights result in 150 trapnights. Using this ratio, catches per trapping line were comparable even if individual stations were rendered inoperative for unforeseen reasons.

Trapping followed the general design and methods used within the Swedish National Monitoring Program of Small Mammals (Hörnfeldt 1994). It was carried out between 30 September and 16 October 2014, starting with the northernmost systems in Västernorrland, near Sundsvall. The target habitat were different types of wetlands, such as Sphagnum patches and marshes, with hydrophilic plants as the dominant species (Gunnarson & Löfroth 2009). In beaver systems and reference systems with an open water body or a lake at their centre, traps were placed as far away from the surrounding forest as possible, to avoid edge effects, and were therefore mostly situated at the edge of the water body. In systems without an open water surface, the whole system represents a potential habitat for small mammals. These systems were mostly water bodies interlaced with islands of vegetation, and transects were placed across the system. Areas that did not fulfil the criteria for a 90 m trapping line due to forest stands or open water getting in the way, two parallel trapping lines of 40 m were used. Depend-

ing on the topography of the system, trapping lines run parallel or perpendicular to the water flow (figure 2).

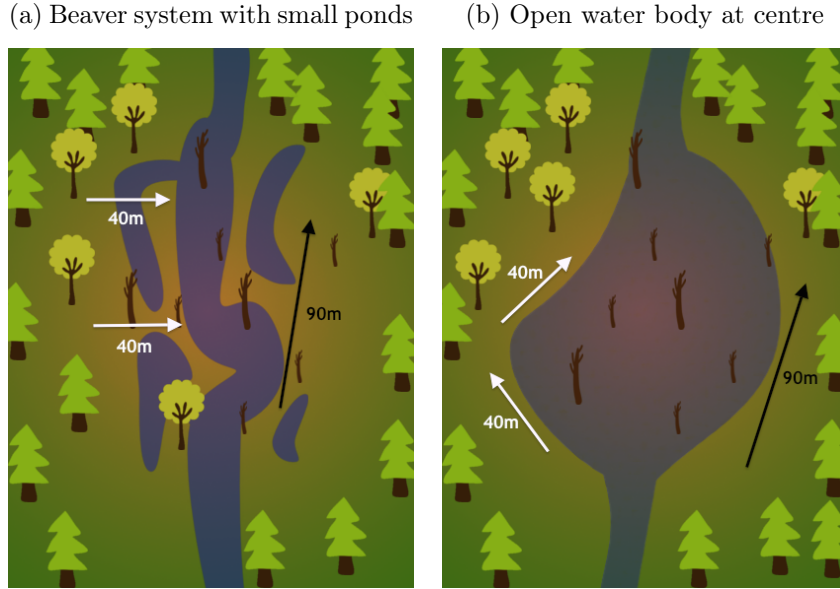


Figure 2: Different types of wetlands with two 40 m trapping lines (white), or one 90 m trapping line (black). Tree design: Freepik.com

Traps were placed on the ground – whenever possible close to structures that small mammals might use for running along them, on visibly used runs or close to holes. As bait I used pieces of dried apple (for mice and voles) and Polish wicks (for shrews) (Hörnfeldt 2004). The traps were checked at an approximate 24-hour interval. All small mammals were labelled, bagged and stored at -20°C until their dissection. Before dissection, the animals were weighed and the species identified on the basis of Richarz (2010) and Wallentinus (1965). The animals were then sexed and their heads cut off (for the extraction of teeth for age determination). The rest of the body was refrozen.

I used snap-trapping and not live-trapping in this study for two reasons: Snap-trapping poses a lower risk for the researcher to contract Hantavirus from the captured animals because the virus is also transmitted via bites (Boone et al. 2014). Also, the animals needed to be dissected in order to gather reliable data on their age and sex. The bodies were frozen and stored for other parts of the research project on beaver systems, such as the analysis of environmental toxins (e.g. mercury) in different tissues.

Christensen & Hörnfeldt studied the effects of destructive sampling on the Swedish vole populations (2003). Voles have been sampled for environmental monitoring for almost 50 years but, according to the authors, there is no risk of over-exploitation. Trapping data from Västmanland shows no notable decline in the number of Eurasian common shrews (*Sorex araneus*) taken by destructive sampling in the past 40 years (Hörnfeldt 2014). It is therefore unlikely that the

present study had any noticeable influence on the local small mammal populations.

2.3 Age Determination and weight

The bank vole (*M. glareolus*) is Sweden's most common mammal. In bank voles, the roots of the molars start to grow when they are approximately three months old. Since the roots never stop growing, but continuously wear off, the length of the root in comparison to the rest of the tooth increases with age. Empirical data on this ratio showed that it is possible to determine the age between three and 16 months (Tupikova et al. 1968; Viro 1974). However, a number of authors have warned about possible problems that occur when applying this method of age determination to field born voles because of dietary differences to laboratory conditions (Gustafsson et al. 1982; Hansson 1983). For the present study, I have therefore used root length in combination with indicators of sexual maturity (uterine scars and testicle size) to sort the voles in the categories *subadults* and *adults*. Voles with root lengths between 0 and 0.29 mm were classified as subadult (0-5 months old, probably born between late April and early September 2014), and those with root lengths of 0.69 mm and above as adults (≥ 8 months, born in or before April 2014) (Viro 1974). Three ambiguous cases were eliminated from the dataset.

For the extraction of the teeth, the lower jaws of all bank voles were boiled at 100°C in 5% aqueous solution of Sodium hydroxide for about 10 minutes to remove most of the tissue and fur. Both first mandibular molars M^1 were then extracted with a set of pincers. The roots of both molars were measured under a Wild Heerbrugg microscope, at a magnification of 2.5. The average root length of each individual was used for the age determination according to Viro (1974). The classification according to age was also used as a basis for comparing the weight of bank voles in the different habitats.

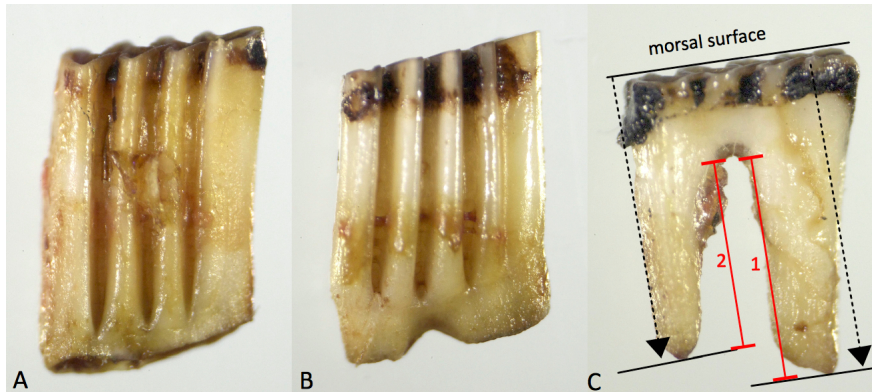


Figure 3: A) Molar (M^1) of subadult bank vole (approx. 0-3 months). No roots visible. B) M^1 of subadult bank vole (approx. 4 months). Root beginning to emerge. C) M^1 of adult bank vole (approx. 16 months or older). Red: measuring line 1 (oral, 2.1 mm) and 2 (aboral, 2.5 mm).

The actual distance that was measured is illustrated in figure 3c. The starting point for each measurement was obtained through parallel translation of the morsal surface to the apical point of each root. From there, the root length was measured perpendicularly.

2.4 Biotope mapping

Habitat heterogeneity was assessed by investigating structural habitat factors. Structural habitat factors were also mapped at the sampling sites to see whether they correlated with variations in abundance and species diversity. The factors surveyed were: vegetation cover, dominant species, water area, area covered by deadwood, and boulders. They were estimated and mapped at each trapping station in May 2015. Since the habitat mapping was carried out in spring, the maximum height of the herbal layer was not reached yet, and could only be roughly estimated. This was done according to plant remains from the previous year and photographs taken in autumn during the small mammal sampling, where vegetation height could be compared to the flags used to mark the trapping stations (see fig.4). The sampling protocol that was used for mapping is given in Appendix B.



Figure 4: System B23 in October 2014, with two trapping station markers.

Vegetation was classified according to height and type (trees, shrubs, dwarf shrubs, grass, herbs, and moss). The vegetation cover for each class was estimated in percent.

Deadwood was classified according to type and diameter:

- standing deadwood (height > 1 m, diameter at one metre > 10 cm),
- stumps (height < 1 m, diameter at cut surface > 10 m),

- fine woody debris (diameter < 10 cm),
- coarse woody debris (diameter > 10 cm).

Cramer & Willig (2005) stress the importance of spatial resolution when investigating habitat heterogeneity. On a macro-level, habitat heterogeneity is usually taken to mean the presence of different habitat types in a landscape (MacArthur & MacArthur 1961; Szacki & Liro 1991). In the present study, habitat heterogeneity was assessed at micro-level. As defined by Morris (1987), this means that the animals' home range is larger than the study area. The home range of bank voles has been shown to be up to 2000 m² (Bergstedt 1966). Shrews in woodland habitats can also have home ranges between over 2000 m² (*S. minutus*) (Kollars 1995). Structural habitat factors were measured at the level of trapping stations, with a total of 1000 m² (100 m x 10 m) mapped per system. It was assumed that, for the most part, home ranges of the mammals trapped in this study overlapped with the mapped area but were not wholly comprised by it.

2.5 Species diversity

Species diversity consists of two components: Species richness and evenness. Species richness in this case is the number of different species per system. Evenness indicates how evenly the abundances of these species are distributed (Tuomisto 2012). In order to obtain a number that accurately reflects the species composition and abundances of each system, it is necessary to include both components in the index chosen for comparison. Out of the many ways of expressing species diversity, I have used the transformed Shannon entropy or Shannon index ($\exp H'$) for comparing the different habitats (Gotelli & Chao 2013). It is based on the Shannon index (H'), which gives the uncertainty of the identity of a species in the dataset:

$$H' = - \sum_{i=1}^n p_i \ln p_i$$

The transformed Shannon index ($\exp H'$) is based on the Shannon index (H'). While the Shannon index is a unit of species diversity, the transformed Shannon index is not. It is a unit of species richness (Gotelli & Chao 2013), and also contains information about evenness. It is a measure of so-called true diversity. True diversity assumes that the dataset consists of equally abundant species (Tuomisto 2011). If a given habitat has three species that are equally abundant, true diversity is 3. If the three species have unequal abundances, true diversity according to Shannon ($\exp H'$), will typically range between 1 and 3.

Let us say we have a community with individuals that belong to two different species – bank voles and wood mice. If we trap nine bank voles and one wood mouse, the calculated $\exp H'$ is about 1.4 (Gotelli & Chao 2013), even though species richness is 2. This means that $\exp H'$ is equal to that of a hypothetical community with only 1.4 species of equal abundances. If we had trapped

five individuals of each species, true diversity would be the same as species richness.

Compared to the untransformed index, the transformed Shannon index has two advantages for us. First, it is not sensitive to the number of individuals in the dataset (Gotelli & Chao 2013). I take this to be an advantage because in this study the number of individuals caught in each system is comparatively small and varies strongly. Secondly, the index is linear, making it more intuitive for comparing the systems than non-linear indices (Jost 2006, 2010).

On the basis of the exponential Shannon index ($\exp H'$), which I used to calculate true diversity, I calculated evenness according to Tuomisto (2012) and Jost (2010): $Evenness = Diversity/Richness$.

2.6 Statistical analysis

All statistical analysis and visualisation was conducted in the open source program R (version 3.1.3).

2.6.1 Multivariate statistics – Principal Component Analysis

The relationship between the structural habitat factors, such as vegetation, water cover and deadwood, was analysed with principal component analysis (PCA). I used the 'vegan' package in R. The PCA was based on a correlation matrix since some of the variables are in different units (metres, percent) and some altogether without unit, in which case using a covariance matrix is not advisable (Jackson 1991). The data was not tested for normality but distributions were visualised as Q-Q plots (function: *qq.norm*) before analysis.

The variables that entered into the PCA were: tree layer 1 (*T1*, over 10 m, [%]), tree layer 2 (*T2*, 4-10 m, [%]), shrub layer (*S*, 1-3 m, [%]), grass layer (*G*, [%]), dwarf shrub layer (*DS*, [%]), herb layer (*H*, [%]), moss layer (*M*, [%]), boulders (*B*, diameter > 10 cm, [%]), maximum height of non-woody plants (*max. height*, [m]), standing deadwood (*STD*, [no unit]), fine woody debris (*FWD*, diameter < 10 cm, [%]), coarse woody debris (*CWD*, [m], diameter > 10 cm), and water area (*W* [%]). For each system, the average for the variables was calculated in order to obtain one value per system for each variable.

I used PCs that explained more than 15% of the variation, so the scores of these components were used for further analysis in connection with the true diversity, evenness, species richness, and catch size data of the systems. The strength of correlation between the components and these variables, which were considered dependent on the structural habitat factors, was explored with the Kendall's τ and the corresponding test (functions: *cor.test(x, y, method = "kendall")*). This coefficient is non-parametric and can be used on small datasets with non-normal distributions (Field 2009).

2.6.2 Univariate statistics

The data on trapping indices, true diversity and species richness in the different system types and beaver system types were compared statistically. Since evenness was at its maximum (1) in systems with only one species, no meaningful analysis could be based on these values, so no tests were run on this data. Species diversity was also omitted from this analysis since this factor is included in true diversity. Furthermore, the age, weight and trapping index of bank voles (*M. glareolus*) as well as the trapping index of field voles (*M. agrestis*) in the system types and beaver system types were compared. Lastly, I analysed the correlation between system size and variables such as trapping index and true diversity using Kendall's τ .

Due to the small sample size (nine beaver systems and four reference systems), statistical analysis was to a large extent limited to non-parametrical tests. The data was not tested for normality because the usual test for small sample sizes (Shapiro-Wilks)(Rochon et al. 2012) has been shown to be inadequate for these purposes. Histograms of most of the data indicated non-normal distribution. However, weight distribution for subadult bank voles in pioneer and recolonized beaver systems was approximately normal. Means, medians and standard deviations were calculated for all variables and sample populations.

To test whether distributions of certain variables differed between the sample populations, I used a Kolmogorov-Smirnov Z test (function: *ks.test*). It is better suited for small sample sizes (≤ 25) than other comparable tests, e.g. Mann-Whitney U test (Field 2009). Only the mean weights of subadult bank voles in pioneer and recolonized beaver systems were compared with Student's t -test because all assumptions (normality, homoscedasticity) were met.

In some cases, I used the Fligner-Killeen-test (function: *fligner.test*) to test for departures from homoscedasticity (homogeneity of variances). It was chosen for its robustness, as it is non-parametric and less sensitive to departures from normality than comparable tests (Wasserstein & Boyer Jr 1991; Crawley 2007). It has been shown to work well on small sample sizes, although the recommended sample size is still ≥ 7 (Donnelly & Kramer 1999), a requirement that is not fully met by my data ($n_1 = 9, n_2 = 4$).

3 Results

3.1 Abundance and diversity

During September and October 2014, I trapped 108 bank voles (*M. glareolus*), 73 field voles (*M. agrestis*), six common shrews (*Sorex araneus*), one pygmy shrew (*Sorex minutus*), three Eurasian water shrews (*Neomys fodiens*), and four wood mice (*Apodemus sylvaticus*) in the 13 systems (figure 5). The presence of carnivorous small mammals, such as weasels (*Mustela sp.*), was obvious from feeding traces on some of the trapped voles, but did not enter into the data.

Systems B11, B13, B23, B24 and B25 all had a trapping index higher than 10, whereas the other beaver systems had indices between 5.33 (B22) and 7.33 (B14 and B26). The reference systems also had values below 10, ranging from 1.33 (R2) to 8.67 (R1). B24 had the highest value: 20.67 and R2 the lowest.

In R2 only field voles were present, and in R5, I exclusively caught bank voles. In the other two reference systems and B22, I caught two species: bank voles (*M. glareolus*) and field voles (*M. agrestis*). B21 also had two species, wood mice and bank voles. In all the other systems, three species could be detected. In addition to bank and field voles, I caught a pygmy shrew in B11. Common shrews were trapped in systems B13, B14 and B24, and water shrews in B23 and B25. In B26, wood mice were detected along with bank and field voles.

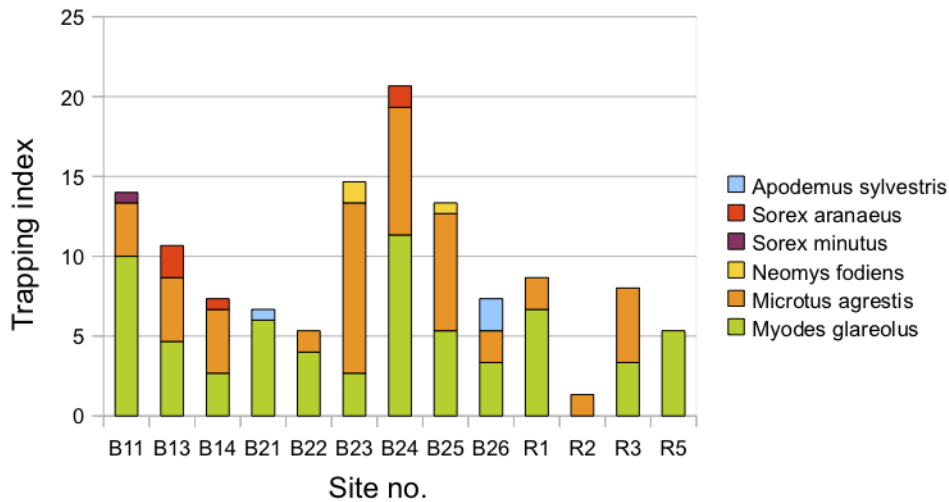


Figure 5: Trapping index (number of individuals caught per 100 trapping nights per study site). System B11 - B26 represent beaver systems and R1 - R5 non-beaver wetland systems.

3.2 Principal Component Analysis of structural vegetation factors

On the structural vegetation data a principal component analysis was conducted. The 14 variables that entered into the PCA were reduced to four principal components. The first two principal components of the PCA together explain 56% of the variation in the data. PC3 (13.85%) and the other nine principal components were excluded for the model for the sake of simplicity. The first principal component explained 36.48%. It was interpreted as a negative variable of ‘beaveriness’, a degree of the influence of beaver activity on the systems. PC2 explained 19.51% of the variation, and appears to be a variable of forest influence as it was dominated by the tree layers and number of stumps.

Table 1: PCA scores of structural habitat factors. Scores ≥ 0.5 are marked blue, scores ≤ -0.5 red.

	PC1	PC2
Tree layer 1	-0.20	0.80
Tree layer 2	0.48	0.63
Shrub layer	0.67	0.27
Grass layer	-0.24	-0.26
Dwarf shrubs	0.85	-0.08
Herb layer	-0.67	0.10
Moss layer	0.85	-0.08
Boulders	-0.16	0.40
Max. height of non-woody plants	-0.12	-0.58
Standing Deadwood	-0.73	-0.11
Stumps	-0.37	0.65
Fine woody debris	-0.71	0.10
Coarse woody debris	-0.81	-0.33
Water	-0.45	0.52

The values for the first principal component decreased with the increase of the beavers’ influence. The component was positively influenced by the reference systems (especially the pioneer systems B23, B24 and B26), and negatively by most of the beaver systems, except for B11 and B21 (see fig. 6 and table 2). Most of the beaver systems clustered in the first and fourth quadrant of the plot, whereas the reference systems formed a cluster in the second and third quadrant. Factors that were most common on lakesides and Sphagnum patches, such as moss (*M*), dwarf shrubs (*DS*), shrubs (*S*), and small trees (*T2*) had a positive influence on PC1 (1. The component was negatively influenced by factors that are typical for beaver systems, such as deadwood (*SDW*, *FWD*, *CWD*), water (*W*) and grass (*G*) (1.

The second principal component (PC2) was dominated by system B22, a forest-system, which had a strong positive influence (table 2). Water surface, high trees, small trees and tree stumps had a strong positive influence on PC2, whereas high

non-woody vegetation had a strongly negative influence on this component (table 1). For all correlations between the structural habitat factors, see the correlation matrix in appendix C.

The correlation between PC1 (a gradient of the beaver’s influence on the systems) and the trapping index was negative ($\tau = -0.42$, $p = 0.05$). PC2 ($\tau = -0.26$, $p = 0.23$) showed little correlation with the trapping index (figures 7a, 7e). True diversity was negatively correlated with the first principal component ($\tau = -0.58$). Kendall’s rank correlation test was significant ($p = 0.006$). $\text{Exp}H'$ is therefore negatively correlated to PC1 (figure 7b). For PC2 ($\tau = -0.12$, $p = 0.58$), the correlation test was not significant (figure 7f). PC1 and species richness were negatively correlated ($\tau = -0.70$, $p = 0.003$) (see figure 7c). Again, the correlation test for PC2 was not significant (PC2: $\tau = -0.06$, $p = 0.78$) (7g). For PC1 and evenness no correlation was indicated ($\tau = 0.29$, $p = 0.18$) (figure 7d). The same went for PC2 ($\tau = -0.10$, $p = 0.62$) (figure 7h). For this last variable, one has to keep in mind that evenness equals 1 for systems with only one species.

Table 2: PCA scores of systems (weighted sums of structural habitat factor scores). Scores ≥ 1 are marked blue, scores ≤ -1 red.

	PC1	PC2
B11	0.26	0.75
B13	-0.57	-0.88
B14	-0.59	-0.12
B21	0.51	-0.14
B22	-0.27	2.48
B23	-1.17	-1.13
B24	-1.16	-0.71
B25	-0.74	1.4
B26	-1.42	-0.4
R1	1.28	-0.42
R2	1.37	-0.44
R3	1.29	-0.95
R5	1.2	0.56

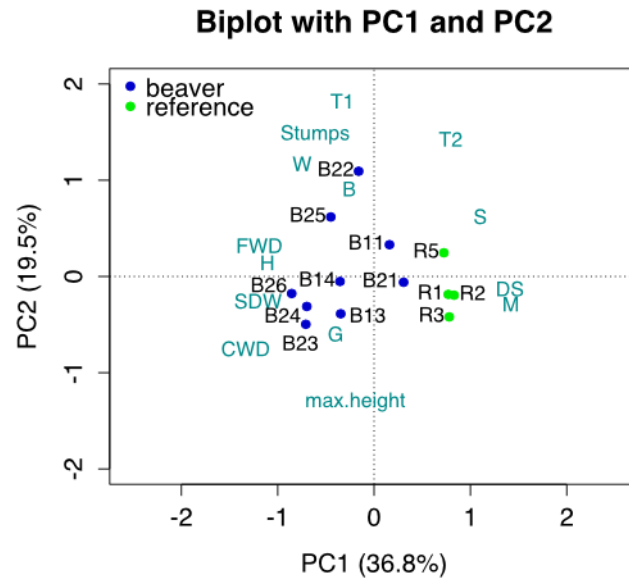


Figure 6: Biplot of principal components 1 and 2 of structural habitat factors. Beaver systems are marked with blue points, reference systems with green points. For abbreviations see 2.6.1. Plotted in R, scaling = 1.

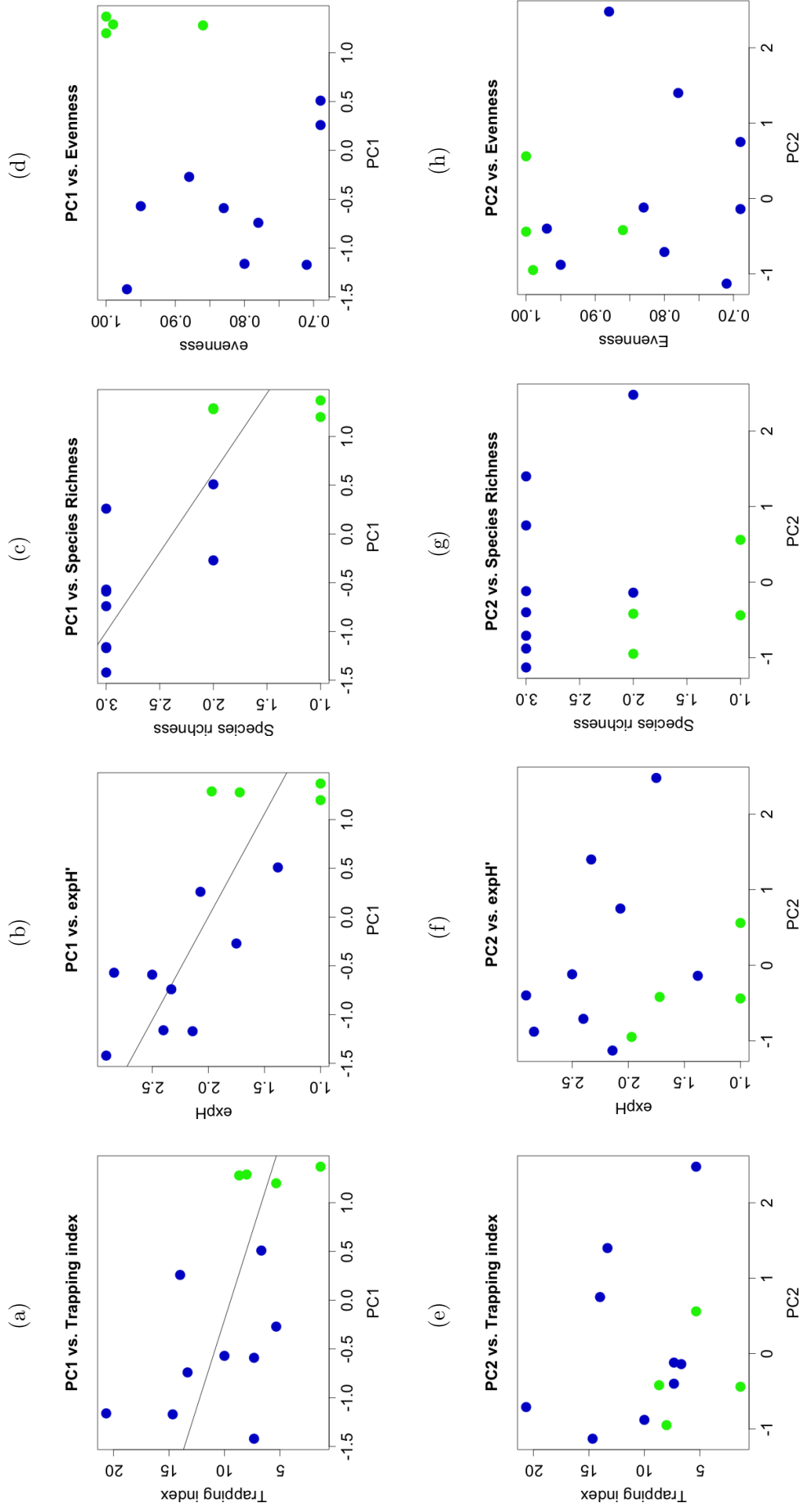


Figure 7: Trapping index, true diversity, evenness, and species richness plotted against 1st and 2nd principal component. Filled green circles denote reference systems, filled blue circles denote beaver systems. Significant correlations ($p < 0.05$) indicated by regression line. Plotted in R.

3.3 Distribution of abundances and species

The two system types (beaver and reference systems) and the beaver system types (pioneer and recolonized systems) were compared on the basis of four variables using the Kolmogorov Smirnov Z test: the trapping index (TI), true diversity ($\exp H'$), the trapping index of field voles (*M. agrestis*) and of bank voles (*M. glareolus*) (tables 3 and 4). The null hypothesis (H_0) was that the distributions of the two sample populations (beaver and reference systems; recolonized and pioneer beaver systems) do not differ. The alternative hypothesis (H_1) was that distributions between the two populations differ in some way (e.g. skewness, variance) (Sokal & Rohlf 1995).

Table 3: Means, medians and standard deviations of different trapping indices and true diversity. TI = trapping index, $\exp H'$ = true diversity, TI_{MA} = trapping index for *M. agrestis*, TI_{MG} = trapping index for *M. glareolus*. \bar{x} = arithmetic mean, M = median, SD = standard deviation.

	Beaver ($n = 9$)				Reference ($n = 4$)			
	TI	$\exp H'$	TI_{Ma}	TI_{Mg}	TI	$\exp H'$	TI_{Ma}	TI_{Mg}
\bar{x}	11.04	2.26	4.52	5.56	5.83	1.42	2.00	3.83
M	10.00	2.33	4.00	4.67	6.67	1.36	1.67	4.33
SD	5.00	0.49	3.80	3.13	3.33	0.50	1.96	2.90

Table 4: Means, medians and standard deviations of different trapping indices and true diversity for recolonized and pioneer beaver systems.

	Recolonized ($n = 6$)				Pioneer ($n = 3$)			
	TI	$\exp H'$	TI_{Ma}	TI_{Mg}	TI	$\exp H'$	TI_{Ma}	TI_{Mg}
\bar{x}	9.44	2.15	3.33	5.45	14.22	2.48	8.00	5.78
M	8.67	2.20	3.67	5.00	14.67	2.40	6.89	3.33
SD	3.61	0.53	2.53	2.51	6.68	0.39	4.44	4.82

First, the trapping indices of the system types were compared. The Kolmogorov-Smirnov Z test returned $p = 0.36$, the Fligner-Killeen test that was run on the data indicated homogeneity of variances ($p = 0.38$). We must therefore assume that there is no significant difference between the system types as far as the trapping index is concerned. Nevertheless, the mean and median of the trapping index were higher in the beaver systems than in the reference systems (table 3). Compared to the recolonized beaver systems, the pioneer systems have a higher mean and median, but also a larger standard deviation (figure 8a, table 4).

For the system types, the Kolmogorov-Smirnov Z test for true diversity returned $p = 0.07$, and the Fligner-Killeen test $p = 0.60$. At a confidence level of 95%, the tests do not indicate different distributions between the two groups. However, the mean and median are higher for the beaver than for the reference systems, even though standard deviations are almost identical (table 3, figure 8c). For the beaver system types, the Kolmogorov-Smirnov Z test does not indicate unequal distributions either ($p = 0.68$). Means and medians are similar (table 4).

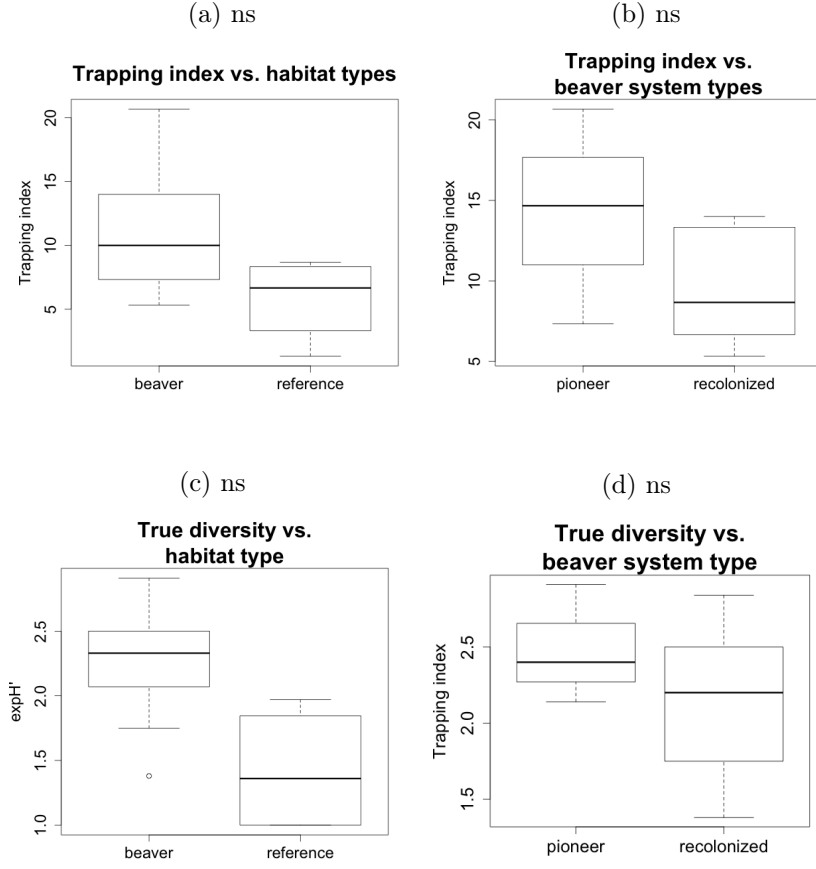


Figure 8: Comparison of true diversity ($\exp H'$) and trapping indices in beaver and reference systems. Boxplots show medians, lower and upper quartile borders (boxes), sample minimum and maximum (whiskers) and outliers (circles). ns = not significant

The Kolmogorov-Smirnov Z test for the trapping indices of bank voles and field voles gives no indication that the populations in the beaver and reference systems have different distributions (field voles $p = 0.72$, bank voles: $p = 0.99$). Distributions are not significantly different in the pioneer and recolonized systems either (field voles: $p = 0.34$, bank voles: $p = 0.70$). However, the mean trapping index for field voles (TI_{Ma}) is higher in the beaver systems than in the reference systems, and the distribution also has a higher standard deviation in the former (table 3 and figure 9a). Within the beaver systems, the mean trapping index for field voles (TI_{Ma}) is higher in the pioneer systems and shows a larger standard deviation (table 4 and figure 9c). For bank voles, the mean and median of the trapping index are similar in the beaver systems and in the reference systems, with a similar standard deviation in both system types (table 3, figure 9b). Recolonized and pioneer systems have similar means for bank voles, but the median is lower and standard deviation is larger in pioneer systems (table 4, figure 9d).

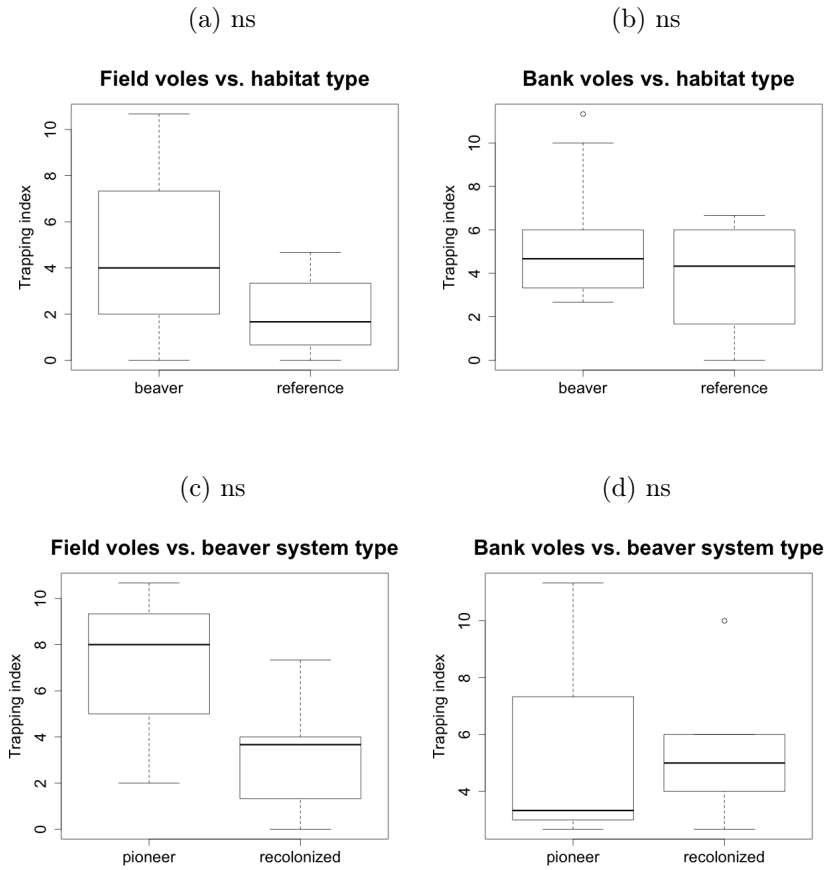


Figure 9: Comparison of trapping indices for field voles and bank voles in beaver and reference systems. Boxplots show medians, lower and upper quartile borders (boxes), sample minimum and maximum (whiskers) and outliers (circles). ns = not significant

3.4 Age distribution of bank voles

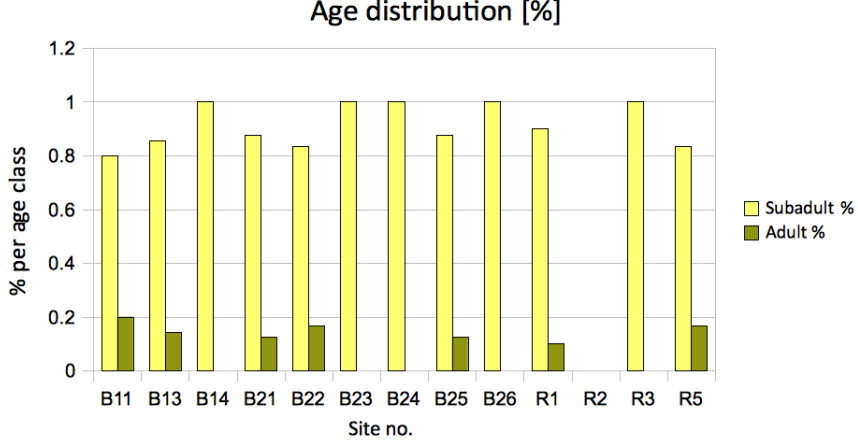


Figure 10: Age distribution of adult and subadult bank voles in percent.

In all systems, the percentage of subadult individuals was higher than that of adults, with no adult bank voles at all in system B14, the pioneer beaver systems (B23, B24 and B26) and systems R2 and R3 (figure 10). Bank voles that were under eight months old showed no signs of maturity and breeding activity and were therefore classified as subadult. In total, 94 of the bank voles were classified as subadults and nine as adults.

The trapping index for adult and subadult bank voles was similar for beaver and reference systems (see figures 11a and 11b). There was no indication that distributions of subadult bank voles differ significantly between the system types (Kolmogorov-Smirnov Z : $p = 0.96$) or the beaver system types ($p = 0.98$). For the distributions of adult voles in beaver and reference systems, the Kolmogorov-Smirnov Z test returned $p = 1$ and for pioneer and recolonized systems $p = 0.12$. There was low correlation between both of the age groups and PC1 (subadults: $\tau = -0.07$, adults: $\tau = 0.19$).

Table 5: Means, medians and standard deviations of subadult and adult bank vole trapping indices in beaver and reference systems. TI_S = trapping index subadults; TI_A = trapping index adults; \bar{x} = arithmetic mean; M = median; SD = standard deviation. For sample population sizes (n) see table 3

	Beaver		Reference		Recolonized		Pioneer	
	TI_S	TI_A	TI_S	TI_A	TI_S	TI_A	TI_S	TI_A
\bar{x}	7.33	0.78	4.75	0.50	6.83	1.17	8.33	0
M	6.00	1.00	5.00	0.50	6.50	1.00	5.00	0
SD	4.44	0.97	3.69	0.58	2.79	0.98	7.57	0

The mean and median for the trapping index of subadult bank voles are higher for the beaver systems than for the reference systems, and standard deviations are similar (table 5). For pioneer and recolonized systems the situation is less

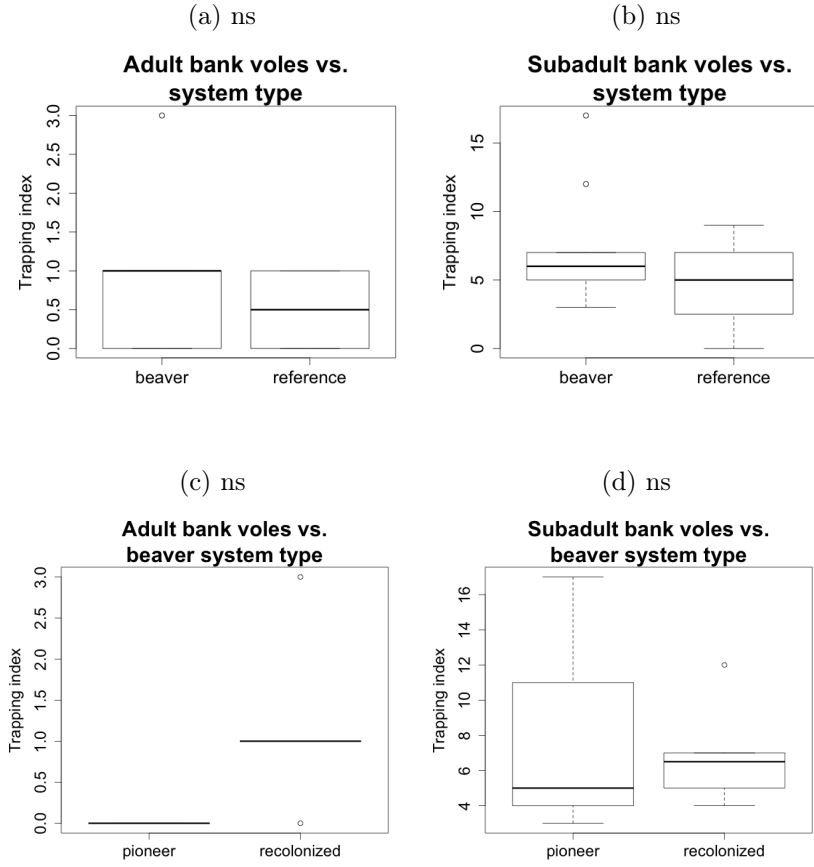


Figure 11: Comparison of adult and subadult bank vole trapping indices in beaver and reference systems. Boxplots show medians, lower and upper quartile borders (boxes), sample minimum and maximum (whiskers) and outliers (circles). ns = not significant

clear. The pioneer systems have a higher mean for subadult bank voles but a lower median than the recolonized systems, and a comparatively large standard deviation. Values for adult bank voles were consistently low over all systems but in pioneer systems no adult voles were caught at all.

3.5 Weight distribution of bank voles

There was no significant difference in weight between subadult bank voles in beaver and reference systems (Kolmogorov-Smirnov Z : $p = 0.51$) (table 6, figure 12). However, the weights of subadult bank voles differed within the beaver systems: Mean weight of subadult voles in pioneer systems was higher than in recolonized systems (figure 12b). For these data, distributions were approximately normal and variances were equal (Fligner-Killeen: $p = 0.84$). Therefore, Student's t -test was used to compare the means of the two groups ($p = 0.001$). Weights of adult bank voles were not compared because of the small sample sizes

($n_1 = 4, n_2 = 2$).

Table 6: Means, medians and standard deviations of weight of subadult bank voles in beaver and reference systems. \bar{x} = arithmetic mean; M = median; SD = standard deviation.

	Beaver	Reference	Recolonized	Pioneer
	$n = 65$	$n = 19$	$n = 40$	$n = 25$
\bar{x}	18.23	18.56	17.60	19.24
M	18.07	17.81	17.55	19.54
SD	2.09	3.12	1.72	2.25

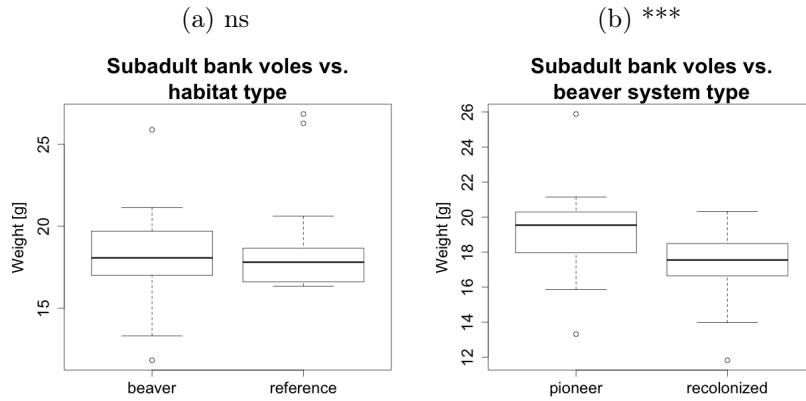


Figure 12: Distribution of subadult voles' weight in grams for the different systems, including outliers. ns = not significant; *** = $\alpha \leq 0.001$

3.6 Possible spatial influences

The beaver systems chosen for this study tended to be larger than the reference systems (figure 13). While the reference systems had an area between 0.5 and 2 ha, the beaver systems were up to 3.2 ha, and about half of them were larger than 1.5 ha (figure 13). Although distributions do not differ significantly (Kolmogorov-Smirnov: $p = 0.61$), it was necessary to investigate the relationship between trapping index, true diversity and the area of the systems.

Correlation between true diversity and system area was low ($\tau = 0.25$), and the same goes for the correlation between system area and trapping index ($\tau = 0.29$). No correlation was therefore indicated between either true diversity or the trapping index and the area of the system (compare figures 14a and 14b).

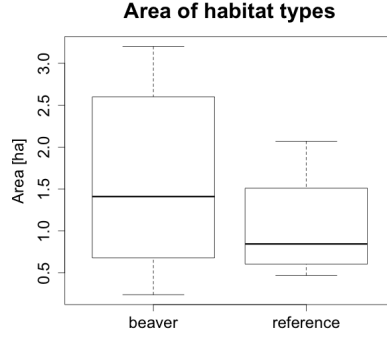


Figure 13: Area of beaver systems and reference systems [ha] as boxplot. Boxplots show medians, lower and upper quartile borders (boxes), sample minimum and maximum (whiskers) and outliers (circles).

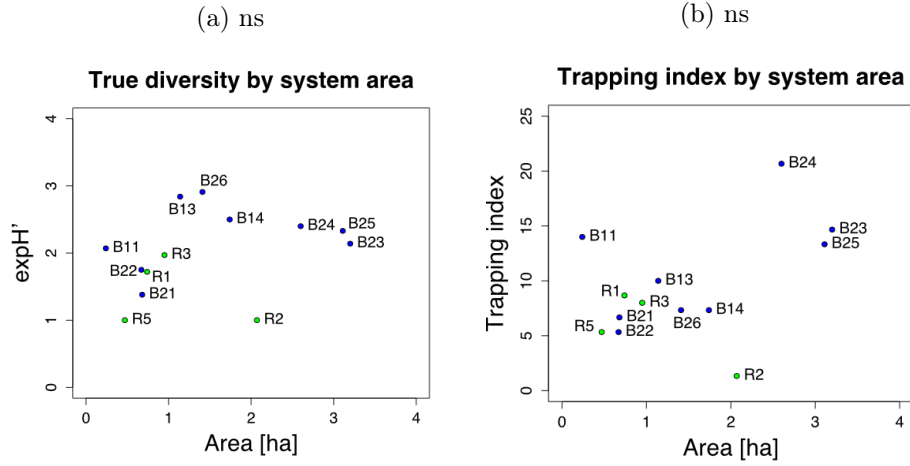


Figure 14: Scatterplots of true diversity and trapping index values by study site area in hectares. Beaver systems are shown in blue, reference systems are shown in green. ns = not significant

4 Discussion

4.1 Habitat heterogeneity

A high amount of deadwood is assumed to lead to better living conditions for small mammals because stratification increases the availability of shelter and food (Hansson 1978; Ecke et al. 2001; Rosell et al. 2005). Habitat heterogeneity at micro-level was therefore assessed on the basis of structural habitat factors, especially on the presence of deadwood. The beaver systems in this study clearly had a higher amount of woody debris and fallen logs than the reference systems (figure 6). The reference systems were associated with vegetation such as dwarf shrubs and mosses whereas beaver systems had a higher percentage of grassy

and herbal vegetation, which provide small mammals with food, shelter and cover from aerial predators. On a micro-level, it can therefore be assumed that beavers have a positive influence on habitat heterogeneity.

4.2 Linking structural habitat factors, abundance, and species diversity

Despite the non-significant results of the Kolmogorov-Smirnov Z tests (at the confidence level of $\alpha = 0.05$), the correlation analysis provides us with valuable information on the relationship of beavers and small mammals. Trapping index, true diversity and species richness were clearly correlated with the influence that beavers have on the systems. PC1, which was negatively influenced by habitat factors associated with beavers (standing deadwood, coarse and fine woody debris), was negatively correlated with all three of the aforementioned variables (table 1). In systems with a strong beaver influence, trapping index, true diversity, and species richness were higher than in those with low influence of beavers and particularly higher than in the reference systems (figure 7). This supports the hypothesis that some small mammal species might find better living conditions in beaver systems than they do in other lakeside wetland habitats. Shrews (*S. minutus*, *S. aranaeus*, *N. fodiens*) and wood mice were trapped in beaver systems only, which indicates that for these species, the reference systems are not attractive habitats.

Why then could no significant differences be detected in the distributions of trapping index and true diversity values between the systems? It is likely that with the present data, the sample size of this study and the tests used, there is a high chance of making a type II error and accepting the null hypothesis when in fact it would be correct to refute it. The power of a statistical test depends on sample size and the size of the effect that can be detected (Sokal & Rohlf 1995; Norman 2010; Nakagawa & Cuthill 2007). If either of these are too small, the test's power is not satisfactory. Although much attention was paid to choosing an appropriate test for the sample sizes and distributions obtained in the sampling, the Kolmogorov-Smirnov Z test has its limitations. It is less powerful than the Mann-Whitney U -test because its null hypothesis is broader (Sokal & Rohlf 1995). However, with the given sample sizes, the power of the Mann-Whitney U -test is also questionable. It is possible that for the Kolmogorov-Smirnov Z test as well sample sizes and/or effect sizes were too small for the test to have sufficient power. Since power was not calculated, I can only speculate about this aspect.

Pearson (1931) and Norman (2010) have suggested that using Student's t -test is appropriate also for skewed data and small sample sizes. On the one hand, using Student's t -test might reduce the probability of making a type II error because it is less conservative than the Kolmogorov-Smirnov Z test. On the other hand, it might increase the type I error rate (Winter 2013). De Winter (2013) proposed that t -tests can be used with small sample sizes if the expected

effect size is large. Nagakawa & Cuthill (2007) refer to an effect size of $d = 1.2$ as 'large' in biology but caution against using benchmark values too rigidly. They also point out the importance of giving confidence intervals. Prevedello et al. (2013), who investigated small mammal studies on food supply and population densities, report 93 effect sizes (Hedge's d) that range between $|0.01|$ and $|7.79|$, and have an average of 1.2. It is therefore unlikely that the present study will have an effect size that would be considered 'large' by de Winter, who mentions effect sizes of up to 32 (2013). This is especially considering that, due to the comparatively small differences in means, the confidence interval would probably be large in comparison to the effect, which again limits the test's explanatory power (Nagakawa & Cuthill 2007). I argue, therefore, that with the present data, the choice was between having a higher chance of making type I or type II errors and not between more or less appropriate null-hypothesis tests. For further research, I therefore suggest increasing the number of reference systems.

As far as the relationship between true diversity, species richness and "beaver-iness" (PC1) is concerned, the results of the correlation analysis support my hypothesis that beavers can have a positive influence on these variables. Systems that had PC1-values over -0.25 (B11, B21, B22 and all reference systems) had low true diversity. B11 was a recently abandoned system surrounded by forest, with low amounts of deadwood in the system itself, B21 was a grass-dominated system close to agricultural area, and B22 was mainly forest. In the reference systems, mosses and dwarf shrubs were the dominant vegetation. The common factor here was the low amount of lying deadwood and woody debris that could provide structural diversity on a micro-level and the presence of dwarf shrubs, which were absent from all other systems. Species that were recorded as dwarf shrubs were: *Alnus viridis*, *Andromeda polifolia*, *Betula nana*, *Calluna vulgaris*, *Empetrum nigrum* and *Vaccinium sp.*. It is possible that the dominance of dwarf shrubs and mosses in these systems limited the availability of other food plants and insects important for small mammals, especially for shrews, and was therefore negatively linked to true diversity and species richness. Species diversity of Lepidoptera, a prey of common shrews (Hansen et al. 2009), is, for example, negatively influenced by upcoming dwarf shrubs (Erhardt & Thomas 1991). Furthermore, Johannesen & Mauritzen (1999) have shown that bank voles tend to avoid shrub-dominated areas, possibly due to interspecific interaction with grey-sided voles. I suggest that beavers are able to create a type of habitat that provides vegetation and structural conditions that favour diversity of small mammals. However, this depends on the specific characteristics of the beaver system, as systems with "atypical" conditions (low amount of grassy and herbal vegetation) are not favourable for small mammal diversity and species richness.

No direct correlation was found between PC2 (forest influence) and trapping index, true diversity and species richness respectively. Most systems, beaver and reference systems alike, were influenced by the surrounding forest vegetation, but this proximity seems to have had no large influence on either of the variables under investigation. Generally speaking, bank voles, *M. glareolus*, are a woodland species, and field voles, *M. agrestis*, a herbivorous grassland species (Hansson

1983). However, the bank vole eats a variety of food, including invertebrates and seeds, and is therefore also found in grasslands (Hansson 1983, 1985). Wood mice, *Apodemus sylvaticus*, despite their name, are found in grasslands as well as woodlands (Montgomery 1989). Common shrews *Sorex araneus* and pygmy shrews *Sorex minutus* in a study by Canova (1992) were shown to occur in a variety of habitats, such as reed beds and woodland. Eurasian water shrews are found in different kinds of wetland and humid habitats (Spitzenberger 1999). All of the species trapped in this study have been known to use woodland habitat. Their diversity and abundance is therefore not likely to be influenced by the presence of forests surrounding the systems to an extent that would be significant.

Looking at the boxplots, however, field voles had a higher trapping index median in pioneer beaver systems compared to recolonized systems, while bank voles seemed to prefer recolonized systems (figure ??). This is not surprising, considering that the pioneer systems were dominated by grasses and reeds, such as *Carex* sp., *Phalaris arundinacea* and *Phragmites australis*. The recolonized systems, especially B22 (which was in a forest), B25 and B11 (which ran parallel to the forest edge), as well as B21, had a higher tree cover than the trapping lines in the pioneer systems. They were also more prone to being invaded by bank voles from the surrounding forest.

As I have stated earlier, home ranges of the small mammal species investigated here may vary in size. They might wholly be comprised in the study systems, or only partly overlap with them. In order to draw more specific conclusions on the use small mammals make of beaver systems, it is necessary to look at the extent to which their home ranges lie in beaver systems, and at how much time they actually spend there. This, however, requires a different trapping design from the one I used. To investigate habitat use I suggest using live traps instead of snap traps and arranging them in a trapping grid instead of a trapping line. This way the small mammals' movements in the landscape can be observed by the researcher. Here, the main challenge might be to find a size for the trapping grid that reflects the animals' ranges of movement in the beaver systems and, possibly, the adjacent forests.

4.3 Assessing habitat quality – age structure and weight of bank voles (*M. glareolus*)

According to Gliwicz (1993), adult bank voles that have survived the winter establish territories in optimal habitats. The adult bank voles trapped in systems B11, B21, B22 and B25 were all older than twelve months. They probably had their home ranges in or close to these systems. Adult bank voles were absent from system B14, the pioneer beaver systems (B23, B24 and B26) and reference systems R2 and R3. This indicates that for bank voles, these systems might constitute suboptimal habitat that is only used when population pressure is high in the optimal habitat. However, Gliwicz (1993) also found that young bank voles born in the summer months and early autumn did not disperse. Since

subadult bank voles were found in all systems, it is difficult to assess whether they dispersed to the habitat they were caught in, were born there, or only moved there in search for food.

Cyclicality is an issue when considering vole abundances in different habitats. It has already been mentioned that in peak years, voles-of-the-year are abundant and typically do not reach breeding maturity (Boonstra 1994 and Tkadlec & Zejda 1998). In this study, over 80% of the voles caught were classified as subadults, due to their age and their reproductive organs' state. It is therefore possible that there was a vole peak in southern and central Sweden in autumn 2014, even though the peak was expected for 2015 (Frauke Ecke, personal communication). Since voles are especially abundant during peak years, and are therefore forced to disperse to suboptimal habitat, it is difficult to make statements about habitat attractiveness based on their numbers during this phase of the cycle.

As far as the weight distribution of subadult bank voles in the systems is concerned, no differences were detected between reference and beaver systems. Independent of how attractive the habitats were for the voles, their quality as far as food is concerned seems to be similar. Subadult voles in pioneer beaver systems were heavier than in recolonized systems. This could be due to the better availability of food or better quality of food. It has been pointed out that habitat attractiveness and habitat quality are not necessarily correlated – animals might find low quality habitat attractive because they misjudge its quality (Kristan 2003). It is also possible that, due to the dominance of grasses in the pioneer systems, bank voles did not find the pioneer systems attractive as a breeding habitat in spring but found good living conditions there later in the year (Gliwicz 1993).

I recommend that a study focused on assessing the quality of beaver systems for small mammals should take care to gather data from different phases of cycles if cyclic species are studied. Also, I suggest focusing on a species associated specifically with wetland habitats, such as the Eurasian water shrew (*Neomys fodiens*) or the European water vole (*Arvicola amphibius*). Another possible focus species is the Eurasian harvest mouse (*Micromys minutus*), whose numbers have declined in Europe, probably due to habitat loss (Aplin et al. 2008). The harvest mouse is difficult to trap and might have been present in the systems without being detected (Harris 1979). It is commonly associated with wetlands and grasslands, showing a preference for *Carex sp.* and ruderal vegetation (Churchfield et al. 1997; Surmacki et al. 2005). Habitat quality could also be assessed on the basis of parasites found on the animals (Cockle & Richardson 2003).

5 Conclusion and recommendations

Due to their ecosystem engineering activities, beavers create ponds and riparian zones littered with deadwood, providing heterogeneous micro-habitats for a variety of small mammal species. I have been able to show in this study that Swedish beaver systems have a higher amount of woody debris than lakeside habitats with comparable riparian zones. The amount of coarse and fine woody debris in this study was positively correlated with small mammal abundance and species diversity, and seemed to be especially important for the presence of shrews. Beavers provided micro-structures that offer shelter and cover to ground-dwelling rodents and insectivores, and were therefore clearly able to enhance habitat heterogeneity and diversify landscape structures to the benefit of small mammal species in the systems studied.

For bank voles (*M. glareolus*), pioneer beaver systems, with their dominant grass layer, apparently offered better living conditions than recolonized beaver systems. However, it was shown that, since the bank vole is a habitat generalist and is ubiquitous in peak years, it is not actually a suitable study species for research questions directed at habitat quality and attractiveness of beaver systems (see also Ulevičius & Janulaitis 2007).

In order to determine habitat quality and attractiveness of beaver systems for small mammals, I recommend focusing on small mammal species other than voles, such as shrews and mice. To avoid unnecessary destructive sampling of voles, I suggest live-trapping, the use of tracking-tubes and nest identification (Glennon et al. 2002). In case of live-trapping, the presence of fur parasites could possibly be used as an indicator of habitat quality, and the method can be combined with the spool-and-line technique as described by Boonstra & Craine (1986).

Further research is necessary to investigate the actual time small mammals spend in beaver systems, and to determine the extent to which trophic interactions play a role in habitat quality for small mammals in beaver systems. Beavers have been shown to have positive as well as negative effects on terrestrial and freshwater invertebrates (Rosell et al. 2005; Bailey & Whitham 2006; Hood & Larson 2014), which might have effects on species further up in the food chain.

It is also advisable to use a higher number of reference systems than were used for this study, in order to improve the sample size for statistical analysis. This recommendation is not only based on the fact that group-wise null hypothesis testing was difficult with the respective sample sizes of $n = 9$ and $n = 4$ for the two groups. Correlations, which were used here to explore the relationship between structural habitat factors and small mammal diversity, can also be displayed better when based on a larger number of data points. One should keep in mind that beaver systems are a very heterogeneous group of habitats. When studying small mammals in beaver systems, correlations are probably better suited to display the gradual relationships of environmental factors and variables such as biodiversity than group-wise comparisons.

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Appendix

A Coordinates of trapline start and end points

Table 7: Coordinates of trapping line start and end points (RT90)

Trapline ID	Start X	Start Y	End X	End Y
11a	6949553	1570501	6949524	1570516
11b	6949484	1570553	6949474	1570579
13a	6912211	1553191	6912231	1553179
13b	6912229	1553161	6912199	1553170
14	6901389	1552187	6901341	1552179
21	6570090	1444850	6629302	1489206
22	6568860	1446471	6568804	1446541
23a	6621009	1516211	6620984	1516229
23b	6620988	1516248	6618339	1512349
24	6618384	1512363	6620970	1516267
25	6629324	1489264	6629302	1489206
26a	6630674	1507311	6630657	1570325
26b	6630651	1507336	6630667	1507320
Ref 1	6907877	1547357	6907817	1547350
Ref 2	6911019	1553402	6911010	1553468
Ref 3a	6629857	1511051	6629834	1511066
Ref 3b	6629831	1511121	6629848	1511142
Ref 4	6573196	1445544	6573162	1445606
Ref 5	6574202	1443515	6574156	1443501
Ref 6	6573205	1439080	6573171	1439026

Note that this table includes coordinates for reference sites 4 and 6, which were excluded from the results and analysis because of continuity issues. The Swedish moose hunting season interfered with the trapping in these locations.

B Mapping protocol of structural habitat factors

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Structural habitat factors		
Site no. / Station no.	Habitat type	Region
GPS coordinates (RT90)		X: Y:
Date	Signs of beaver activity	Type of water body
Comments (e.g. beaver activity, special landscape features...)		

Tree layer 1 (%)	Tree layer 2 (%)	Shrub layer (%)	Grasses (%)	Moss (%)
Dwarf shrubs (%)	Herbs (%)	Boulders > 10cm (%)	Max. height (cm) of herbal layer	Stumps
Standing dead wood	FWD, $\varnothing < 10\text{cm}$ (%)	CWD, $\varnothing > 10\text{cm}$ (running m)	Water (%)	

Dominant species

Species	Dominance (%)	Species	Dominance (%)

C Correlation matrix

Table 8: Correlation matrix of structural habitat factors

	T1	T2	S	G	DS	H	M	B	max. height	SDW	Stumps	FWD	CWD	
T1	1.00	0.03	-0.21	-0.10	-0.25	0.32	-0.21	0.23	-0.29	0.23	0.49	0.29	0.16	0.29
T2	0.03	1.00	0.67	-0.23	0.43	-0.13	0.43	0.05	-0.16	-0.18	0.05	-0.17	-0.38	-0.08
S	-0.21	0.67	1.00	-0.25	0.57	-0.40	0.57	-0.02	-0.27	-0.41	-0.12	-0.21	-0.55	-0.25
G	-0.10	-0.23	-0.25	1.00	-0.33	-0.03	-0.37	0.36	0.21	0.00	0.24	0.01	0.22	-0.10
DS	-0.25	0.43	0.57	-0.33	1.00	-0.39	0.85	-0.30	-0.19	-0.51	-0.34	-0.57	-0.78	-0.30
H	0.32	-0.13	-0.40	-0.03	-0.39	1.00	-0.25	-0.06	0.05	0.44	0.24	0.32	0.50	0.21
M	-0.21	0.43	0.57	-0.37	0.85	-0.25	1.00	-0.35	-0.27	-0.38	-0.44	-0.39	-0.68	-0.32
B	0.23	0.05	-0.02	0.36	-0.30	-0.06	-0.35	1.00	-0.09	-0.15	0.42	0.14	0.00	-0.06
max.height	-0.29	-0.16	-0.27	0.21	-0.19	0.05	-0.27	-0.09	1.00	0.03	0.00	-0.17	0.22	-0.13
SDW	0.23	-0.18	-0.41	0.00	-0.51	0.44	-0.38	-0.15	0.03	1.00	0.21	0.30	0.56	0.31
Stumps	0.49	0.05	-0.12	0.24	-0.34	0.24	-0.44	0.42	0.00	0.21	1.00	0.23	0.32	0.32
FWD	0.29	-0.17	-0.21	0.01	-0.57	0.32	-0.39	0.14	-0.17	0.30	0.23	1.00	0.47	0.40
CWD	0.16	-0.38	-0.55	0.22	-0.78	0.50	-0.68	0.00	0.22	0.56	0.32	0.47	1.00	0.43
W	0.29	-0.08	-0.25	-0.10	-0.30	0.21	-0.32	-0.06	-0.13	0.31	0.32	0.40	0.43	1.00

T1 = tree layer 1; T2 = tree layer 2; S = shrub layer; G = grass layer; DS = dwarf shrub layer; H = herb layer; M = moss layer;

B = boulders; max.height = maximum height of non-woody vegetation; SDW = standing deadwood; FWD = fine woody debris;

CWD = coarse woody debris