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**Faculty of Natural Resources and Agricultural Sciences**

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Uppsala 2014

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**Credits:** 30 hec
**Level:** Second cycle, A2E
**Course title:** Independent Project/Degree project in Biology – Master's thesis
**Course code:** EX0565
**Programme/education:** Master Program in Limnology Uppsala University

**Place of publication:** Uppsala
**Year of publication:** 2014
**Online publication:** http://stud.epsilon.slu.se
**Cover photos:** Beaver pond No. 2 north of Luleå, Joel Lönnqvist 2013

**Keywords: beaver pond, *Castor fiber*, aquatic plants, hydrophytes, helophytes, macrophytes, catchment, nitrogen, landscape, plant dispersal**

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## Abstract

The European beaver *Castor fiber* is considered an ecosystem engineer and a key species because of its dam building behavior. Little is known about the factors affecting plant diversity in beaver impounded streams. This study aimed to investigate if local and landscape variables affect plant diversity of beaver ponds. Plant inventories were performed in 12 different ponds in three different latitudinal regions and the vegetation data collected was compiled into groups according to Raunkiear life form and dispersal traits. Landscape variables related to the catchments of the beaver ponds were processed in a geographic information system (GIS). The total plant diversity in the beaver ponds could not be explained by landscape variables while diversity of water-associated terrestrial plants grouped together with aquatic plants did show correlations with landscape variables. The median richness was the same upstream as downstream for the total plant species. All other water-associated groups, however, had greater median richness downstream the beaver pond than upstream. This study concluded that landscape variables such as total stream length in the catchment, total number of lakes in the catchment and catchment size is correlated with the diversity of aquatic and water-associated terrestrial plants in beaver ponds. It was also concluded that streams and their riparian zones have lower median plant richness upstream than downstream a beaver pond.

**Keywords**: beaver pond, *Castor fiber*, aquatic plants, hydrophytes, helophytes, macrophytes, catchment, nitrogen, landscape.

## Glossary

**Total** – All the plant species found
**FM** – Terrestrial plants with a seed floating time greater than a week and macrophytes
**M** – Macrophytes
**FHy** –Terrestrial plants with a seed floating time greater than a week and hydrophytes
**Hy** – Hydrophytes

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# Introduction

Current trends show that the populations of many mammalian species worldwide are in decline and an increasing number of species are being threatened by extinction. With this known, reintroductions of species to areas where they were historically present but have now gone extinct are being applied on a large scale as a measure of conservation (Hoffman et al. 2011). However, whereas the effects of reintroductions have been extensively studied on the species level, there is surprisingly little research on the effects species reintroductions have on the ecosystem level (Armstrong & Seddon 2008). It has been argued that the aims of reintroductions should focus on ecosystem functioning rather than on species composition and prioritization should be given to species that act as ecosystem engineers. For making guidelines and predicting the success of future reintroductions, research on the impacts of historical reintroductions and their effects on ecosystem functioning are of great relevance (Armstrong & Seddon 2008).

In late 19th century the European beaver *Castor fiber* was exterminated in Sweden but after successful reintroductions the population has grown and has now recolonized much of its former range (Hartman 1993). This provides a unique opportunity to study which effects a reintroduction of an ecosystem engineer has on its environment.

## *Beaver population in Europe and Sweden*

In the early 20$^{th}$ century, the European beaver had been decimated into eight fragmented populations consisting of about 1200 specimens (Halley & Rosell 2003). This great decline in numbers was due to a long period of overexploitation caused by the high demand for priced castoreum and beaver pelts (Rosell et al. 2005). In Sweden, the beaver population had gone extinct sometime in the early 1870s and when a national ban on hunting was established in 1873 it was already too late for the population to recover. After the beaver had been extinct for about fifty years, two beavers from southern Norway were transferred from their last remaining population in Scandinavia and reintroduced to western Sweden (Hartman 1993). Between 1922 and 1939 80 beavers were released in different sites throughout Sweden and recolonization began (Ellegren et al. 1993).

Similar introductions took place, and are still taking place, in other parts of Europe and this together with relieves on the hunting pressure has led to a steady increase of both the population and its distribution range. Beaver populations are continuously expanding their range into habitats that until recently have been without beavers for up to 1000 years (Halley & Rosell 2003). Since the population went through a bottleneck in the early 20$^{th}$ century, the genetic variation within the current populations is small. The success of the beaver reintroduction programs shows that even though the genetic variation in the founder population is low, a reestablishment of a population can be successful (Ellegren et al. 1993).

## *Beaver as an ecosystem engineer*

The definition of ecosystem engineering species according to Jones et al. (1994) is as follows: "Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials." Beavers are well known for their tree-felling and dam-building behaviors that lead to profound modifications of the hydrology of waterways, creating wetlands that can remain for hundreds of years (Jones et al. 1994). As a result of this behavior, organic matter and sediments are held in the wetlands, water chemistry is altered, the riparian zone changes its structure and the downstream habitats are changed. This might also have a cascading effect on the constitution and diversity of other organisms (Jones et al. 1994).

If an ecosystem engineer is to increase the species richness at a landscape level, it has to create patches with combinations of conditions that are not present elsewhere in the landscape. Furthermore, the species present in the engineered patches should not be present in patches that are left unmodified. There should be no assumptions made that an engineered patch should hold higher or lesser species richness than an unmodified one. Instead, research on species richness in patches have found that patches modified by ecosystem engineers can have both higher and lower species richness than patches which have been left untouched (Jones et al. 1997). The habitat patch dynamics created in the landscape by beavers in interaction with the terrain through foraging and dam-building create an alternating abundance of habitats for hydrophytes, fish, reptiles, birds and woodland herbs and trees (Picket et al. 2000).

## *Landscape effects*

The landscape altering effects of the North American beaver *Castor canadensis* has been studied extensively while the European beaver has received less attention. The European beaver's dam-building behavior is similar to its North American relative (Rosell et al. 2005). The only study performed on the hydrogeomorphic effects of the European beaver concluded that beavers create large wetlands, extend the areas of open water surfaces and increase the calm reaches of streams through damming. Also, beavers were found to increase the total water flow length of the streams by diverting the flow onto floodplains. When diverting the waterways it often leads to the creation of many smaller streams that later on merge and rejoin the original stream. With time, this multi-channeled drainage network leads to gradual avulsion, and eventually the relocation of the stream channel. The heterogeneity of streams increases by the constant altering of the water table, changing stream velocity and maintaining floodplains (John & Klein 2004, Burchsted et al. 2010). The depositions of sands and organic silts are intensified within beaver ponds through sedimentation and the channel-bed and ditches have been recognized as places where the highest amounts of sediments are deposited while smaller amounts get stored on the submerged floodplains (John & Klein 2004). One study examined aerial photos of an area which had no or very few beavers initially, but 60 years later a large beaver population was established and as a consequence it had changed 13 % of the landscape from forest to meadows and ponds (Naiman et al. 1994).

By constantly altering depth of the water table, flooding areas, and alternating between colonizing and abandoning patches, the beavers create disturbance that increases landscape-level heterogeneity (Johnston & Naiman 1987, Wright et al. 2003). Beaver meadows are sites that have previously been flooded by beavers and when abandoned, turned into wet meadow-like patches of habitat that differ from the surrounding landscape (Figure 1, p 13) (Wright et al. 2002). Species are different in their ways of colonizing and adapting to different abiotic conditions, therefore, internally heterogeneous patches are more likely to have higher species richness than internally homogenous patches (Hutchinson 1959). Beaver ponds could be regarded as islands in the island biogeography sense. The biogeography theory suggests that the bigger and the less isolated an island is, the more species it will hold (Macarthur & Wilson 1967). This is due to the fact that larger, less isolated islands receive greater rain of dispersing life forms than more isolated and smaller ones (Simberloff & Wilson 1969).

## *Hydrological and geomorphological effects*

Beaver activities are likely to have been playing a significant role as a driving factor of floodplain development along low order rivers in Central Europe during the quaternary period (John & Klein 2004). When making assessments of the ecological status of streams and developing waterway restoration projects, the desired goal is often to return to the unaltered or pristine state of a stream (European Union 2000). What should be kept in mind then is that historical times saw beaver populations which were so large that they had a major impact on making the landscape in the northern boreal zone what it is today. The concept of the unaltered stream ecosystem should recognize the ecosystem engineering roles of beavers, as watersheds with beavers are considerably different biogeochemically than those without beavers (Naiman et al. 1988).

When constructing dams in streams beavers extensively alter the stream morphology and water flow, and create aquatic or semiaquatic habitats that without the presence of beavers would be terrestrial. The construction of a beaver dam has multiple effects on the hydrology, not only locally, but also in the catchment as a whole (Woo & Waddington 1990, James et al. 2005 and Jones et al. 1994). Streams with woody debris dams retain water 1.5–1.7 times longer (Ehrman & Lamberti 1992) than streams with a minimal amount of woody debris, and it has been argued that beaver dams can have a great effect on the water retention time within rivers (Gurnell 1998).

Having beaver dams in a watershed has shown to cause lesser annual discharge due to greater evaporation and increased groundwater recharge

(Westbrook et al. 2006). The ponds created above beaver dams serve as reservoirs keeping water discharge at generally stable levels with lesser fluctuations. The ponds can serve as a source of water for the discharge during droughts while it impairs the effects of flood peaks in time of deluge (Westbrook et al. 2006, Correll et al. 2000).

Beaver activities through damming and flooding create patches of varying water table depth and heterogeneous patches containing soils with varying water content. Studies in mountainous regions of North America have shown that the presence of beaver ponds has a great impact on the groundwater flow patterns over vast areas (Westbrook et al. 2006.) In a study performed in a lowland area with flat topography, however, no beaver-induced influence on groundwater flow was shown (Woo et al. 1990). Beaver induced inundation does not only occur upstream the dam but new areas of surface waters have been observed to form downstream the dams. This is made possible through a rise in groundwater table and the diversion of the stream over the floodplain and then back again to the original course (Westbrook et al. 2006.) By maintaining the soil waterlogged for prolonged periods of time, the many processes altering the water table caused by beaver dams are of great importance for the shifts in soil types and beavers are playing a crucial part in the formation and sustention of riparian wetlands (Westbrook et al. 2006).

### *Sedimentation*

Beaver inhabited streams compared to non-beaver inhabited streams have been shown to have greater primary production, probably due to the greater nutrient availability caused by sediment retention and processing of organic matter in the hyporheic zone (Coleman & Dahm 1990). The beaver ponds hold large quantities of sediments just upstream the dam which is retained there during the time the dam is maintained and the beavers are active (Visscher et al. 2013). The thickness of the sediments is greater just upstream the pond and seems to be more evenly distributed if there are dams both in the upstream and downstream ends of the pond. The low velocities through these ponds probably influence sediment distribution (Visscher et al. 2013). The filtering effects linked to increased sedimentation in beaver ponds and the creation of more heterogeneous waterways, give beavers great potential to contribute to catchment management as well as wetland and stream restoration (Burchsted et al. 2010, Visscher et al. 2013).

### *Effects on water chemistry*

The shifts in hydrology alter the chemical element storage from the forested vegetation into soils of wetlands and meadows and sediments of ponds and macrophytes play an important role in changing the water chemistry by settling bottom sediments, and storing and taking up nutrients (Engel 1990). There are strong connections between nutrient retention and biotic uptake, increased evotranspiration and lowered stream flow (Devito et al. 1989). Since the creation of beaver dams does increase evotranspiration (Westbrook 2006), lower stream flow (Woo & Waddington 1990) and biotic uptake on a longer time scale it could be argued that beaver ponds potentially serve as both sources and sinks for essential nutrients and carbon (Francis et al. 1985).

In Canada, peat deposits and beaver ponds were identified as likely sources of nutrient exports downstream (Dillon et al. 1991). The export was also controlled by seasonal changes in water flow; for example summer months with little flow and high biotic activity seemed to retain the nutrients while the winter and spring months with high run off and little nutrient assimilation showed net exports (Dillon et al. 1991). Increasing fertility of a pond raises the level of intraspecific competition of plants and competition for nutrients becomes of less importance while competition for light becomes the limiting factor (Ray et al. 2001).

Damming of a stream influences the stream's annual discharge and velocity, and the wetlands and ponds created after damming generally have lower water flow than the stream stretches previous to damming. This allows for greater sedimentation rates of particles and compounds with various different compositions. Nutrient rich sediments have the potential to stay in the pond instead of being transported further downstream in the catchment towards its final destination in the sea (Correll et al. 2000). Having low flow, shallow waters and nutrient rich water could promote the presence and growth of periphyton, plankton and macrophytes (Correll et al. 2000). It is also expected that these organisms would actively take up nutrients like nitrates, phosphates and silicates, explaining why we would see a greater nutrient retention in systems with beaver activities as opposed to systems without (Correll et al. 2000).

Beaver ponds are sinks for inlet nitrogen in the form of nitrates but usually act as sources of nitrogen in the form of ammonium (Cirmo & Driscoll 1996, Maret et al. 1987, Devito et al. 1989, Correll et al. 2000). A study in an agricultural stream in Canada found median nitrate levels to be lower in riparian areas of the stream after beaver dams had been created (Hill & Duval 2009). The median values of ammonia increased after dam construction and levels were higher especially during the autumn and spring flood (Hill & Duval 2009). In two second order catchments in a coastal plain in North America, the influence of stream discharge on the temporal variations in concentrations of total organic phosphorous, total organic nitrogen, total organic carbon and total suspended solids became less evident after beaver ponds had been built (Correll et al. 2000). In three large beaver systems in a mountainous region in the US, beaver ponds retained the nutrients during periods of high flow, whereas nutrient retention during times of low flow was less recognizable (Maret et al. 1987).

While nitrates have been shown to be retained within the pond, ammonium exports have been shown to be the same as or exceed the imports (Devito et al. 1989). The same study found neither export nor import of total nitrogen, dissolved organic carbon or total phosphorous, although nutrients seemed to be retained during the summer and autumn months and then released in winter and spring (Devito et al. 1989). Beaver ponds differed from the conifer swamps study-sites in the way that they retained nitrates while passing through or exporting ammonium. The coniferous swamps retained both ammonium and nitrates. Devito et al. (1989) showed equal fluxes of dissolved organic carbon over the beaver ponds while the coniferous swamps showed a > 90 % export than import of DOC.

## *Detrimental effects on ecosystems*

Some studies surveying the beaver's effects on plant diversity have found that the selective grazing and ever-changing riparian zones which the beaver creates leads to a disturbance that is favorable to biodiversity (Parker et al. 1998, Correll et al. 2000, Wright et al. 2002, Wright et al 2003). However, one study in Ontario, Canada showed that the beaver did not act as a keystone species, yet instead it favored the dominant species of woody plants through its selective grazing by removing deciduous trees and leaving conifers (Donkor & Fryxell 1999). Nevertheless, Donkor & Fryxell (1999) also mention the gaps that beavers create can be recolonized by regenerated stems of beaver food species and others. This, together with the damming and flooding activities, significantly alter the composition and structure of boreal forests in the long term (Donkor & Fryxell 1999).

Ever since the beaver recovered from very low populations in the early 20$^{th}$ century it has recolonized much of its former range (Rosell et al. 2005). Today its habitat is to a great extent being controlled by humans for forestry, agriculture and residents and conflicts between beavers and humans interests are inevitable (Parker et al. 1998). The main concerns are beaver activities in intensely forested areas with tree-felling and the inundations of large areas of forest as a result of their dams. A study in mountainous Norway estimated the damages beavers cause on productive forest in an area. It was concluded that beavers often inundate areas which are not considered productive forest area, like peat bogs. When summed up, it was estimated that damages caused by beavers on forest would reduce the landowner's income by 0.1 % in the end (Parker et al. 1998). The landowner in particular in the study had a large amount of land (3469 ha) and is likely to tolerate a 0.1 % income reduction. However, the mean size of privately owned forest in Norway is only 2.5 ha and the many small landowners can experience a considerably greater proportional damage to their land and are more likely to have a hostile attitude towards beavers (Parker et al. 1998).

### *Beavers and diversity of aquatic plants*

Beaver meadows and other wetlands are patchily distributed across the landscape and the structure and composition of the plant communities within them are largely affected by propagule dispersal, either through hydrochory (Honnay et al. 2001) or zoochory (Mueller & Van der Valk 2002, Wright et al. 2003). Wetlands can differ in plant composition and richness due to their relative distance to other wetlands in the surroundings with similar habitats (Wright et al. 2003). Macrophytes have a central role in the ecology of river habitats since they greatly influence nutrient cycling, sedimentation processes and transfers of energy (Baatrup-Pedersen & Riis 1999).

The role of interspecific competition is most likely of great importance for the role of richness, diversity and composition in relation to time (Ray et al. 2001). Therefore, when a beaver pond is created, the species richness will increase in the early successional stages while it decreases in the later stages due to intraspecific competition over resources (Wright et al. 2003).
The sediment/water interface in beaver ponds compared to sediments of free-flowing stretches of streams is enriched with nitrate which enhances nitrogen fixation by primary producers. A study examining subarctic streams in Canada estimated the nitrogen fixation by micro-organisms in sediments and revealed that the estimated accumulation of total nitrogen is nine to 44 times greater in the beaver dammed than in other parts of a stream (Francis & Naiman 1985).

Many fish, amphibian and bird species depend on macrophytes for refuge and food since they also host a wide diversity of invertebrates (Nummi 1989, Schriver et al. 1995). The diversity and presence of macrophytes is mostly affected by the flow, depth and chemical composition of the water it is growing in (Baatrup-Pedersen & Riis 1999). Therefore, macrophytes can serve as indicators of the quality of sediments and water in a system as a whole (Carbiener et al. 1989) and the Water Framework Directive (WFD) (European Union, 2000) includes macrophytes as one of the biological quality elements required for the assessment of ecological status of rivers.

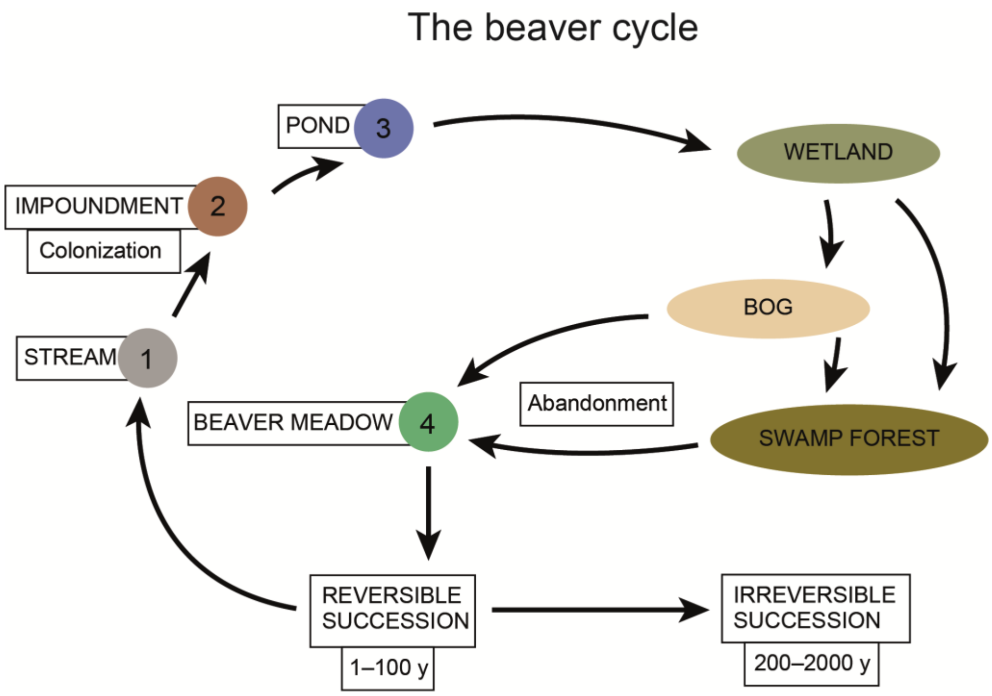



**Figure 1** The successional stages of riverine beaver ponds. 1. The unaltered free flowing stream before arrival of beavers. 2. Beavers colonize the stream and impound it with woody debris. 3. The impoundment leads to flooding the stream banks upstream and beaver pond is established. The beaver pond can go through various stages of different wet ecosystems until it gets abandoned (due to e.g. disease, fire or emigration). After abandonment the beaver meadow (4.) can persist for a long period of time. Illustration drawn by Joel Lönnqvist based on Naiman et al. (1988). Layout by Franciska Sieurin.

The damming activities of beavers cause two successional stages along the riparian zones in an impoundment. The raising of the water table causes the first stage of shallow wetland or pond that gradually gets colonized by plants preferring this kind of habitat. Years or decades later, the beavers abandon the area and stop maintaining the dam which gradually leads to its collapse (figure 1). This in turn leads to lowering of the water table allowing terrestrial plants to colonize the drained mud flats (Nummi 1989). The low flow and often shallow nature of beaver ponds together with retaining nutrients and sediments make beaver ponds favorable habitats for macrophytes (Corell et al. 2000, Rosell et al. 2005).

Initially the macrophyte community composition is dictated by which plants disperse their propagules the best and colonize the new habitat. On a longer time scale, competition over resources and changes in sediments become more important for which species are present or dominant in the community (Barko et al. 1991). Beaver dams can last long after abandonment (Gurnell 1998) and the resulting beaver meadow wetlands (figure 1) can then function as a seed bank for future re-colonization of the dam (Little et al. 2012). Ray et al. (2001) looked at the succession of macrophytes in isolated beaver impounded bogs in Minnesota, USA. The study showed that free-floating and easily dispersed species dominated the ponds in the early stages (4–6 years old), while submerged elodeid macrophyte species dominated in the intermediate stages of succession

(10–40 years old). The first 40 years during beaver pond succession saw a steady increase in macrophyte richness and diversity. However, the oldest ponds studied (> 40 years) showed a slight stabilization or even a decline in macrophyte diversity, probably due to competition over resources between the well-established species (Ray et al. 2001). Little et al. (2012) took into account wetland size and water chemistry when they concluded that the vegetation prior to flooding as well as water chemistry and the geomorphic setting determined pond vegetation the most. The existing information on plant communities in stream impounded beaver ponds is scarce. This could be due to the fact that very few – if any – have tried to study the influences of the landscape as a source of diversity when studying the beaver as en ecosystem engineer.

## *Aims of the study and scientific questions*

The effects beaver ponds have on plant dispersal and the origin of plant communities in ponds are not well studied. This study aimed to explore the relationships between landscape variables and the diversity of plants in beaver ponds located on streams. The first hypothesis was that a larger amount of similar habitats within the catchment would produce greater plant diversity in the pond. A pond with a larger catchment would be able to get colonized by more plant species and therefore be able to host a more diverse plant community than a pond with a smaller catchment. Lakes are habitats for aquatic plants so the more lakes there are in a catchment, the likelier it is that more species will flow downstream to the beaver pond and colonize it, and thereby put the foundation for a more species diverse plant community. Streams are just like lakes sources of aquatic plants and therefore the more abundant they are within the catchment, the greater the input of propagules being transported downstream from them into the pond. The second hypothesis was, that the plant diversity would be higher downstream than upstream the pond. Based on these hypotheses two main scientific questions were formulated:

1) Is the diversity of the pond affected by the amount of similar habitats within the catchment?

2) Is there any difference in diversity upstream compared to downstream the beaver pond?

# Materials and methods

## *Study sites*

This study is a part of a 3-yrs research project called BABI (The reintroduction of European beavers – a plus for biodiversity or detrimental for the environment?) at the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences. The project aims to get a holistic view on the impact of beavers on the environment in Sweden.

**Table 1** Beaver pond coordinates. Coordination system: RT90 2.5 gon V.

| Pond | X coord | Y coord |
|---|---|---|
| 1 | 1784112 | 7342479 |
| 2 | 1773300 | 7359348 |
| 3 | 1779376 | 7361205 |
| 11 | 1570373 | 6949391 |
| 13 | 1552491 | 6911542 |
| 14 | 1552137 | 6901107 |
| 21 | 1444813 | 6570007 |
| 22 | 1446373 | 6568658 |
| 23 | 1516043 | 6620943 |
| 24 | 1512213 | 6618273 |
| 26 | 1489263 | 6629208 |
| 25 | 1507137 | 6630607 |

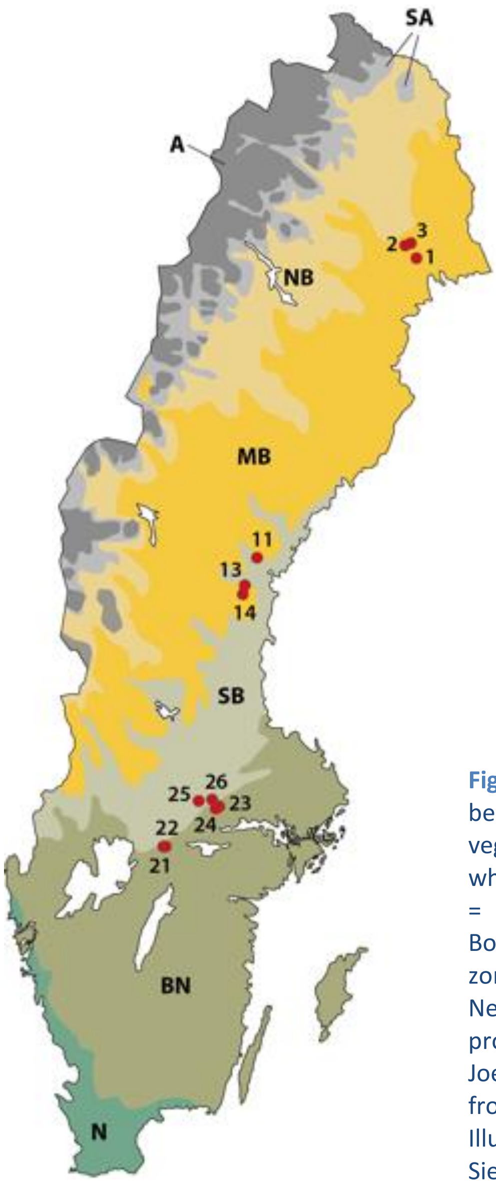



**Figure 2** Map of Sweden with the numbered beaver ponds in red and the different vegetation zones according to Sjörs et al. (1999) where A = Alpine belts, SA = Subalpine belt, NB = Northern Boreal sub-zone, MB = Middle Boreal sub-zone, SB = Southern Boreal sub-zone, BN = Boreo-Nemoral zone and N = Nemoral (temperate) zone. This map was produced in the ArcGIS software (ESRI 2010) by Joel Lönnqvist 2013 with the zonal borders from Sjörs (1999). Final layout made in Adobe Illustrator (Adobe Systems, 2013) by Franciska Sieurin.

Beaver ponds selected for the research project were accessible, active, had clear upstream and downstream sites and came from three different regions, representing three different vegetation zones (figure 2, Sjörs 1999) (Levanoni 2013). The beaver pond data was filtered and after inspecting 120 different locations in the field, 12 beaver ponds that met the requirements were selected (figure 2). The three northernmost ponds represent the middle boreal sub-zone and are located northwest of the town of Luleå (Norrbotten County), while the middle three in the Sundsvall region (Västernorrland County) are located on the border between the middle boreal sub-zone and the southern boreal sub-zone. The remaining four (Västmanland County) and two (Örebro County) ponds lie on the border of the southern boreal sub-zone and the boreonemoral zone. The distance between the northernmost sampling site in Norrbotten and the southernmost in Örebro is about 840 km and the regions have 140 and 180 days long vegetation periods respectively (Sjörs 1999). All the catchments of the selected beaver ponds were dominated by coniferous or mixed forest with varying wetland influences. Some agricultural elements (~ 2–5 %) were found in the southern catchments (figure 3).

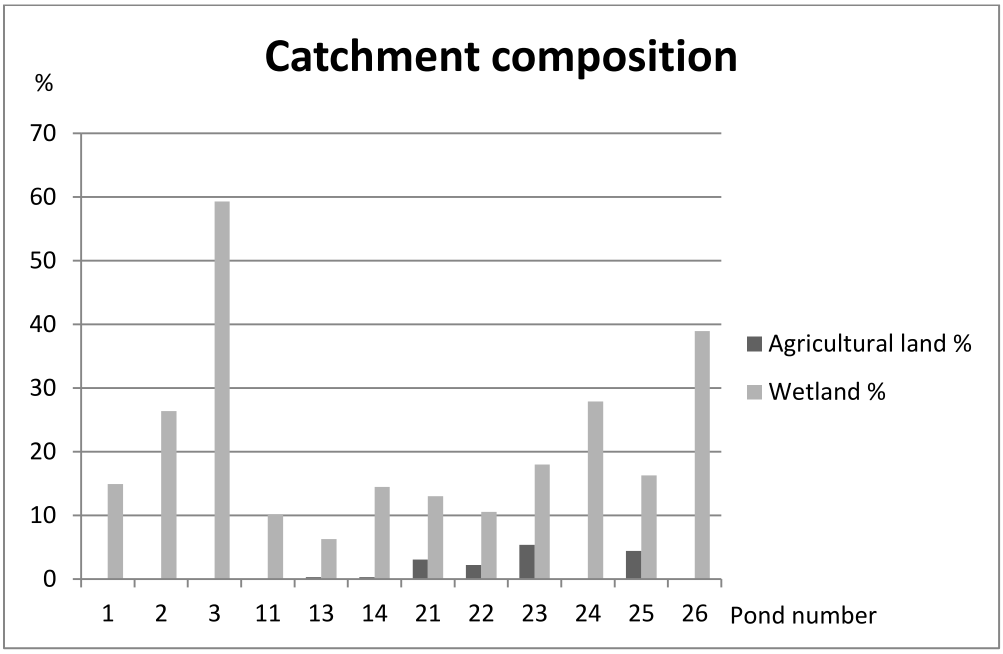



Figure 3 Percentage cover of agricultural land and wetlands in the beaver pond catchments. Ponds 1–3 were located in the northern, 11–14 in the middle and 21–26 in the southern region. Land cover data provided from SLU map database and calculated by Joel Lönnqvist with the help of ArcGIS (Esri, 2010).

In this study a beaver pond comprises the area hydrologically influenced by the beaver dam. In general this implies inundated areas, but not necessarily ponds with an open water surface. By investigating aerial photos (Lantmäteriet) of the selected areas in the ArcGIS software, polygons correspondent to the areas and shapes of the beaver ponds were created (Levanoni 2013). To determine the shape and size of the beaver ponds, the outer boundary of a pond was set to be either non-flooded dry land or land with healthy trees with green leaves or needles. In older ponds without dead trees the boundaries of the pond area were determined by observing the presence of flooded land. Delineating of beaver ponds was facilitated by evident signs of beaver activity like the dam itself, the beaver lodge, logs and snags.

## *Field Sampling*

In each of the 12 chosen beaver systems an inventory of the flora was performed, both in the beaver pond itself and in the upstream and downstream locations. Two ponds were surveyed by Joel Lönnqvist and Frauke Ecke while the remaining ten ponds were surveyed by Joel Lönnqvist and Wilhelm Osterman. The ponds were submitted to an inventory that included the occurrence and cover abundance of the species while the upstream and downstream surveys only recorded occurrence of species.

The materials used most for the field work were; a 1 $m^2$ wooden frame for sampling, a small rubber boat, three pairs of waders, a dry suit, protocol (both normal and water resistant), one plant press and a pair of modified garden rakes which were used for sampling the submerged vegetation. To avoid sampling the same area more than once, and in order to keep the right distance between sampling plots a GPS (Garmin) was used to take to coordinates of every sampled plot or site. A waterproof camera was brought to document the appearance and flora of the ponds. To prevent missing out on any of the possible habitats in the beaver pond influenced by depth, shading, flow etc., a stratified sampling method which differed slightly depending on the presence or absence of open water was used (figure 4).

In ponds with open water eight different zones for stratified sampling were created. One outer riparian edge zone stretching 15 meters from the pond border inwards was created, leaving an inner zone being the rest of the open water. These two zones were then each divided into four smaller zones leaving us with eight zones in total to be sampled. Every zone received an evenly distributed number of inventory plots distributed by throwing the square 1 $m^2$ wooden frame at random. However because of inaccessibility, difficult terrain and tall vegetation in the ponds lacking well-defined open water the ponds were sampled without using the zonal division. Instead, the plots were spread by blind throwing the inventory frame at random, with inter-distances of the frames being 15–30 meters in the largest ponds while in the smallest pond the distance was 7–15 meters.

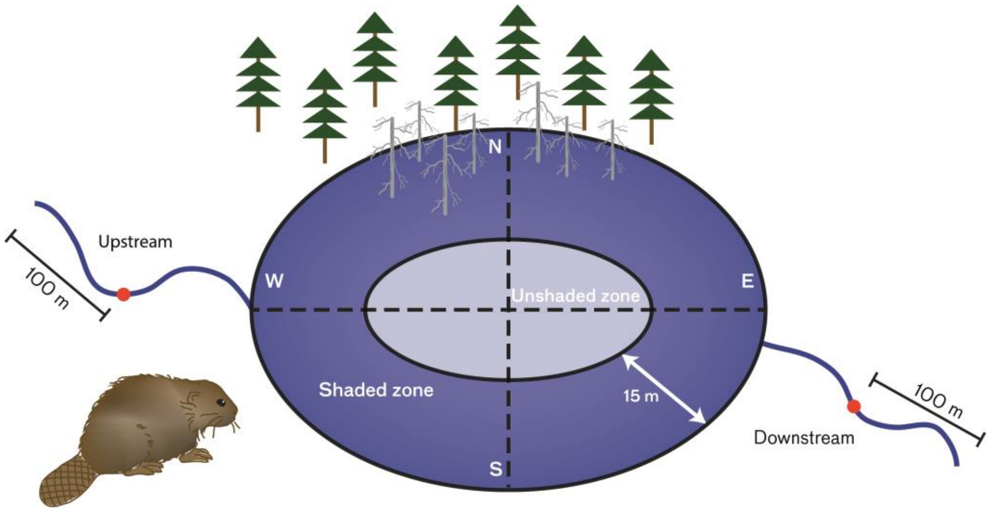



**Figure 4** Illustration of a beaver pond with open water. The pond was divided into a "shaded zone" close to the shore and an "unshaded zone" being the rest of the pond. These were then divided into eight smaller sub-zones which got the plant plots distributed evenly among them. Red markers mark positions of the water data loggers and 100 m bars show the distance where upstream and downstream inventories were performed.
Joel Lönnqvist 2013, layout by Franciska Sieurin.

The Largest ponds with an area > 3000 m$^2$ received a maximum number of 30 plots while the smallest < 1600 m$^2$ received a minimum number of 16 plots corresponding to covering 1 % of the pond area in ponds 1600–3000 m$^2$. Within every plot the different plant species and their cover abundance at a percentage scale were recorded, with a maximum cover-abundance of every individual species of 100 %. Many plots were multiple-layered with plants growing in different layers, which led to that the combined cover of all species in one plot could be > 100 %. To avoid missing out on rare species, not only the plants found in the plots but all the species observed within a pond were recorded. This produced a whole-pond species lists for every pond. After collecting data in a pond, the abundance of every species was estimated on a scale ranging from 1–3 with 1 being a rare species and 3 being one of the dominating species in the pond. Species that never occurred in a plot but were still present in a pond were recorded and were given abundance estimations. When compiling the data these species were given a percentage cover depending on their estimated abundance value. An estimated abundance value of 1 got 0.01 % while 2 got 0.05 % and 3 got 1 %.

## *Species identification*

The inventory was conducted between the 2013-07-04 and the 2013-08-06 starting with the southern ponds and then proceeding to the middle and finally the northernmost. This period was chosen since it coincides with the peak of the vegetation during the summer, which facilitates species identification. In ponds with open and transparent water, aqua scopes and snorkeling with a dry suit was used in order to detect vegetation at greater depths. When the visibility in the water was too poor a modified garden rake with the width of 25 cm and a distance of 7–11 cm between the teeth was used instead. This was done in order to sample submerged plants for accurate determination of species and abundance cover. During most of the survey the surveyors were wading or snorkeling with the exception of pond no. 14 where a small inflatable rubber boat was used. When species determination was not possible on site (*Callitriche* spp., *Myriophyllum* spp., and *Salix* spp.), a plant press was used for storing the specimens until correct determination could be made later on. The hawkbits from the *Hieracium* complex were not determined further than to sections.

### *Sampling the upstream and downstream sites*

Loggers to measure water chemistry had previously been placed upstream and downstream the beaver ponds. The sites of the loggers had been chosen so that no beaver activity, like accumulated woody debris and damming, could be found within 100 m upstream or downstream the logger respectively (Levanoni 2013). In each site, an inventory stretch was made, starting at the water logger and ending 100 meters upstream or 100 meters downstream of it respectively (figure 4). In these particular stretches of the stream only the occurrence of plant species was recorded. All the submerged, emergent and terrestrial plants growing in the water or in the riparian zone were noted. The riparian zone was the area exposed to alterations in water flow, defined as the area stretching 0.4 m perpendicular to the stream channel. In all the inventories we used Swedish floras and keys for accurate species identification (Mossberg & Stenberg, 2010, Krok et al. 2013).

### *Data management and grouping*

After the collection, the data was compiled and arranged into different groups according to Raunkiear's definitions of plant life forms based on the over-wintering buds with the help of Ellenberg et al. (1992). The several strictly terrestrial life forms recognized in the beaver ponds belonged to the groups recognized as the herb-chamaephytes, the geophytes, the hemicryptophytes, nanophanerophytes, phanerophytes, therophytes and the woody chamaephytes. These plant forms are not especially adapted to the wet conditions of the beaver pond but are rather a reflection of the surrounding drier forests and meadows. These groups include many woody tree species (*Picea abies*, *Populous tremula*, *Betula* spp. etc.) as well as heathers (*Vaccinium* spp. *Calluna vulgaris* etc.), grasses (*Deschampsia* spp. *Molinia caerulea.* etc.), and sedges (*Carex pallescens*, *Scirpus sylvaticus* etc.). In this thesis, these groups form part of the total amount of plants but since they are not typical for the beaver pond habitat they were not analyzed further separately. Most vascular plants of the dataset belonged to the semi-aquatic life forms named helophytes. They are usually rooted in soil and sediments, and are often only partially submerged with the majority of the plant above water. This group includes some sedges (*Carex rostrata, Carex nigra, Carex chordorrhiza* etc.), grasses (*Calamagrostis* spp. *Phragmites australis* etc.), burr-reeds (*Sparganium* spp.), tufted loosestrife (*Lysimachia thyrsiflora*), and bog arum (*Calla palustris*).

The strictly aquatic plants known as hydrophytes are constituted of the smaller groups elodeids, lemnids, and floating-leaved vegetation. The lemnids (*Hydrocharis morsus-ranae* and *Lemna minor*) are not rooted in soil or sediments and float freely on the surface of open waters. The floating-leaved vegetation (*Nuphar lutea, Nymphea alba* and *Potamogeton natans*) also floats on the water surface of ponds but stay anchored with roots in the sediments. The elodeids (*Callitriche* spp., *Myriophyllum* spp., *Utricularia* spp., *Potamogeton alpinus,* etc.) are usually completely submerged and grow in the water attached to the sediments.

Plants which disperse their seeds by water could be affected by beaver activities in a similar way to that of the macrophytes. Since the creation of a beaver pond resets plant succession (Little et al. 2012), they provide the submerged substrate for wet soil seed banks, which can be colonized by water dispersing plants. While most macrophytes disperse hydrochorously by floating vegetative propagules, especially during times of flood drift, the helophytes – on the other hand – are dispersing their seeds floating on the water surface (Coops & Velde 1995, Cellot et al. 1998). The success of seed hydrochory is connected to the seed buoyancy time (Afzelius et al. 1954, Skoglund 1990, Nilsson et al. 1991), and plants with seeds that have a longer floating time are more frequent on river banks and riparian zones than those with shorter (Johansson et al. 1996). Therefore, additionally to the groupings depending on the Raunkiaer life forms, the plant species were sorted depending on their seed floating time according to Romell (Afzelius et al. 1954). For this study, all the plants which had a floating time greater than a week were defined as possible water dispersers and were grouped together with macrophytes to form a group of their own. In the end, five composed groups were used in order to compare the diversity and richness of the beaver ponds (table 2).

**Table 2** Organization of the group categories used in the study.

| *Group* | *Plants included* |
|---:|---|
| **Total** | All plant species found in the inventory |
| **FM** | Terrestrial plants with a seed floating time > a week and macrophytes |
| **M** | Macrophytes (hydrophytes and helophytes) |
| **FHy** | Terrestrial plants with a seed floating time > a week and hydrophytes |
| **Hy** | Hydrophytes |

## *Landscape variables*

In order to get data from landscape variables, vector based terrain maps and raster digital elevation maps (DEMs) provided by SLU were used to define the catchments. Using the “spatial analyst” tool in the ArcGIS software (ESRI 2010), it was possible to calculate the “flow direction” and “flow accumulation” of the DEM. By placing a “pour point” at the same location as the beaver dam, the shape and size of the beaver pond’s watershed could be calculated. The watershed shapefile was then joined with information from the terrain map in order to obtain the land use of the watershed. A circular buffer zone shapefile with its center in the beaver dam and the radius of 1 km was also created and merged with the watershed shapefile (figure 5). This was done in order to account for the dispersal of water plants by zoochory. By joining the shapefile of the watershed (including the buffer zone) with the information from the terrain map, the number of lakes and total stream length could be obtained. This was done for all 12 beaver ponds.

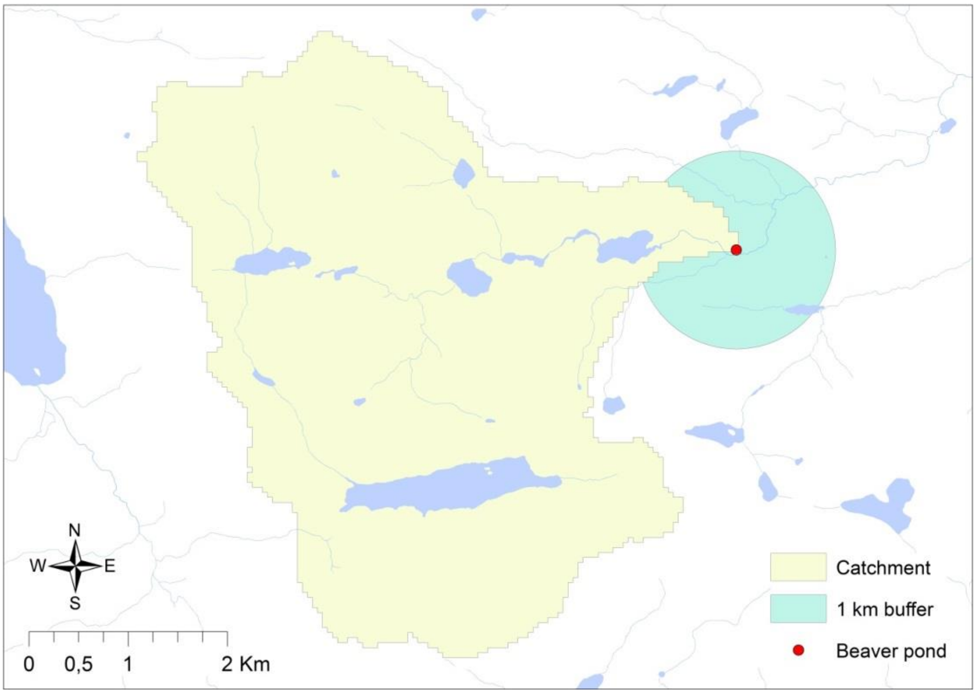



**Figure 5** Watershed of beaver pond number 13. The landscape variables were calculated by making maps in the software ArcGIS (ESRI 2010). The catchment area and the radius buffer zone are shown before merging them. Streams and lakes are shown in blue. The map was made by Joel Lönnqvist 2013 with data from SLU database.

The plant data collected in the beaver ponds enabled the calculation of Shannon's diversity-indices for the different ponds (Shannon, 1948). Since the data collected in the upstream/downstream sites did not contain any information about abundance of species, only species richness was used for them.

## *Water chemistry variables*

The water chemistry data used in this thesis was collected in the months of May, September and November in 2012 and in March and April 2013 (Levanoni 2013). Chemistry data on total nitrogen, nitrites/nitrates total phosphorous and pH was collected from the waters of the actual beaver ponds, as well as in the upstream and downstream sites (Levanoni 2013) (figure 4 p 18). Averages of this data and extreme values were picked out to represent the water chemistry of the ponds in the analysis. The average extreme values were used for the explaining of diversity and richness in the pond while average values from the above mentioned months were used in comparisons between the upstream and downstream sites.

## *Statistical analysis*

All the diversity, richness, landscape and chemistry parameters of the compiled data were tested for normality. Since several of the parameters had data with a non-normal distribution, non-parametric tests were used for most parts of the analyses (table 3). The statistical analyses were performed in the statistical software Minitab 16 (Minitab Inc, 2012).

**Table 3** Statistical tests used and justifications.

| **Statistical test** | **Parameters tested** | **Justification** |
|---|---|---|
| Anderson-Darling test | All data compiled; plant diversity, plant richness, landscape parameters and chemistry parameters | To test normality |
| Spearman correlation | Plant diversity, plant richness, landscape parameters and water chemistry parameters | Non normal data. The test was made like parametric Pearson correlation but using the ranked data |
| Wilcoxon signed rank test for paired data (one and two sided) | Plant richness upstream and downstream. Water chemistry | Non normal data |
| Multiple linear regressions | Plant diversity, plant richness, landscape parameters and chemistry parameters | To find the most important factors for pond diversity. Log and Box-Cox transformations of the data used to achieve normality of the residuals |
| Kruskal-Wallis tests | Plant diversity and plant richness | Non normal data (small sample sizes) |

## *Pond similarity*

Similarity indices were calculated and similarity plots were produced with the help of the software PAST (Harper & Ryan 2001). The pond similarity plots were based on the Bray-Curtis similarity index using non-metric multidimensional scaling and the scatter plots were produced in Minitab.

# Results

## *Dominating species and their abundance*

**Table 4** The three most dominant species in each pond and their Raunkiaer life form. G = geophyte, He = helophyte, El = elodeid, P = phanerophyte, Z = woody chamaephyte. Abundance of species in a pond is expressed as average % coverage. For complete species list with Raunkiear life forms and see floating times see appendix 1 pp 41–43.

| Region | No. | Most abundant | Second most abundant | Third most abundant | Species richness |
|---|---|---|---|---|---|
| North | 1 | *Hippuris vulgaris* H 2.2 % | *Sparganium emersum* H 1.6 % | *Carex chordorrhiza* H 1.3 % | 41 |
| North | 2 | *Carex aquatilis* H 11.3 % | *Menyanthes trifoliata* H 10.8 % | *Carex lasiocarpa* H 9.1 % | 55 |
| North | 3 | *Calamagrostis canescens* H 3.5 % | *Vaccinium vitis-ideae* Z 2.6 % | *Betula pubescens* P 2.2 % | 37 |
| Middle | 11 | *Callitriche hamulata* El 11.9 % | *Potamogeton berchtoldii* El 2.3 % | *Lysimachia thyrsiflora* H 1.2 % | 33 |
| Middle | 13 | *Calamagrostis canescens* H 7.6% | *Carex acuta* H 7.2% | *Phalaris arundinacea* H 7.1% | 49 |
| Middle | 14 | *Carex rostrata* H 7.5 % | *Sparganium angustifolium* El 1.7 % | *Calamagrostis canescens* H 1.6 % | 34 |
| South | 21 | *Calamagrostis canescens* H 5.8 % | *Carex nigra* H 3.8 % | *Scirpus sylvaticus* G 3.4 % | 99 |
| South | 22 | *Scirpus sylvaticus* G 4.8 % | *Potamogeton alpinus* El 3.8 % | *Mentha* spp. G 3.8 % | 68 |
| South | 23 | *Calla palustris* H 24.4 % | *Hydrocaris morsus-ranae* L 13.0 % | *Carex rostrata* H 6.1 % | 36 |
| South | 24 | *Sparganium natans* H 7.5 % | *Phragmites australis* H 7.2 % | *Carex rostrata* H 6.5 % | 70 |
| South | 25 | *Carex rostrata* H 9.5 % | *Calamagrostis canescens* H 4.3 % | *Lysimachia thyrsiflora* H 4.1 % | 39 |
| South | 26 | *Lysimachia thyrsiflora* H 2.9 % | *Phragmites australis* H 2.3 % | *Calamagrostis canescens* H 1.7 % | 60 |

## *Landscape and nutrients effects on diversity*

Both Shannon's diversity index and the species richness of the Total group were positively correlated with the ratio of total nitrogen to total phosphorus (table 5). Species richness of the FM group was positively correlated with stream length as well as to ratio of total nitrogen to total phosphorus (table 5). Shannon's diversity and species richness of the FM group were both positively correlated with nitrites/nitrates (table 5). Species richness of the group showed a positive correlation with the stream length. The diversity of the M group was shown to be positively correlated with the amount of lakes in the catchment, the catchment area, as well as the levels of nitrites/nitrates and quotient of total nitrogen and total phosphorus (table 5). Richness of the M group showed a significant correlation only with the nitrite/nitrate (table 5). The diversity index of the FHy group did not show any significant correlations with any of the landscape nor water chemistry parameters. The richness of the same group was positively correlated with the total stream length of the catchment, nitrites/nitrates levels and the ratio of total nitrogen to total phosphorus (table 5). The diversity and richness of the Hy group had no correlations with neither landscape nor water chemistry variables (see Appendix 2 pp 44–49 for plotted data). Nitrites/nitrates had a strong positive significant correlation with total stream length in the catchment; Spearman correlation coefficient 0.8 and $p < 0.01$.

**Table 5** Spearman correlation matrix. D = diversity; R = richness; ns = non-significant; * = $p < 0.05$; ** = $p < 0.01$. N = 12 for all variables. **Total** = All plant species found in the inventory, **FM** = Terrestrial plants with a seed floating time > a week and macrophytes, **M** = macrophytes, **FHy** = Terrestrial plants with a seed floating time > a week and hydrophytes, **Hy** = Hydrophytes. For plotted correlations go to Appendix 2 p 44–49.

| | Total | | FM | | M | | FHy | | Hy | |
|---|---|---|---|---|---|---|---|---|---|---|
| | D | R | D | R | D | R | D | R | D | R |
| **Catchment size** | 0.32 ns | 0.34 ns | 0.52 ns | 0.51 ns | 0.65 * | 0.45 ns | 0.29 ns | 0.32 ns | 0.27 ns | 0.09 ns |
| **Stream length** | 0.28 ns | 0.27 ns | 0.53 ns | 0.61 * | 0.57 ns | 0.54 ns | 0.38 ns | 0.61 * | 0.33 ns | 0.42 ns |
| **Number lakes** | 0.47 ns | 0.41 ns | 0.51 ns | 0.39 ns | 0.60 * | 0.36 ns | 0.23 ns | 0.16 ns | 0.10 ns | -0.06 ns |
| **$NO_2 + NO_3$** | 0.44 ns | 0.45 ns | 0.63 * | 0.66 * | 0.62 * | 0.61 * | 0.51 ns | 0.74 ** | 0.23 ns | 0.50 ns |
| **Tot- N/P** | 0.66 * | 0.59 * | 0.66 * | 0.64 * | 0.62 * | 0.53 ns | 0.43 ns | 0.59 * | 0.07 ns | 0.11 ns |

The multiple linear regression analyses, with diversities of the groups as response and the landscape and water chemistry variables as independent variables did not show any significant regressions. Therefore it was not possible to see which of the different landscape and water chemistry parameters had greater effects on diversity.

## *Regional differences in diversity*

There were no difference in Shannon's diversity index of any of the plant groups when comparing the three geographical regions north, middle and south (table 6). There was no difference in the richness's of the Total group, FM, FHy and Hy groups when comparing regions. It was found that macrophyte richness differed between regions (table 6). The southern region had a significantly larger estimated median (9.25) than the middle region (4) ($p < 0.05$) (figure 6).

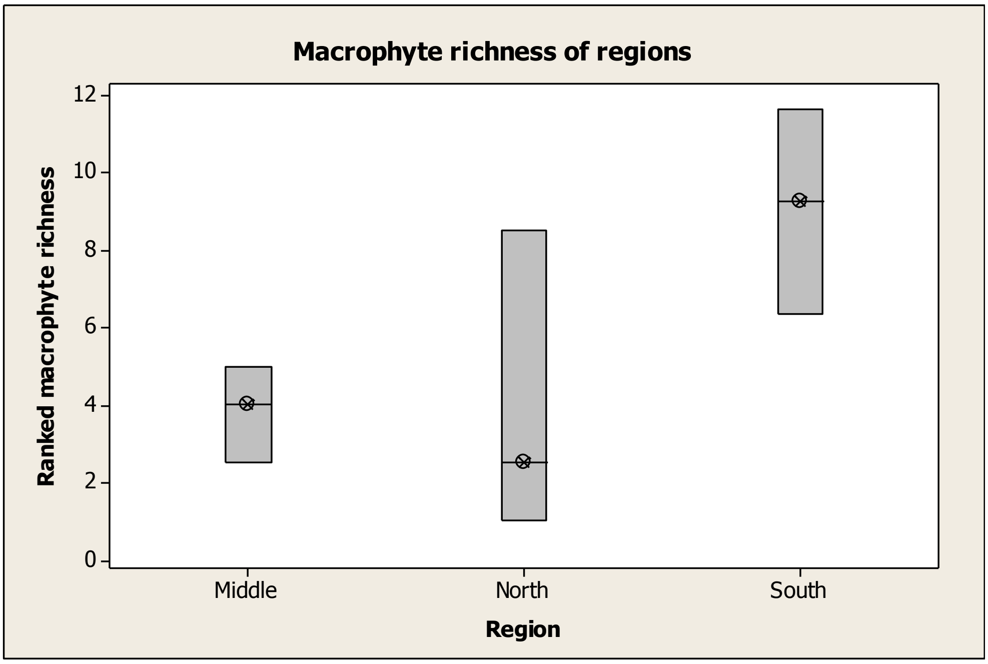



**Figure 6** Box-plot of the ranked macrophyte richness values of the three regions middle, north and south with percentiles and symbols showing medians.

**Table 6** Kruskal-Wallis test of HM richness between regions where N = sample size, H = test statistic, DF = degrees of freedom, P = P-value and P adj = P adjusted for ties. * = $p < 0.05$

| Region | N | Avg rank | H | DF | P | P adj. |
|---|---|---|---|---|---|---|
| North | 3 | 3.8 | | | | |
| Middle | 3 | 4.0 | | | | |
| South | 6 | 9.1 | | | | |
| Total | 12 | 6.5 | 6.16 | 2 | * | * |

## *Upstream and downstream richness*

There was no difference in total species richness between the upstream and downstream sites. The tests of all the other groups (FM, M, FHy, and Hy) did show there was a difference in richness between the upstream and downstream sites and that richness was lower upstream than downstream (table 7).

**Table 7** Results of Wilcoxon signed rank test for matched data. Where U = upstream richness D = downstream richness N = sample size P = p-value, ns = non-significant * = $p < 0.05$ ** = $p < 0.01$, Total = All plant species found in the inventory, FM = Terrestrial plants with a seed floating time > a week and macrophytes, M = Macrophytes, FHy = Terrestrial plants with a seed floating time > a week and hydrophytes, Hy = Hydrophytes.

| Group | Hypothesis | N | Upstream median | Downstream median | T | p |
|---|---|---|---|---|---|---|
| Total | U = D vs U ≠ D | 12 | 50 | 50 | 24 | ns |
| FM | U = D vs U < D | 12 | 21 | 26.5 | 4.5 | ** |
| M | U = D vs U < D | 12 | 14.75 | 20.25 | 2.5 | ** |
| FHy | U = D vs U < D | 12 | 16.0 | 20.0 | 4 | ** |
| Hy | U = D vs U < D | 12 | 1.75 | 2.0 | 3 | * |

## *Upstream and downstream water chemistry*

Average levels of total phosphorus were higher downstream than upstream. Average total nitrogen levels were also higher downstream than upstream while the nitrites/nitrates levels in the water did not change significantly after passing through the beaver dam. There was no difference in the ratio of tot-N/tot-P comparing the two sites (table 8).

**Table 8** Results of Wilcoxon signed rank test for matched data where U = Upstream nutrient levels D = Downstream nutrient levels N = sample size p = p-value, ns = non-significant, * = $p < 0.05$, and ** = $p < 0.01$.

| Nutrient | Hypothesis | N | Upstream median | Downstream median | T | p |
|---|---|---|---|---|---|---|
| tot-P | U = D vs U < D | 11 | 12.7 | 13.9 | 10 | * |
| tot-N | U = D vs U < D | 11 | 446.2 | 485 | 10 | * |
| $NO_2$+$NO_3$ | U = D vs U ≠ D | 11 | 67.5 | 65.3 | 28 | ns |
| tot-N/P | U = D vs U ≠ D | 11 | 39.87 | 33.19 | 53 | ns |

## *Pond similarity*

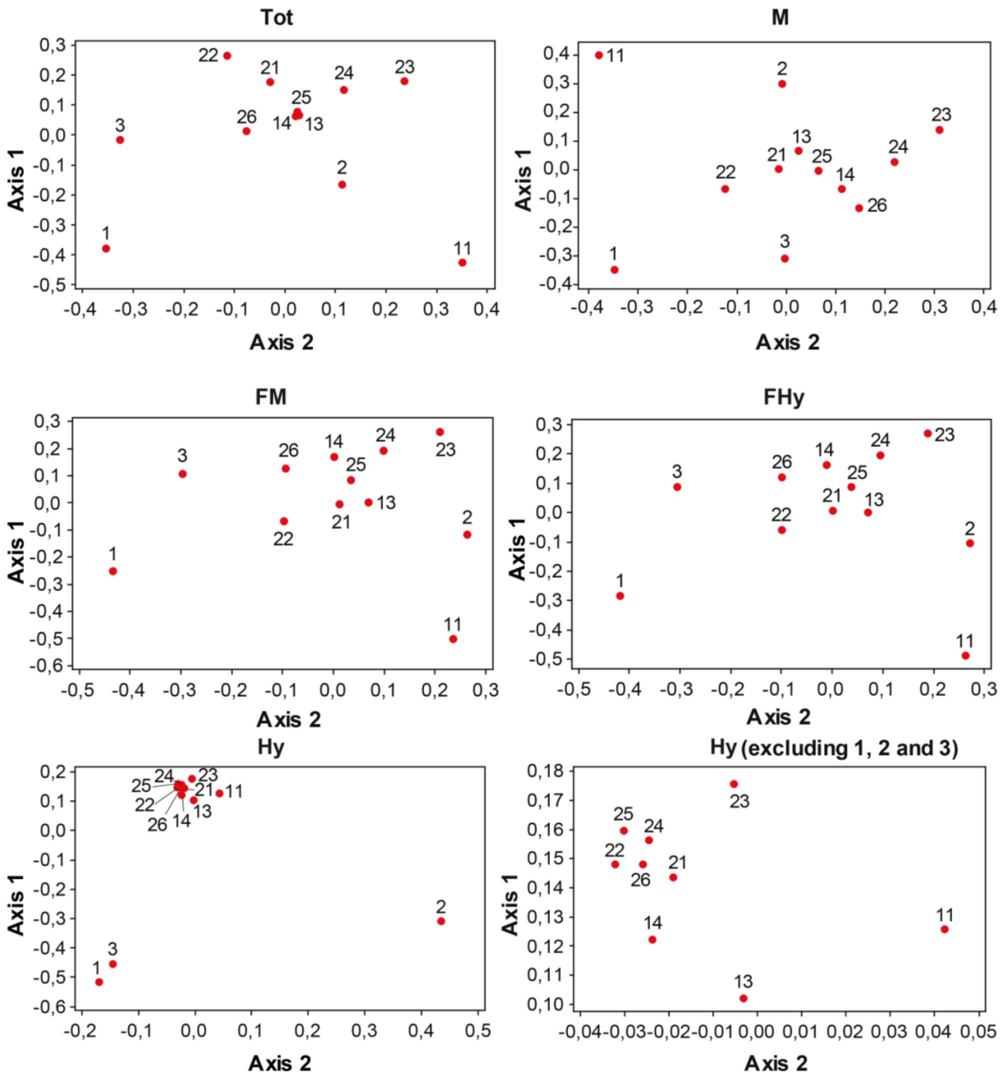



**Figure 7** Pond similarity based on Bray-Curtis similarity index. Where Tot = total amount of plants, M = macrophytes, FM = terrestrial plants with a floating time greater than a week and macrophytes, FHy = terrestrial plants with a floating time longer than a week and hydrophytes and Hy = hydrophytes. Similarity plots were made with the species occurrence and abundance data. Values were calculated in the software PAST (Harper & Ryan 2001) and scatter plots were produced in Minitab.

Pond number 1 had open water and deeper parts which separate it from other ponds. Pond number 11 consisted of drained mud flats dominated by *Callitrichie hamulata* and no other pond had a similar species composition. Pond number 3, one small and recently inundated pond (Levanoni 2013), stands out in most plant groups. The regional similarities are most evident in the Hy group with the northernmost ponds number 1, 2 and 3 standing out from the rest (figure 7). Looking at Hy (excluding 1, 2 and 3), the middle region ponds (number 11, 13 and 14) differentiate themselves from the southern region (number 22, 25, 24, 26, 21 and 23) (figure 7). *Calla palustre* and *Hydrocaris morsus-ranae* dominated pond number 23 which had the highest plant abundance of all ponds and a different species composition which can be seen in all groups examined (figure 7).

# Discussion

## Catchment effects on plant diversity and richness

As beavers colonize, abandon and recolonize ponds they create ephemeral ponds which might last for a period of time, only to later disappear and reappear again (Ray et al. 2001). When a pond is flooded, most of the terrestrial species drown and disappear while aquatic species start colonizing the new habitat. There are several ways to colonize a newly impounded beaver pond. If the area of the pond has been impounded before, there is a chance that a seed bank of aquatic species remain in the soil waiting to sprout, colonize and start a new plant community succession. If there is no seed bank of previous hydrophile plant inhabitants within the pond, the new colonizing species will mostly rely on propagule dispersal from surrounding habitats (van der Valk 1981). Because nearly all wetland species have propagules that float at least for a short period of time (Sculthorpe 1967), and many also have wind-dispersed seeds, long-lived seeds are often found in the substrate throughout wetlands even in areas where the adult plants of a species never have grown (van der Valk and Davis 1976, 1978). Lippert & Jameson (1964) recognized the importance of having permanent waters in the nearby area, acting as sources of aquatic organisms for colonization of a temporary pond. More permanent aquatic habitats (wetlands, lakes and rivers) can act as sources of propagules and the variable degree of connectivity with these affect the succession of a pond (Ray et al. 2001). In many terrestrial plant species dispersal takes place with the help of wind or animals, but most of the aquatic species rely on water for their dispersal between similar habitats (Wright et al. 2003).

There were signs of the catchment variables having an influence on the plant diversity and richness of the ponds. The total stream length within the catchment had significant positive correlations with the richness of the groups FM and FHy. This was in line with the hypothesis that rivers in the catchment act as sources of these plant groups for the colonization of beaver ponds. The number of lakes within the catchment had a positive correlation with the diversity of the M group, which could imply that lakes and their riparian zones lying upstream beaver ponds in the same catchment act as sources of helophyte and macrophyte species. The number of lakes and total length of rivers within the catchment were strongly correlated with size of the watershed. Therefore, it is not surprising to find that catchment size was the most important explanatory variable for the diversity of the M group. It was not expected however, to see that catchment size did not have any significant effect on the diversity or richness of any of the other groups. It could be argued that other plant groups do not rely as much on hydrochorous dispersal downstream from the catchment, but rather rely on other means of propagule dispersal which could have other sources of origin. Although, the richness of the FM group was correlated with stream length and was therefore also expected to have a correlation with catchment size, but this was not the case.

Bornette et al. (1998) recognized that frequency of inundation was as an important factor connected to the disturbing scouring the effect, but so was nutrient level, turbidity, groundwater connectivity and the configuration of the water body in the landscape. Retention structures determine whether or not plant propagules become established (Bornette et al. 1998). They also found that submerged and floating macrophytes respond differently to connectivity and the degree of connectivity seems to determine whether vegetative or sexual reproduction predominate (Bornette et al. 1998). The relationship between plant diversity and connectivity is complex and depends on several interacting factors (Bornette et al. 1998, Ward et al. 2002). The intermediate disturbance hypothesis (IDH) suggests that an intermediate level of disturbance, connectivity in this case, should favor high plant diversity. The highest or lowest degrees of connectivity might favor the diversity of other organism groups (fish, amphibians), but the intermediate degree of connectivity favors the plant diversity (Ward et al. 2002). With a higher degree of connectivity there is a greater likelihood of having competitive species entering the pond and outcompeting less competitive species leading to a less diverse community (Bornette et al. 1998). This might help explain why no pervading patterns on plant diversity were seen when looking at number of lakes, stream length and the size of the catchments.

## *Nitrites/nitrates levels and its effects on diversity*

Beaver systems have been shown to affect the availability and distribution of chemical compounds throughout the watershed (Naiman et al. 1994) and macrophytes also play an important role for water chemistry of streams (Engel 1990). Nitrites/nitrates had some of the strongest significant correlations of any variables together with the diversity and richness of the FM and M groups. The FHy group had significant correlations with nitrites/nitrates only for richness. Still, these trends contradict previous studies made on nitrates impact on aquatic plants (Tracy et al. 2003, Barker et al. 2008). The relationships between nitrates and plant species richness both in terrestrial and aquatic ecosystems have been studied, and most say that when the nitrate load increases in a system, the nitrophilic species will grow fast, become large and abundant and outcompete other species (James et al. 2005). Therefore it is unexpected to see the reoccurring positive correlation between the nitrites/nitrates levels in the ponds and the species diversity. There are other explanations than the nitrites/nitrates level itself that might influence. For example the two southernmost ponds, number 21 and 22 had nitrites/nitrates levels that were about five times higher (> 250 µg/l) than the average of the other ponds (51 µg/l). Pond number 21 had the highest diversity index for the total amount of plant species while pond number 22 had the second highest. The species richness of pond number 21 was 99 species which was the highest by all followed far behind by number 24 which only had 70 species and pond number 22 with 68 species. The high nitrites/nitrates levels of pond number 21 and 22 are probably explained by that number 21 has agricultural areas within 45 m

(SLU maps, ArcGIS 2010) of the pond itself and number 22 lies further downstream on the same stream as number 21. They share large parts of their catchments, and their water chemistry is similar (see appendix). Raised levels of nitrogen and especially nitrites/nitrates in streams are often of agricultural origins (Vitousek & Aber 1997, Mayer et al. 2002). All the ponds in the southern region except pond number 26 had agricultural land in the catchments while the middle and northern regions did not have any agricultural land in their catchments.

There is a regional difference with the northern ponds 1, 2 and 3 being located around 840 km north of the southernmost number 21 and 22. The pattern of species diversity could be explained by the well-documented tendency that species richness decrease with increasing latitude (Stephen 1989). So the correlation seen between nitrites/nitrates, and diversity could actually be explained by the latitudinal differences instead, although this was not supported by the results looking at the diversity of the regions. Only the southern region proved to have significantly greater species richness for the HM group and this does not completely support the tendency. Ponds number 21 and 22 are old ponds that have been abandoned and recolonized (Osterman 2013, unpublished material). This probably means that they have had time to build up a greater seed bank when they were in use, and then when recolonization occurred they had an edge over newly colonized dams for starting a species diverse plant community. Beaver ponds have been found to act as filters, that through increased sedimentation and plant nutrient uptake, reduce the nitrate levels in the stream water, both in watersheds with relatively low nutrient load of anthropogenic origin (Maret et al. 1987, Corell et al. 2000), and in streams with raised nutrient levels (Klotz 2010). This study however, did not show any significant difference between the upstream mean nitrites/nitrates levels and the downstream nitrites/nitrates values which implies that the beaver ponds may not have any effect on the levels of nitrate. It has to be kept in mind that water chemistry data was lacking from the most nutrient retaining summer months (July, August). If this data had been available a different pattern might have been distinguishable.

### *The species richness of the upstream and downstream sites*

Beavers significantly alter the structure and composition of riparian plant communities along the streams it impounds (Hood & Bayley 2009). The results showed no difference in richness between upstream and downstream sites when looking at total amount of plants found (Total). This is in line with the statement from Jones et al. (1994), which says a patch modified by ecosystem engineer does not necessarily have higher over all species richness than a patch which has been left untouched. The other four groups (FM, M, FHy and Hy), which are all more or less bound to wet habitats, showed a greater species richness downstream than upstream the beaver ponds. The riparian habitat upstream beaver ponds had the same overall plant richness as the riparian habitats downstream. The richness of aquatic plants (M, Hy), however, was greater in the downstream habitats suggesting the beaver dams and ponds favor macrophytes not only in the actual ponds but also in the downstream riparian zones. This did not support the hypothesis that beaver ponds would act as filters inhibiting plants from hydrochorous dispersal downstream the pond. Instead it suggests that beaver ponds act as sources of propagules. It could also be suggested that instead of favoring dispersal, the altered hydrology and stream morphology downstream the pond favors the aquatic plant diversity.

In order to explore this more thoroughly further research which takes these parameters into account would be needed. An interesting finding is that average nutrient levels (tot-N tot-P) were higher downstream the beaver pond. When examining the explanatory variables for the diversity and richness of the pond, nutrients were found to have positive correlations with several of the plant groups. Therefore, it is remarkable to see a similar pattern in the upstream and downstream. Although nitrites/nitrates were the only nutrients examined which stayed the same upstream as downstream, the levels in the pond were correlated with the levels of total nitrogen. Stream order, water discharge, different vegetation zones, the much varying habitats and stream morphology of upstream and downstream sites are parameters that were not considered in this study but could still have effects on the plant communities. Further research on the topic should aim to consider these in order to find out what is affecting plant diversity in beaver ponds the most.

## Conclusion

The relationship between plant diversity and landscape factors is complex where several factors act together to determine succession and diversity. In this study the nitrites/nitrates levels showed unexpected positive correlations with plant diversity that could only partly be explained by regional differences. The two following summarized statements are put forward in order to answer the two scientific questions asked in the introduction (p 14):

1) The total plant diversity in stream impounded beaver ponds cannot be predicted by landscape variables derived from the catchment. However, the diversity of water-bound plants in a beaver pond is positively correlated with total stream length, total number of lakes and the total size of the catchment.

2) This study concludes that riparian zones upstream beaver ponds have lesser aquatic plant species richness than riparian zones downstream beaver ponds. It is likely that the hydrological alterations that beaver ponds induce favor aquatic plants downstream the ponds, although propagule dispersal from the ponds could have an important role as well.

## Acknowledgements

I gratefully acknowledge Dr. Frauke Ecke for her valuable input, guiding supervision and time in the field. I would also like to thank PhD student Oded Levanoni for the help with GIS, water chemistry data and sharing knowledge. I send my appreciations to my fellow colleague Wilhelm Osterman, for keeping the spirits up during the field work and making it such an enjoyable time. I also thank Franciska Sieurin for the help with the layout of the illustrations and graphs and thanks to Brenda Vidal for help in the last moment.

## References

Adobe Systems. (2012) Adobe Illustrator CS 6.

Afzelius, K., Dahlgren, O., Halle, T., Hultén, E., Johansson, N., & Lindfors, T., Romell, L. G., Svensson, C., & Söderberg, H. (1954). Växternas spridningsmöjligheter. In *Växternas liv, åttonde bandet 2:a upplagan* (pp. 98–132).

Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution*, *23*(1), 20–5.

Baattrup-Pedersen, A., & Riis, T. (1999). Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology*, *42*, 375–385.

Barker, T., Hatton, K., O'Connor, M., Connor, L., & Moss, B. (2008). Effects of nitrate load on submerged plant biomass and species richness: results of a mesocosm experiment. *Fundamental and Applied Limnology / Archiv für Hydrobiologie*, *173*(2), 89–100. doi:10.1127/1863-9135/2008/0173-0089.

Barko, J., Gunnison, D., & Carpenter, S. (1991). Sediment interactions with submersed macrophyte growth and community dynamics. *Aquatic Botany*, *41*, 41–65. Retrieved from http://www.sciencedirect.com/science/article/pii/0304377091900387.

Bornette, G., Amoros, C., & Lamouroux, N. (1998). Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology*, 267–283. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2427.1998.00273.x/full.

Burchsted, D., Daniels, M., Thorson, R., & Vokoun, J. (2010). The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. *BioScience*, *60*(11), 908–922. doi:10.1525/bio.2010.60.11.7.

Carbiener, A. R., Trémolières, M., Mercier, J. L., Ortscheit, A., & Carbiener, R. (1989). Aquatic Macrophyte Communities as Bioindicators of Eutrophication in Calcareous Oligosaprobe Stream Waters (Upper Rhine Plain , Alsace) communities as bioindicators of eutrophication Aquatic macrophyte stream waters (Upper Rhine plain , Alsace), *86*(1), 71–88.

Cellot, B., Mouillot, F., & Henry, C. (1998). Flood drift and propagule bank of aquatic macrophytes in a riverine wetland. *Journal of Vegetation*

*Science*, *9*, 631–640. Retrieved from http://onlinelibrary.wiley.com/doi/10.2307/3237281/abstract.

Cirmo, C. P., & Driscoll, C. T. (1996). The impacts of a watershed $CaCO_3$ treatment on stream and wetland biogeochemistry in the Adirondack mountains. *Biogeochemistry*, *32*(3), 265–297.

Coleman, R. L., & Dahm, C. N. (1990). Stream geomorphology : Effects on periphyton standing crop and primary production. *Journal of the North American Benthological Society*, *9*(4), 293–302.

Coops, H., & Velde, G. (1995). Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshwater Biology*, *34*(1), 13–20. doi:10.1111/j.1365-2427.1995.tb00418.x.

Correll, D., Jordan, T., & Weller, D. (2000). Beaver pond biogeochemical effects in the Maryland Coastal Plain. *Biogeochemistry*, *49*(3), 217–239. Retrieved from http://link.springer.com/article/10.1023/A:1006330501887.

Devito, K., Dillon, P., & Lazerte, B. (1989). Phosphorus and nitrogen retention in five Precambrian shield wetlands. *Biogeochemistry*, *8*(3), 185–204. Retrieved from http://link.springer.com/article/10.1007/BF00002888.

Dillon, P. J., Molot, L. A., & Scheider, W. A. (1991). Phosphorus and nitrogen export from forested stream catchments in central Ontario. *Journal of Environmental Quality*, *20*, 857–864.

Donkor, N. T., & Fryxell, J. M. (1999). Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. *Forest Ecology and Management*, *118*(1-3), 83–92. doi:10.1016/S0378-1127(98)00487-3.

Ecke, F. (2013). Unpublished material from Frauke Ecke, SLU, Uppsala, Sweden.

Ehrman, T. P., & Lamberti, G. A. (1992). Hydraulic and particulate matter retention in 3$^{rd}$-order Indiana stream. *Journal of the North American Benthological Society*, *11*(4), 341–349.

Ellegren, H., Hartman, G., Johansson, M., & Andersson, L. (1993). Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(17), 8150–8153.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1992) *Indicator values of plants in Central Europe* (*Zeigerwerte von Pflanzen in Mitteleuropa*).Verlag Erich Goltze, Göttingen. (In German).

Engel, S. (1990). Ecosystem responses to growth and control of submerged macrophytes: A literature review. *Technical bulletin*, *170*(Wisconsin Department of Natural resources), 1–20. Retrieved from http://digital.library.wisc.edu/1711.dl/EcoNatRes.DNRBull170.

ESRI. (2010) ArcMap 10.1 Redlands, CA: Environmental Systems Research Institue.

European Union (2000) Water Framework Directive (Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy).

Francis, M., Naiman, R., & Melillo, J. (1985). Nitrogen fixation in subarctic streams influenced by beaver (Castor canadensis). *Hydrobiologia*, *121*, 193–202. Retrieved from http://link.springer.com/article/10.1007/BF00017543.

Grime, J. P., Hodgson, J. G., & Hunt, R. (1988). *Comparative Plant Ecology: A functional approach to common British species* (pp. 1–742).

Gurnell, A. M. (1998). The hydrogeomorphological effects of beaver dam-building activity. *Progress in Physical Geography*, *22*(2), 167–189. doi:10.1177/030913339802200202.

Halley, D., & Rosell, F. (2003). Population and distribution of European beavers (Castor fiber). *Lutra*, *46*(2), 91–101. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Population+and+distribution+of+European+beavers+(Castor+fiber)#0.

Harper, D., & Ryan, P. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontología Electronica*, *4*(1), 1–9. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:PAST+:+PALEONTOLOGICAL+STATISTICS+SOFTWARE+PACKAGE+FOR+EDUCATION+AND+DATA+ANALYSIS#0.

Hartman, G. (1993). Long-Term Population Development of a Reintroduced Beaver (Castor fiber) Population in Sweden. *Conservation Biology*, *8*(3), 713–717.

Hill, A. R., & Duval, T. P. (2009). Beaver dams along an agricultural stream in southern Ontario, Canada: their impact on riparian zone hydrology and nitrogen chemistry. Hydrological Processes *1336*(February), 1324–1336. doi:10.1002/hyp.

Hoffmann, M., Belant, J. L., Chanson, J. S., Cox, N. a, Lamoreux, J., Rodrigues, A. S. L., Schipper, J., & Stuart, S. N. (2011). The changing fates of the world's mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *366*(1578), 2598–610. doi:10.1098/rstb.2011.0116.

Honnay, O., Verhaeghe, W., & Hermy, M. (2001). Plant community assembly along dendritic networks of small forest streams. *Ecology*, *82*(6), 1691–1702. Retrieved from http://www.esajournals.org/doi/abs/10.1890/0012-9658(2001)082%5B1691:PCAADN%5D2.0.CO%3B2.

Hood, G. A., & Bayley, S. E. (2009) A comparison of riparian plant community response to herbivory by beavers (*Castor canadensis*) and ungulates in Canada's boreal mixed-wood forest. *Forest Ecology and Management, 258*(9), 1979–1989.

Hutchinson, G. (1959). Why are there so many kinds of animals? *The American Naturalist*, *93*(870), 145–159. Retrieved from http://bio.classes.ucsc.edu/bio160/bioe_108_summer_10/Bio160readings/Homage to Santa Rosalia.pdf.

James, C., Fisher, J., Russell, V., Collings, S., & Moss, B. (2005). Nitrate availability and hydrophyte species richness in shallow lakes. *Freshwater Biology*, *50*(6), 1049–1063. doi:10.1111/j.1365-2427.2005.01375.x.

Johansson, M. E., Nilsson, C., & Nilsson, E. (1996). Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, *7*(Table 1), 593–598. Retrieved from http://onlinelibrary.wiley.com/doi/10.2307/3236309/abstract.

John, S., & Klein, A. (2004). Hydrogeomorphic effects of beaver dams on floodplain morphology : avulsion processes and sediment fluxes in upland valley floors. *Quaternaire*, *15*, 219–231.

Johnston, C. A., & Naiman, R. J. (1987). Boundary dynamics at the aquatic-terrestrial interface : The influence of beaver and geomorphology, *Landscape Ecology 1*(1), 47–57.

Jones, C., Lawton, J., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386. Retrieved from http://www.jstor.org/stable/10.2307/3545850

Klotz, R. L. (2010). Reduction of High Nitrate Concentrations in a Central New York State Stream Impounded by Beaver Reduction of High

Nitrate Concentrations in a Central New York State Stream Impounded by Beaver. *Northeastern Naturalist*, *17*(3), 349–356.

Krok, T., Almquist, S., Jonsell, L., & Jonsell, B. (2013). *Svensk Flora: Fanerogamer och Kärlkryptogamer.* 29th ed. Liber. (pp 1–592).

Lantmäteriet (2013) Maps and geographic information. http://www.lantmateriet.se/.

Levanoni, O. (2013). Personal communication with Oded Levanoli, SLU, Uppsala, Sweden.

Lippert, B. E., Jameson D. L., (1964) Plant Succession in Temporary Ponds of the Willamette Valley, Oregon. *American Midland Naturalist 71*(1), 18–197.

Little, A., Guntenspergen, G., & Allen, T. (2012). Wetland vegetation dynamics in response to beaver (*Castor canadensis*) activity at multiple scales. *Ecoscience*, *19*(3), 246–257. doi:10.2980/19-3-3498.

Macarthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography* (pp. 1–203).

Maret, T., Parker, M., & Fannin, T. (1987). The effect of beaver ponds on the nonpoint source water quality of a stream in southwestern Wyoming. *Water Research*, *21*(3), 263–268. Retrieved from http://www.sciencedirect.com/science/article/pii/0043135487902041.

Mayer, B., Boyer, E. W., Jaworski, N. A., van Breemen, N., Howarth, R. W., Seitzinger, S., Billen, G., Lajtha, K., Nadelhoffer, K., Van Dam, D., Hetling, L. J., Nosal, M., & Paustian, K. (2002). Sources of nitrate in rivers draining sixteen watersheds in the northeastern US: Isotopic constraints. *Biogeochemistry*, 171–197. Retrieved from http://link.springer.com/article/10.1023/A:1015744002496.

Minitab, Inc. (2012) Minitab 16 Statistical Software.

Mossberg, B., & Stenberg, L. (2010). *Den nya Nordiska floran* (pp. 1–928).

Mueller, M. H., & Valk, A. G. (2002). The potential role of ducks in wetland seed dispersal. *Wetlands*, *22*(1), 170–178. doi:10.1672/0277-5212(2002)022[0170:TPRODI]2.0.CO;2.

Naiman, R. J., Pinay, G., Johnston, C. A., & Pastor, J. (1994). Beaver Influences on the Long-Term Biogeochemical Characteristics of Boreal Forest Drainage Networks. *Ecological society of America*, *75*(4), 905–921.

Naiman, R., Johnston, C., & Kelley, J. (1988). Alteration of North American streams by beaver. *BioScience*, *38*(11), 753–762. Retrieved from http://www.jstor.org/stable/10.2307/1310784.

Niklaus, P. a., Kandeler, E., Leadley, P. W., Schmid, B., Tscherko, D., & Körner, C. (2001). A link between plant diversity, elevated CO 2 and soil nitrate. *Oecologia*, *127*(4), 540–548. doi:10.1007/s004420000612.

Nilsson, C., Gardfjell, M., & Grelsson, G. (1991). Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany, 69*, 2631–2633. Retrieved from http://www.nrcresearchpress.com/doi/pdf/10.1139/b91-328.

Nummi, P. (1989). Simulated effects of beaver on vegetation invertebrates and ducks. *Annales Botanici Fennici*, *26*, 43–52.

Osterman , W. (2013). The effect of local environmental factors on plant communities in Swedish beaver ponds (Unpublished).

Parker, H., Haugen, A., Kristensen, Ø., Myrum, E., & Kolsing, R. (1998). Landscape use and economic value of Eurasian beaver (*Castor fiber*) on a large forest in southeast Norway. *Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark College*, *N-3800*, 1–18.

Penning, W. E., Dudley, B., Mjelde, M., Hellsten, S., Hanganu, J., Kolada, A., van den Berg, M., Poikane, S., Phillips, G., Willby, N., & Ecke, F. (2008). Using aquatic macrophyte community indices to define the ecological status of European lakes. *Aquatic Ecology*, *42*(2), 253–264. doi:10.1007/s10452-008-9183-x

Pickett, M., Cadenasso, C., & Jones, C. (2000). Generation of heterogeneity by organisms: creation, maintenance, and transformation. In *The Ecological Consequences of Environmental Heterogeneity: The 40th Symposium of the British Ecological Society* (pp. 33–52).

Ray, a. M., Rebertus, a. J., & Ray, H. L. (2001). Macrophyte succession in Minnesota beaver ponds. *Canadian Journal of Botany*, *79*(4), 487–499. doi:10.1139/cjb-79-4-487.

Rosell, F., Bozser, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers Castor fiber and Castor canadensis and their ability to modify ecosystems. *Mammal Review*, *35*(3), 248–276. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2907.2005.00067.x/full.

Schriver, P., Bøgestrand, J., Jeppesen, J., & Søndergaard, M. (1995) Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology 33*(2), 255–270.

Shannon, C. (1948). The matematical theory of communication. *Bell Labs Technical Journal*, *27*(3), 379–423.

Simberloff, D., & Wilson, E. (1969). Experimental Zoogeography of Islands: The Colonization of Empty Islands. *Ecology 50*, 278–296. http://dx.doi.org/10.2307/1934856.

Sjörs, H., Rydin, H., Snoeijs, P., & Diekmann, M. (1999). Swedish plant geography: Dedicated to Eddy van der Maarel on his 65th birthday. *Acta Phytogeographica Suecica*, *84*, 9–13. Retrieved from http://uu.diva-portal.org/smash/record.jsf?pid=diva2:565333.

Skoglund, J. (1990). Seed Banks, Seed Dispersal and Regeneration Processes in Wetland Areas. *Acta Universitatis Upsaliensis*, *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science* (253), 1–20.

Smith, M., Driscoll, C., Wyskowski, B., Brooks, C., & Cosentini, C. (1991). Modification of stream ecosystem structure and function by beaver (Castor canadensis) in the Adirondack Mountains, New York. *Canadian Journal of Zoology*, *69*(1), 55–61. Retrieved from http://www.nrcresearchpress.com/doi/pdf/10.1139/z91-009.

Stevens, G. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, *133*(2), 240–256. Retrieved from http://www.jstor.org/stable/10.2307/2462300.

Tracy, M., Montante, J. M., Allenson, T. E., & Hough, R. A. (2003). Long-term responses of aquatic macrophyte diversity and community structure to variation in nitrogen loading. *Aquatic Botany*, *77*(1), 43–52. doi:10.1016/S0304-3770(03)00071-8.

Van der Valk, A. (1981). Succession in wetlands: a Gleasonian approach. *Ecology*, *62*(3), 688–696. Retrieved from http://www.jstor.org/stable/10.2307/1937737.

Visscher, M. De, Nyssen, J., Pontzeele, J., Billi, P., & Frankl, A. (2013). Spatio-temporal sedimentation patterns in beaver ponds along the Chevral river , Ardennes , Belgium. *Hydrological Processes*, *10*, 1–14. doi:10.1002/hyp.

Vitousek, P., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H., & Tilman D. G., (1997). Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, *7*(November 1996), 737–750. Retrieved from http://www.esajournals.org/doi/full/10.1890/1051-0761(1997)007%5B0737:HAOTGN%5D2.0.CO;2.

Ward, J. V., Tockner, K., Arscott, D. B., & Claret, C. (2002). Riverine landscape diversity. *Freshwater Biology*, *47*(4), 517–539. doi:10.1046/j.1365-2427.2002.00893.x.

Westbrook, C. J., Cooper, D. J., & Baker, B. W. (2006). Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. *Water Resources Research*, *42*(6), n/a–n/a. doi:10.1029/2005WR004560.

Woo, M., & Waddington, J. (1990). Effects of beaver dams on subarctic wetland hydrology. *Arctic*, *43*(3), 223–230. Retrieved from http://www.jstor.org/stable/10.2307/40511261.

Wright, J., Flecker, A., & Jones, C. (2003). Local vs. landscape controls on plant species richness in beaver meadows. *Ecology*, *84*(12), 3162–3173. Retrieved from http://www.esajournals.org/doi/abs/10.1890/02-0598.

Wright, J., Jones, C., & Flecker, A. (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, *132*(1), 96–101. doi:10.1007/s00442-002-0929-

# Appendix 1

## *Species list*

**Table 1** Key for species list (table 2 pp 41–43). With the Raunkiear life forms R, according to Ellenberg et al. (1992) and seed floating times t, according to Romell (Afzelius et al. 1954).

| R | Raunkiaer life form | t | Floating time of the seed |
|---|---|---|---|
| El | Elodeid | 1 | Up to an hour |
| L | Lemnid | 2 | Hours |
| Fl | Floating-leaf plants | 3 | Days |
| He | Helophyte | 4 | Weeks |
| Y | Herb-chamaephyte | 5 | Months |
| G | Geophytes | 6 | Six months |
| Hc | Hemicryptophyte | 7 | Years |
| N | Nanophanerophyte | U | Unknown |
| Ph | Phanerophytes | | |
| T | Therophytes | | |
| Z | Woody chamaephytes | | |

**Table 2** Species list with all the plant species found in the 12 beaver ponds. Where R = Raunkiear life form and t = floating time of the seed (See table 1 for explanation).

| Species | R | t |
|---|---|---|
| *Achillea ptarmica* | Hc | 2 |
| *Agrostis canina* | Hc | U |
| *Agrostis stolonifera* | He | 3 |
| *Alchemilla micans* | Hc | 3 |
| *Alisma plantago-aquatica* | He | 4–7 |
| *Alnus glutinosa* | Ph | 4–7 |
| *Alnus incana* | Ph | 5 |
| *Andromeda polifolia* | Z | U |
| *Anemone nemorosa* | G | 2 |
| *Angelica sylvestris* | G | 5–7 |
| *Anthriscus sylvestris* | Hc | 2 |
| *Athyrium filix-femina* | G | U |
| *Betula nana* | Z | 1 |
| *Betula pubescens* | Ph | 2–5 |
| *Bidens tripartita* | He | 3–5 |
| *Calamagrostis arundinacea* | Hc | U |
| *Calamagrostis canescens* | He | U |
| *Calamagrostis purpurea* | He | U |
| *Calla palustre* | He | 6 |
| *Callitriche coph/palu* | El | U |
| *Callitriche hamulata* | El | U |
| *Callitriche stagnalis* | El | 1 |
| *Calluna vulgaris* | Y | 1 |
| *Calta palustris* | He | 4–5 |
| *Campanula cervicaria* | Hc | U |
| *Campanula patula* | Hc | U |
| *Campanula persicifolia* | Hc | 1 |
| *Campanula rotundifolia* | Hc | 2 |
| *Cardamine pratensis* | Hc | U |
| *Carex acuta* | He | 6–7 |
| *Carex aquatilis* | He | 7 |
| *Carex brunescens* | Hc | U |
| *Carex buxbaumii* | Hc | U |
| *Carex canescens* | He | 5–7 |
| *Carex cespitosa* | He | U |
| *Carex chordorrhiza* | He | U |
| *Carex echinata* | G | U |
| *Carex elata* | He | 4–5 |
| *Carex flava* | Hc | 6–7 |
| *Carex lasiocarpa* | He | 5 |
| *Carex limosa* | He | 5 |
| *Carex magellanica* | He | U |
| *Carex nigra* | He | U |
| *Carex ovalis* | Hc | U |
| *Carex pallescens* | Hc | 3–5 |
| *Carex pilulifera* | Hc | 1–3 |
| *Carex rostrata* | He | 4–5 |
| *Carex sp.* | Hc | U |
| *Carex vaginatum* | G | U |
| *Carex vesicaria* | He | 4–5 |
| *Carex viridula* | Hc | U |
| *Carex vulpina* | He | 7 |
| *Cicuta virosa* | He | 5 |
| *Cirsium helenioides* | Hc | U |
| *Cirsium palustre* | Hc | U |
| *Cirsium vulgare* | Hc | 2 |
| *Comarum palustre* | He | U |
| *Convallaria majalis* | G | U |
| *Cornus suecica* | N | U |
| *Crepis paludosa* | Hc | 2 |
| *Deschampsia cespitosa* | Hc | U |
| *Deschampsia flexuosa* | Hc | U |

| Species | R | t |
|---|---|---|
| *Eleocharis mammilata* | Hc | U |
| *Elymus canina* | Hc | U |
| *Elytrigia repens* | G | U |
| *Empetrum nigrum* | Z | 3 |
| *Epilobium adenocaulon* | Hc | U |
| *Epilobium angustifolium* | Hc | 3 |
| *Epilobium lactifolium* | Hc | U |
| *Epilobium palustre* | Hc | 1 |
| *Epilobium parviflorum* | Hc | 1 |
| *Equisetum arvense* | G | U |
| *Equisetum fluviatile* | He | U |
| *Equisetum palustre* | G | U |
| *Equisetum pratense* | G | U |
| *Equisetum sylvaticum* | G | U |
| *Eriophorum angustifolium* | He | 3 |
| *Eriophorum vaginatum* | He | 3 |
| *Filipendula ulmaria* | Hc | 4–5 |
| *Fragaria vesca* | Hc | U |
| *Frangula alnus* | N | U |
| *Galeopsis speciosa* | T | U |
| *Galeopsis tetrahit* | T | 1 |
| *Galium boreale* | He | U |
| *Galium palustre* | He | 5–6 |
| *Galium trifidum* | He | U |
| *Geranium sylvaticum* | Hc | 1 |
| *Geum urbanum* | Hc | 5 |
| *Geum vivale* | Hc | 3 |
| *Glyceria fluitans* | He | 3 |
| *Gnaphalium uliginosum* | He | 1 |
| *Gymnocarpium dryopteris* | G | U |
| *Hieracium foliosa* | Hc | 1 |
| *Hieracium sect.Hieracium* | Hc | 3 |
| *Hieracium sect.sylvaticum* | Hc | 1 |
| *Hieracium tridentata* | Hc | 1 |
| *Hieracium umbellatum* | Hc | U |
| *Hieracium vulgata* | Hc | U |
| *Hippuris vulgaris* | He | 7 |
| *Hydrocharis morsus-ranae* | L | 1 |
| *Hypericum maculatum* | Hc | 1 |
| *Iris pseudacorus* | He | 4–7 |
| *Juncus articulatus* | Hc | 1–4 |
| *Juncus bufonius* | T | 1 |
| *Juncus bulbosus* | El | U |
| *Juncus conglomeratus* | He | 5 |
| *Juncus effusus* | He | 1 |
| *Juncus filiformis* | Hc | U |
| *Juniperus communis* | Y | 4 |
| *Lathyrus linifolius* | G | U |
| *Lemna minor* | L | 5 |
| *Leontodon autumnalis* | Hc | 1–4 |
| *Leucanthemum vulgare* | Hc | U |
| *Linnea borealis* | Z | U |
| *Luzula multiflora* | Hc | 3–4 |
| *Luzula pilosa* | Hc | U |
| *Lychnis flos-cuculi* | Hc | 1 |
| *Lycopodium annotinum* | Y | U |

| Species | R | t |
|---|---|---|
| *Lycopodium annotinum* | Y | U |
| *Lycopodium clavatum* | Y | U |
| *Lycopus europaeus* | He | 3–7 |
| *Lysimachia thyrsiflora* | He | 4 |
| *Lysimachia vulgaris* | Hc | 1–5 |
| *Lythrum salicaria* | Hc | 1 |
| *Maianthemum bifolium* | G | U |
| *Matteuccia struthiopteris* | Hc | U |
| *Melampyrum pratense* | T | 1 |
| *Melampyrum sylvaticum* | T | 1 |
| *Melica nutans* | Hc | U |
| *Mentha sp.* | Hc | 3 |
| *Menyanthes trifoliata* | He | 5 |
| *Molinia caerulea* | Hc | 3 |
| *Mycelis muralis* | Hc | U |
| *Myosotis laxa* | He | U |
| *Myosotis scorpioides* | He | U |
| *Myrica gale* | N | 7 |
| *Myriophyllum alterniflorum* | El | 1 |
| *Myriophyllum sibiricum* | El | 1 |
| *Myriophyllum spicatum* | El | 1 |
| *Nuphar lutea* | Fl | 3 |
| *Nymphea alba* | Fl | 3 |
| *Oxalis acetosella* | G | 1 |
| *Paris quadrifolia* | G | 4 |
| *Parnassia palustris* | Hc | 3–4 |
| *Pedicularis palustre* | He | 5 |
| *Persicaria lapathifolia* | T | U |
| *Persicaria maculosa* | T | U |
| *Peucedanum palustre* | He | 5 |
| *Phalaris arundinacea* | He | 3–4 |
| *Phegopteris connectilis* | G | U |
| *Phleum pratense* | Hc | 3 |
| *Phragmites australis* | He | 4 |
| *Picea abies* | Ph | U |
| *Pinus sylvestris* | Ph | 2–4 |
| *Platanthera chlorantha* | G | U |
| *Poa pratensis* | Hc | 4 |
| *Poa trivialis* | Hc | 3 |
| *Poaceae sp.* | Hc | U |
| *Populus tremula* | Ph | U |
| *Potamogeton alpinus* | El | 3 |
| *Potamogeton berchtoldii* | El | U |
| *Potamogeton gramineum* | El | U |
| *Potamogeton natans* | Fl | U |
| *Potamogeton obtusifolius* | El | U |
| *Potentilla erecta* | Hc | 1 |
| *Potentilla norvica* | T | U |
| *Prunella vulgaris* | Hc | U |
| *Prunus padus* | Ph | 1 |
| *Pteridium aquilinum* | G | U |
| *Pyrola media* | Hc | U |
| *Pyrola rotundifolia* | Hc | U |
| *Ranunculus acris* | Hc | 3 |
| *Ranunculus auricomus* | Hc | 3 |
| *Ranunculus flammula* | He | 3 |

| Species | R | t |
|---|---|---|
| *Ranunculus lingua* | He | 1 |
| *Ranunculus repens* | Hc | 3–7 |
| *Rhododendron tomentosum* | Z | U |
| *Rorippa palustris* | T | U |
| *Rosa villosa* | Z | 3 |
| *Rubus arcticus* | Hc | U |
| *Rubus chamaemorus* | Hc | 3 |
| *Rubus idaeus* | N | 3 |
| *Rubus saxatilis* | Hc | U |
| *Salix aurita* | N | U |
| *Salix caprea* | N | U |
| *Salix cinerea* | N | U |
| *Salix glauca* | N | U |
| *Salix hastata* | N | U |
| *Salix lapponum* | N | U |
| *Salix myrsinifolia* | N | U |
| *Salix myrtilloides* | N | U |
| *Salix pentandra* | N | U |
| *Salix phylicifolia* | N | U |
| *Salix repens* | N | 3 |
| *Salix sp.* | N | U |
| *Sambucus racemosa* | N | 1 |
| *Scirpus sylvaticus* | G | 1 |
| *Scutellaria galericulata* | He | 7 |
| *Senicio viscosus* | T | 1 |
| *Senico sylvaticus* | T | 1 |
| *Solanum dulcamara* | He | 1 |
| *Solidago virgaurea* | Hc | 1 |
| *Sonchus oleraceus* | T | U |
| *Sorbus aucocaria* | Ph | 4 |
| *Sparganium angustifolium* | El | 7 |
| *Sparganium emersum* | He | 7 |
| *Sparganium erecta* | He | 7 |

| Species | R | t |
|---|---|---|
| *Sparganium glomeratum* | He | 7 |
| *Sparganium natans* | He | 7 |
| *Stachys palustris* | G | 1 |
| *Stellaria alsine* | He | 1 |
| *Stellaria gramineum* | Hc | 1 |
| *Stellaria palustris* | He | 1 |
| *Succisa pratensis* | Hc | U |
| *Taraxacum sp.* | Hc | 3–4 |
| *Thalictrum flavum* | Hc | 3 |
| *Trientalis europaea* | G | U |
| *Trifolium repens* | Y | 1 |
| *Tussilago farfara* | G | U |
| *Typha latifolia* | He | 3 |
| *Urtica dioica* | Hc | 3 |
| *Utricularia intermeida* | El | U |
| *Utricularia minor* | El | U |
| *Utricularia stygia* | El | U |
| *Utricularia vulgaris* | El | U |
| *Vaccinium myrtillus* | Z | U |
| *Vaccinium oxycoccus* | Z | U |
| *Vaccinium uliginosum* | Z | U |
| *Vaccinium vitis-idaea* | Z | U |
| *Valeriana sp.* | Hc | 3–5 |
| *Veronica officinalis* | Y | 1 |
| *Veronica scutellata* | He | 1 |
| *Viburnum opulus* | N | 1 |
| *Vicia cracca* | Hc | 1 |
| *Viola canina ssp.montana* | Hc | 3 |
| *Viola epipsila* | Hc | 2 |
| *Viola palustris* | Hc | 2 |
| *Viola riviniana* | Hc | 1 |

# Appendix 2

## *Correlation plots*



## *Plant groups*

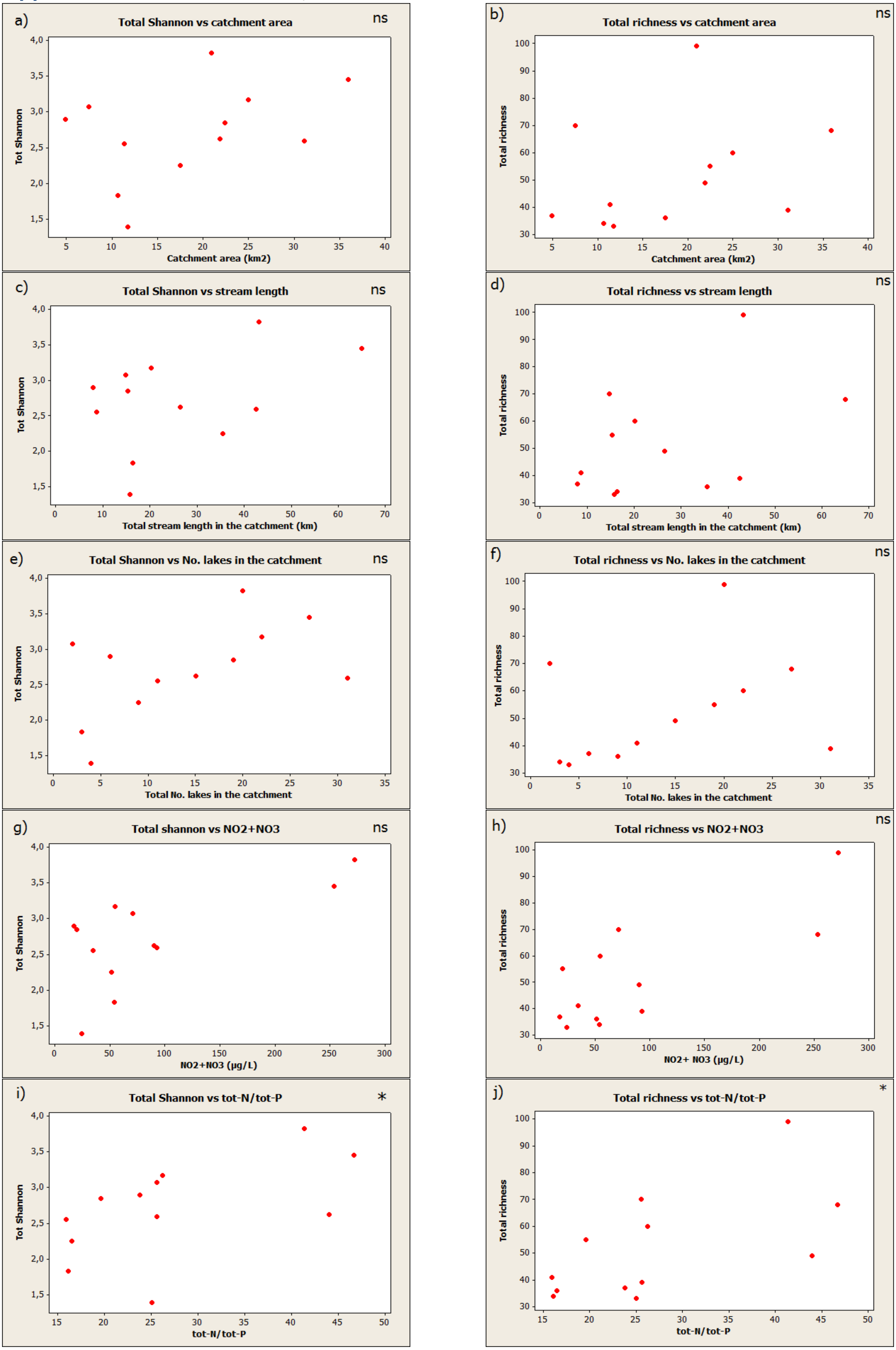
**Total** – All the plant species found
**FM** – Terrestrial plants with a seed floating time greater than a week and macrophytes
**M** – Macrophytes
**FHy** –Terrestrial plants with a seed floating time greater than a week and hydrophytes
**Hy** – Hydrophytes

## *Correlation plot variables in 2.1–2.5*

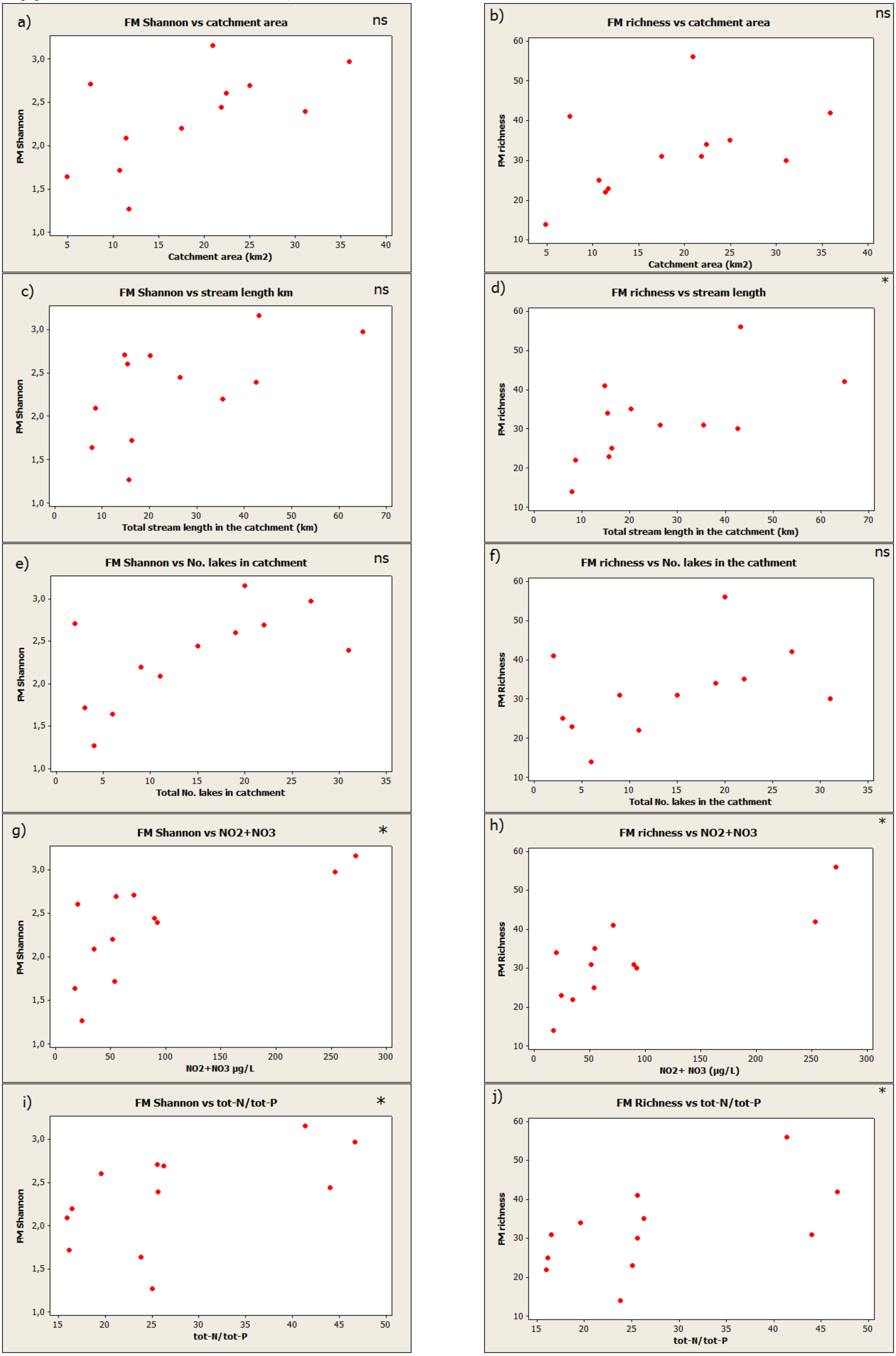
**Shannon's diversity index of plant group** in left columns (figures a, c, e, g, and i)
**Richness of plant group** in right columns (figures b, d, f, h, and j)
**Catchment area** (figures a and b)
**Stream length** (figures c and d)
**No. lakes in the catchment** (figures e and f)
**$NO_2$ + $NO_3$ (nitrites/nitrates)** (figures g and h)
**tot-N/tot-P** (figures i and j)

**Birch gnawed by beaver** Downstream beaver pond No. 13 outside of Sundsvall. Joel Lönnqvist 2013.

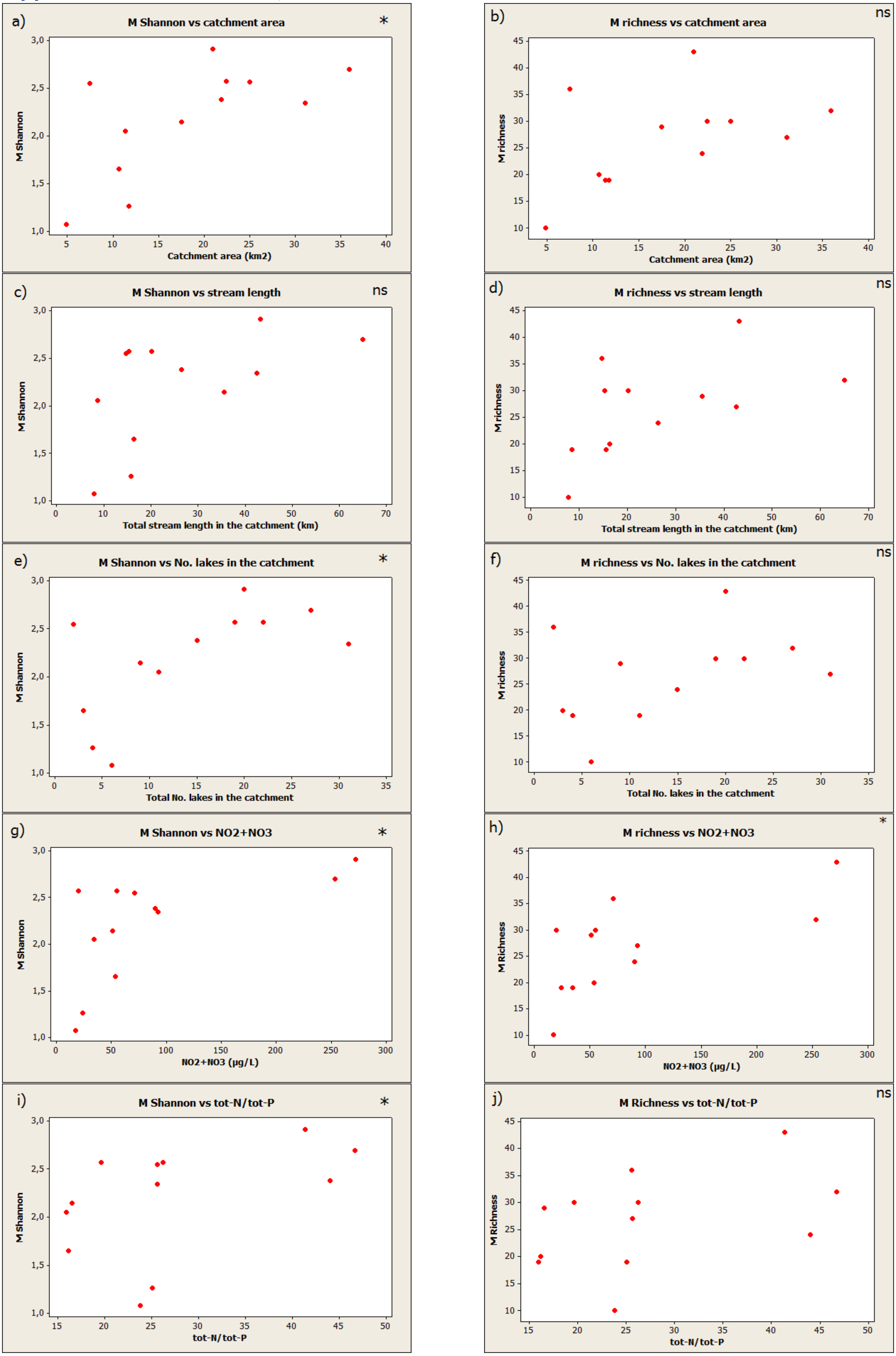
## *Appendix 2.1* **Total** correlation plots



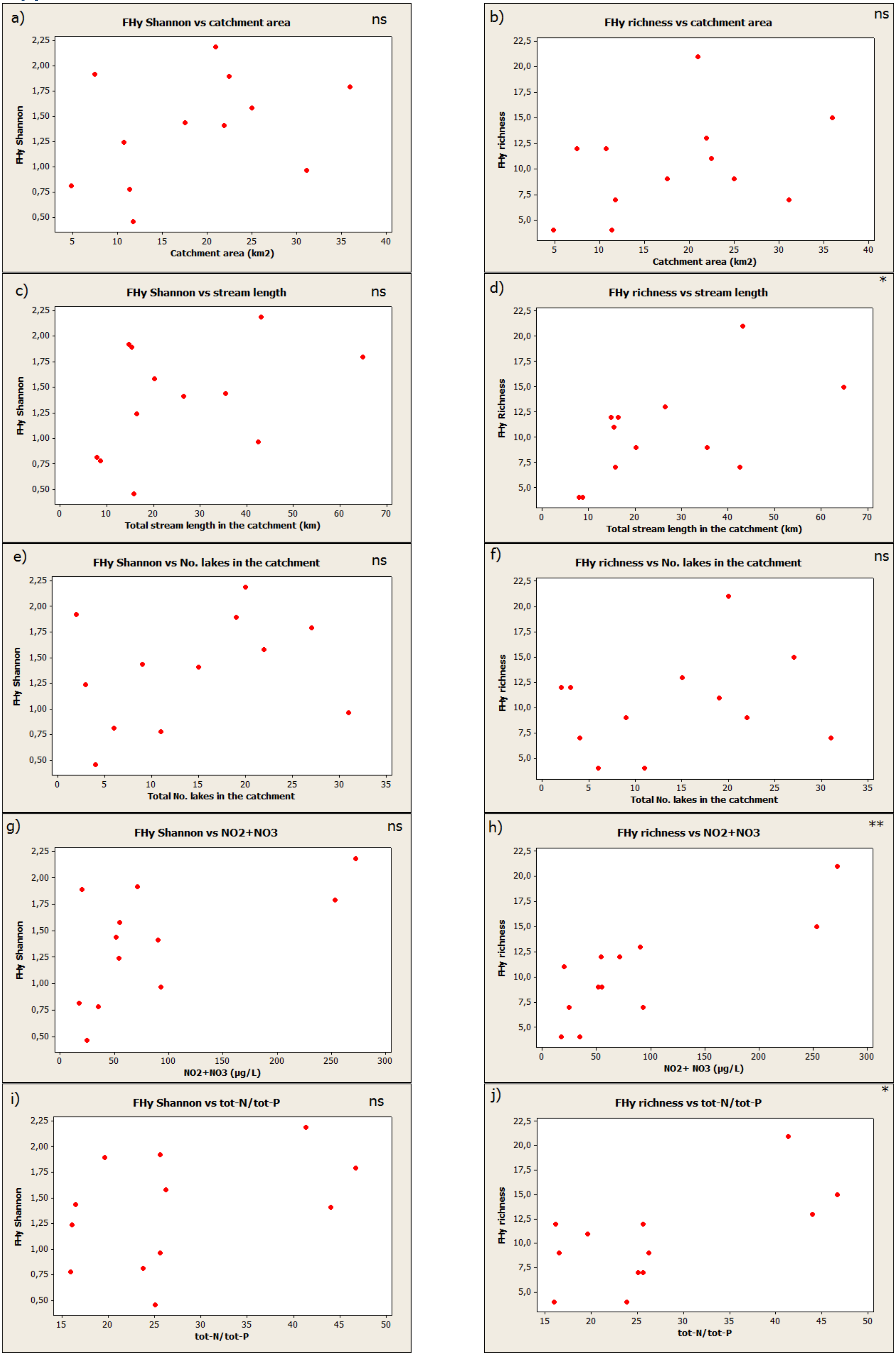
## *Appendix 2.2* **FM** correlation plots



## *Appendix 2.3* **M** correlation plots



## *Appendix 2.4* **FHy** correlation plots



## *Appendix 2.5* **Hy** correlation plots