Using functional traits to improve the understanding of the relationship between lake management and ecosystem function. A case study on lake Ringsjön in Southern Sweden.

Annegreet Veeken
Master Sustainable Development (Global Change and Ecosystems)
Faculty of Geosciences
Utrecht University

Supervised by
Dr. Maria João Ferreira Dos Santos, Faculty of Geosciences, Utrecht University
Dr. Erik Andersson, Stockholm Resilience Centre, Stockholm University
Dr. Romina Martin, Stockholm Resilience Centre, Stockholm University

Second reader:
Dr. Jerry van Dijk, Faculty of Geosciences, Utrecht University

May 29, 2017

Utrecht University

Stockholm Resilience Centre
Sustainability Science for Biosphere Stewardship

Stockholm University

Acknowledgements

I would like to thank Romina for making it possible for me to do this research at the Stockholm Resilience Centre. I was happy to be able to work in this open, inspiring environment and it has been a valuable time for me. Thank you for welcoming me at the Centre and for your support and feedback, even while you were on your maternity leave, I have appreciated it.

Furthermore, I owe my thanks Erik, who supervised me during my time at SRC, and Maria who supervised me during the whole process. Thank you for your ideas, feedback and help developing this research.

Abstract

Human well-being is dependent on the health of the ecosystem we are provided by. To make the connection between humans and nature clear, the concept of ecosystem services has become mainstream. However, the provisioning of ecosystem services is complex and this makes it difficult to use ecosystem system service approaches to inform management decisions. The use of species traits may be a way forward in understanding the influence of management on ecosystem functioning.

In this study a framework of response and effect traits is used to examine the effects of long-term management on the ecosystem functioning of lake Ringsjön in Southern Sweden. Furthermore, a measurement of overlap between response and effect traits in this framework was used to predict the response of ecosystem function to the drivers.

The framework showed to be effective in explaining some of the management effects on species composition of Ringsjön. It was found that the management actions taken in Ringsjön resulted in a greater diversity in the functional traits of macrophyte. The measurement of overlap between response and effect traits gave insights on how the change species composition could result in changes in ecosystem function.

Overall, this study shows how a framework of functional traits can be applied and give a more detailed understanding of managed freshwater ecosystems.

Introduction

One of the major challenges in this era is to ensure and improve the well-being for the current and future world population. People ultimately rely on nature for both basic needs, as food and water, and the cultural and recreational needs that are important for human well-being (MEA, 2005). In present days, few ecosystems remain untouched by humans. The interactions between human and nature are complex. This makes it difficult to manage ecosystems for the benefit of human well-being (Bennett et al., 2015). New methods are therefore needed to improve the understanding of the impact we have on the ecosystems we are provided.

Ecosystem services as the currency of social-ecological systems

The interconnectedness of humans and nature can be defined as a social-ecological system. To make the connection between the social and the ecological system more visible and tangible, the concept of ecosystem services has become mainstream in both policy and science. Ecosystem services are here described as "the benefits humans obtain from their interaction with nature" (Reyers et al., 2013). Ecosystem services encompass both basic human needs, such as the provision of food, and the more cultural or spiritual meanings humans ascribe to nature (TEEB, 2010).

The provisioning of ecosystem services is dependent on a set of linked processes, which together can be named the ecosystem services cascade (Haines-Young & Potschin, 2010). This cascade distinguishes between ecosystem function and ecosystem services, ecosystem function being the capability of an ecosystem to perform a certain process that supports an ecosystem service, leading to an ecosystem service potential (Palomo et al., 2016; Spangenberg et al., 2014). Whether an ecosystem service potential leads to the actual provision of an ecosystem service depends on a complex of natural and human factors (e.g. labour, technology, institutions)(Palomo et al., 2016; Bennett et al., 2015). Because of this complexity, management strategies may have very different effects on the ability of ecosystems to provide multiple, sometimes conflicting, ecosystem services (Villa et al., 2014). To use ecosystem service approaches as a tool for management and decision-making, a thorough understanding of the ecosystem functions that lie at the base of ecosystem service provision is needed.

The biodiversity-ecosystem function relationship

Multiple studies have established a positive relationship between biodiversity and the provision of ecosystem services (see Balvanera et al., 2006 and references therein). However, these studies often narrow down biodiversity to species richness, while biodiversity can be viewed in a much broader sense of taxonomic, compositional, structural and functional variety. The exact role that biodiversity plays in sustaining ecosystem services is poorly understood and long-term effects of biodiversity loss are therefore difficult to predict (Durance et al., 2016). It can be argued that not the number of species per se but rather the underlying variety in functional traits drives the positive relationship between biodiversity and ecosystem service provision (Campbell et al., 2012). While species richness may be important for maintaining an ecosystem's resilience (Kotschy et al., 2015) the functional abilities of particular species or the richness of functional traits maybe as important in sustaining ecosystem function (Haines-Young & Potschin, 2010; Durance et al., 2016).

The use of species traits may be a way forward in getting a greater understanding of the influence of management on ecosystem functioning and ecosystem service potential. Trait-based approaches are relatively new in ecology, but considerable progress has been made in recent years (Hevia et al., 2017). Species trait analysis assumes that ecosystem processes can be predicted by the presence of relevant species traits. For instance, leaf chemistry has been linked to decomposability of plants and the feeding habits of macroinvertebrates have been related to nutrient cycling (Bello et al., 2010). Ecosystem function can be influenced by species at multiple trophic levels, and the abundance of functional traits in one level can alter the composition of traits in the next (Bello et al., 2010; Suding et al., 2008).

Two groups of functional traits can be distinguished; response and effect traits. Response traits define how a community responds to a driver of change (Suding et al., 2008). They encompass both the direct response of the driver and the indirect response of trophic interactions within the community (Suding et al., 2008). Effect traits determine how a change in community composition relates to ecosystem functioning (Suding et al., 2008) and therefore ecosystem service potential. One functional trait can be responsible for either response or effect, or both. For instance, response traits relating to dispersal are not directly responsible for driving ecosystem function while traits like trophic position may relate to both response and effect (Suding et al., 2008; Figure 1).

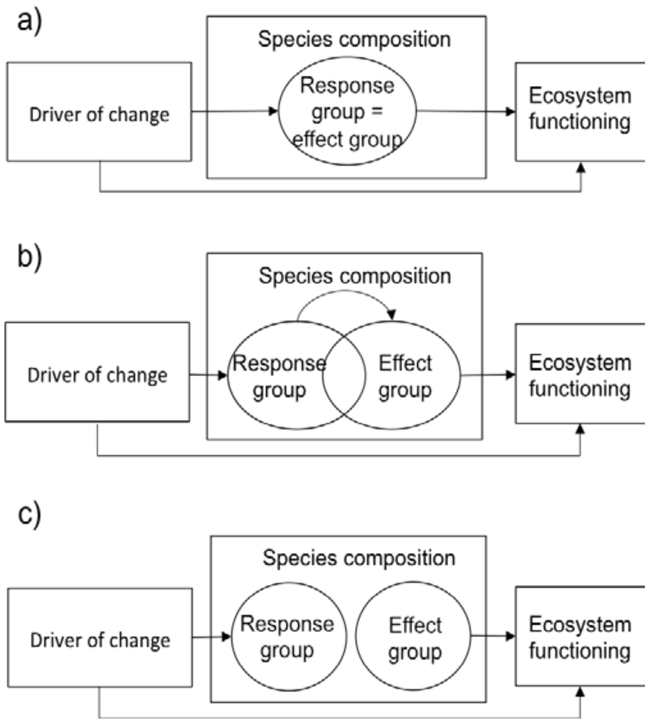


Figure 1 Schematic representation of species groups (with corresponding response traits) that respond to a driver of change and species groups (with corresponding effect traits) that affect ecosystem function. Depending on the driver and ecosystem function response and effect groups (species with similar traits) may entirely overlap (a) partly overlap (b) or be completely different (c) (adopted from Suding et al., 2008).

The degree of overlap between response and effect trait groups has been proposed as an indicator of the resilience of an ecosystem (Suding et al., 2008). When response and effect trait groups overlap entirely, it is expected that the ecosystem function will respond proportionally to the driver (Figure 1a). Consequently, when response and effect groups are completely non-overlapping, it is expected that the driver will not affect ecosystem function (Figure 1c). Interestingly, when response and effect groups overlap partly (Figure 1b), in other words when species with a same effect on ecosystem function respond differently to a driver, then resilience of ecosystem function can be expected (Suding et al., 2008).

Although this method has not been applied in only a few studies it could give important insights into the relationship between driver and ecosystem functions (Hevia et al,. 2017)

The case study: Lake Ringsjön

Here a case study is used to assess the usefulness of functional traits to predict changes in ecosystems and inform decision-making for the management of ecosystem services. The case study is carried out in lake Ringsjön in southern Sweden. Freshwater ecosystems provide a variety of ecosystem services that are important for humans, such as the provision of fish and regulating hydrological and biogeochemical cycles (MEA, 2005). One of the most prominent ways in which humans influence freshwater ecosystems is eutrophication (Søndergaard & Jeppesen, 2007).

Lake Ringsjön has been experiencing problems due to eutrophication since the 1960s. The eutrophication in lake Ringsjön lead to an ecosystem with turbid waters, a domination of algae and great amounts of cyprinid fishes (mostly roach and white bream). Because of its geographical location and its beautiful surroundings the lake used to be a recreational area of high local and regional interest. In the 1960's up to 4000 fishing licenses per year were sold, the lake was appreciated as a swimming lake and famous for bird watching. Also commercial fishing has a long history in the lake. Furthermore, from 1963 to 1987 lake Ringsjön served as a drinking water source for several large cities in Scania. As a direct result of the deteriorating water quality, all of these activities declined (Bergman & Hansson, 1999).

The main sources of nutrients to lake Ringsjön are agriculture, private households and municipality's sewage treatment plants. The exact contribution of each source is unknown. To restore the water quality of Ringsjön, two management actions have been taken: biomanipulation and reduction of the nutrient load to the lake. Biomanipulation is a way of altering the food web to decrease algae concentration and has been carried out in Ringsjön in the 1990's and since 2005. With biomanipulation great amounts of cyprinid fish are removed to favour zooplankton grazing. Multiple measures have been implemented to decrease nutrient load to the lake, ranging from the improvement of private sewage systems to the construction of wetlands. Since the beginning of the monitoring program in 1978, nutrient concentrations have been steadily decreasing and water clarity increased (Figure 2) (Ekologgruppen, 2015).

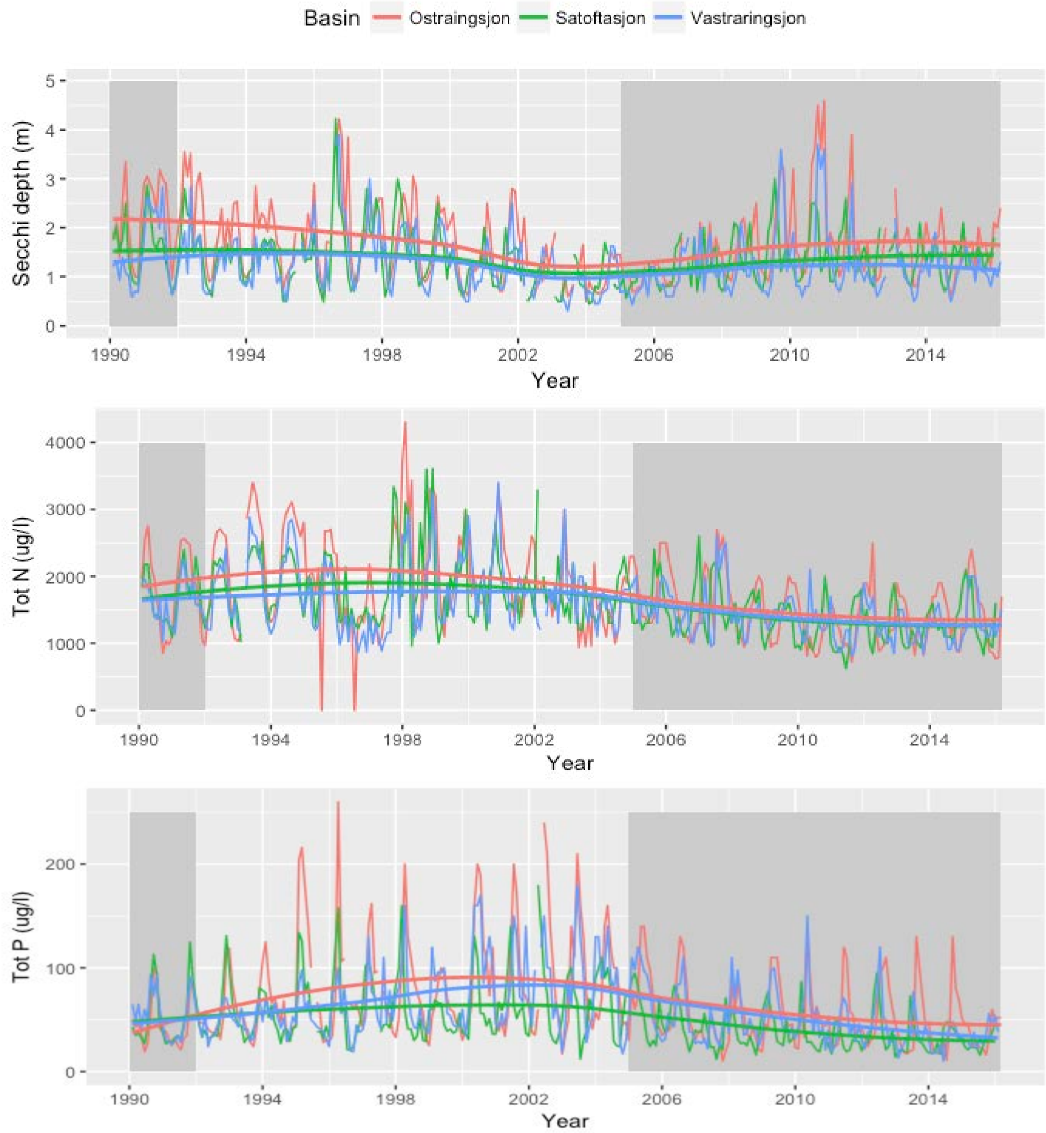


Figure 2 Water quality in the three basins of Ringsjön during the growing season (March-September) from 1992 to 2015. a) Secchi depth (m) b) Total nitrogen (ug/l) c) Total phosphorous (ug/l). Grey areas indicate the periods of biomanipulation.

In this study, I hypothesize that a framework of response and effect traits can be used to identify the effects of long-term management on the ecosystem functioning and ecosystem services potential of freshwater ecosystems. I test this hypothesis in lake Ringsjön. More specifically, I will build my framework by first asking: (i) Which response traits about management impacts on freshwater species composition are found in literature? And (ii) Which effect traits that relate to the desired functions of freshwater ecosystems are defined in literature? Thereafter I will use existing biodiversity and water quality data from Ringsjön and trait databases to answer the following question: (iii) Can the identified response traits explain the past effects of management on biodiversity of lake Ringsjön? Finally, I will determine the overlap between response and effect trait groups to answer the following question (iv) Does the overlap between response and effect traits provide an indication for the resilience of the ecosystem functions of lake Ringsjön?

Methodology

Literature review

Two management measures in lake Ringsjön were under review in this investigation: the biomanipulation and the reduction of nutrient load to the lake (Figure 3). These management actions could alter species composition by (i) improved light conditions (because of decreased algae and decreased benthic feeding), (ii) decreased nutrients and (iii) decrease in cyprinid fish (Bergman & Hansson, 1999; Bornette & Puijlon, 2011). The ecosystem functions that were investigated here are: nutrient cycling, nutrient retention, sediment retention and food and habitat provision for larger animals. These functions were chosen because Ringsjön historically was an important lake for swimming, fishing, bird watching and drinking water provision (Bergman & Hansson, 1999) and these ecosystem services are again desired for the lake (Marcus Ohlsson, Ringsjön's Vattenrad, pers. communication).

The search engines Web of Science and Google Scholar were used to find literature on relevant traits to the identified drivers and functions, i.e., response and effect traits for each of the drivers and ecosystem functions, respectively. Key word combination consisted of search terms for traits (e.g. *trait*, *attribute*), the species group (*macrophytes* or *macroinvertebrates*), the driver (e.g. *light*, *eutrophication*, *nutrients*, *fish*) or the function (e.g. *water purification*, *sediment retention*, *herbivory*). A judgement of the confidence of the relationship between a trait and a driver or a trait and an ecosystem function was based on: the judgement of the authors on the reported effect and other articles reporting the same.

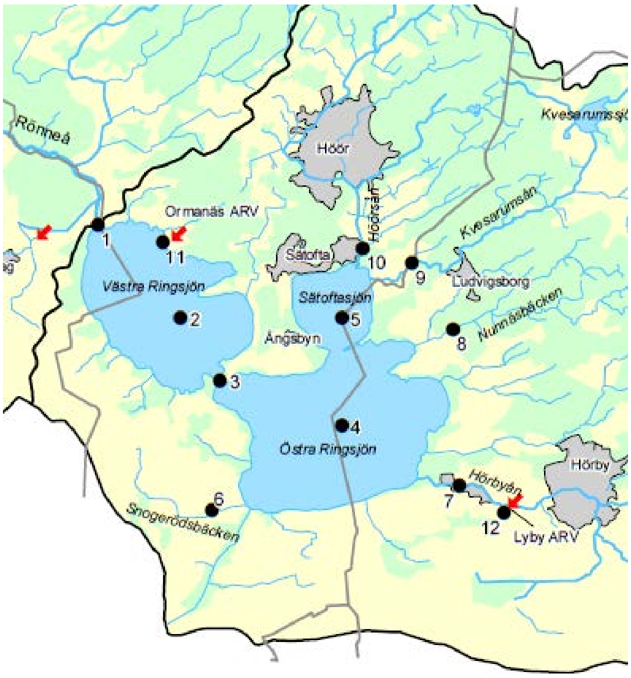


Figure 3 Map of the study area with surrounding municipalities. Black dots show sampling sites and red arrows indicate sewage treatment plants.

Site description & data availability

Lake Ringsjön is situated in the Southern part of Sweden (55°53'01.9"N 13°31'20.4"E) and consists of three connected basins (figure 3). Lake Ringsjön has been of great interest to scientists and water managers; multiple studies about the lake therefore exist, especially about the first biomanipulation attempt (see i.e. Bergman & Hansson, 1999 and ABG, 2014).

To find out how management has affected the nutrient concentrations and light conditions, data on water quality was obtained from the Ringsjön's water board (Ringsjön Vattenrad). Since 1966, water quality was assessed (almost) every month and in each basin. Species richness and abundance of macrophytes and macroinvertebrates has been repeatedly measured by Ekologgruppen since 1992, and is available for download (www.ringsjon.se). Additionally, a study from 1947 that investigated macrophyte diversity in lake Ringsjön was used for comparison with the contemporary data (ABG, 2014). The species were used as input for the trait database search. An overview of the data is found in table 1.

Table 1 An overview of the water quality variables and measurements of biodiversity that were used in this study.

Variable	Unit	Sampling point(s)	Time series
Water quality			
Secchi depth	m	3 (every basin)	Monthly, since 1966
Nitrogen concentration	Total N in µg/l	3 (every basin)	Monthly, since 1966
Phosphorous concentration	Total P in µg/l	3 (every basin)	Monthly, since 1966
Biodiversity			
Macrophytes	Number of species & number of transects	72	Number of species: 1947, Number of species and transects: 1992, 1993, 1996, 2001, 2002, 2004, 2006, 2009, 2012, 2013, 2015
Macroinvertebrates	Number of individuals / m^2	1	Important groups: 1992, 1994, 1994, 1996 All species: 2005, 2007, 2011, 2013, 2014
Biomanipulation	kg/ha	Västra Ringsjön	2005, 2006, 2007, 2008, 2011, 2012

Data on traits of macrophytes was obtained from Willby et al. (2000). Willby et al. (2000) contains only morphological traits and life history traits and provided a complete data set for 15 of the 17 species found in the lake in recent years. Also data on the traits of the species present in 1947 was obtained from Willby et al. (2000) and proved to be complete for 26 of the 32 species. Twelve traits were used in the subsequent analysis (table 2). These traits were subdivided into trait categories (hereafter called attributes) with a score that varies from 0 to 2, '0' indicating absence of an attribute, '1' indicating occasional exhibition of an attribute and '2' the presence of an attribute. In addition, the TRY database (Kattge et al., 2011) was used to complement the trait data with information on biochemical traits of macrophytes, but proved incomplete for most of the species. The biochemical plant traits were therefore excluded from analysis. A table of the trait values can be found in appendix F.

Data on macroinvertebrate traits was downloaded from freshwaterecology.info (Schmidt-Kloiber & Hering, 2015)(table 3). This database compiles data from multiple sources and provided an almost complete data set for the analysis. Every attribute has a score from 0 to 5, with 0 meaning no affinity for an attribute and 5 indicating the highest affinity for an attribute. Macroinvertebrates that were only recorded once during the 1992-2015 period were excluded.

Table 2 Macrophyte traits used in this study (adopted from Willby et al., 2000).

Trait	Attribute	Code
Growth form	Free-floating, surface	Frflsr
	Free-floating, submerged	Frflsb
	Anchored, floating leaves	Anflle
	Anchored, submerged leaves	Ansule
	Anchored, emergent leaves	Anemle
	Anchored, heterophylly	Anhete
Vertical shoot architecture	Single apical growth point	Siapgr
	Single basal growth point	Sibagr
	Multiple apical growth point	Muapgr
Leaf area	Small (< 1 cm2)	LA 1
	Medium (1±20 cm2)	LA 2
	Large (20±100 cm2)	LA 3
	Extra large (> 100 cm2)	LA 4
Morphology index ((length+lateral spread)/2)	(1) 2	MI 1
	(2) 3-5	MI 2
	(3) 6-7	MI 3
	(4) 8-9	MI 4
	(5) 10	MI 5
High belowground: aboveground biomass	-	Root
Number of reproductive organs $year^{-1}$ $individual^{-1}$	Low (< 10)	RO 1
	Medium (10-100)	RO 2
	High (100-1000)	RO 3
	Very high (> 1000)	RO 4
Perennation	Annual	Annual
	Biennial/short lived perennial	Shlipe
	Perennial	Perenn
Evergreen leaf	-	Winter
Amphibious	-	Amphib
Body flexibility	Low (< 45°)	BF 1
	Intermediate (> 45-300°)	BF 2
	High (> 300°)	BF 3

Leaf texture	Soft	Soft
	Rigid	Rigid
	Waxy	Waxy
	Non-waxy	Nowaxy
Fruit size	< 1 mm	F1
	1-3 mm	F2
	> 3 mm	F3

Table 3 Macroinvertebrate traits that were used in this study.

Trait	**Attribute**	**Code**
Feeding habit	Grazers and scrapers	Gra
	Miners	Min
	Xylophagous taxa	Xyl
	Shredders	Shr
	Gatherers/collectors	Gat
	Active filter feeders	Aff
	Passive filter feeders	Pff
	Predators	Pre
	Parasites	Par
	Other feeding types	Oth
Locomotion type	Swimming/skating	Sws
	Swimming/diving	Swd
	Burrowing/boring	Bub
	Sprawling/walking	Spw
	(Semi)-sessil	Ses
	Other	Oth
Preferred substrate	Flags/boulders/cobbles/pebbles	Fbcp
	Gravel	Grvl
	Sand	Sand
	Silt	Silt
	Macrophytes	Macp
	Microphytes	Micp
	Twigs/roots	Twro
	Organic detritus/litter	Odli
	Mud	Mud
Size	<= 0.25 cm	<= 0.25 cm
	> 0.25 - 0.5 cm	> 0.25 - 0.5 cm
	> 0.5 - 1 cm	> 0.5 - 1 cm
	> 1 - 2 cm	> 1 - 2 cm
	> 2 - 4 cm	> 2 - 4 cm
	> 4 - 8 cm	> 4 - 8 cm
	> 8 cm	> 8 cm

Data analysis

All data analyses were performed in R Studio Version 0.99.903 with the package "ggplot2", "data.table" and "plyr". The abundance of traits was calculated by the sum of species abundance possessing the highest score of the trait ('2'). The literature review results were then used to split traits into response and effect. To assess whether water quality changes affected the abundance of response traits, the abundances of relevant response traits were correlated with water quality data using a Pearson correlation method.

As the trait scores are ordinal, the Kruskal-Wallis test was used to test the differences in trait value before the eutrophication (1947), after the first biomanipulation (1992), before the second biomanipulation (2005) and the most recent recording (2015). To show the differences visually, mean trait value was calculated and displayed in barplots.

To examine the effect of species abundance on the trait composition, the mean trait value was weighted by the abundance and displayed in line graphs.

Also for the macroinvertebrates mean trait value was calculated, however only using data from 2005 till the present. Barplots were made displaying the density of the species groups (ind/m^2), the number of transects in which vegetation is present, and the biomass of cyprinids (kg/ha). The differences in trait value were again tested using the Kruskal-Wallis test.

Several steps were necessary to calculate the overlap of response and effect traits. First, the proportion of species belonging to a trait was calculated from the affinity scores. For example, a species scoring '2' for two growth form categories was assigned 0.5 for each category. Second, the overlap between the traits was calculated with the following formula and weighted for the species abundances (adapted from Lepš et al., 2006).

$$O = \sum_{j=1}^{n} \frac{\min(M_{trait\ 1,j}\ , M_{trait\ 2,j})}{k}$$

Were O is the mean value for overlap between traits for the species in a given year, ranging from 0 to 1. M_{trait} is the value for the trait for the jth species and k the number of species.

Results

<u>Literature study</u>

From twelve peer-reviewed publications, 13 traits for macrophytes and macroinvertebrates were obtained and linked to drivers of change in lake Ringsjön. Table 4 shows the candidate list of the identified response traits to reduction of nutrient load and biomanipulation. The response traits for macrophytes mostly relate to a species' ability to efficiently capture light and utilize nutrients from the sediment. For macroinvertebrates response traits link to the release of predation due to the biomanipulation or the indirect effect of increased macrophyte cover (Table 4).

Table 4 List of response traits as the results of the literature study.

Driver	Abiotic effect	Biotic effect	Response trait	Effect	Species group	Certainty	Justification	Reference
Reduction of nutrient load to lake	Increased light	Decrease in phytoplankton (Chl a)	Morphological index, leaf area, growth form	++	Macrophytes	Well established	Traits relate to light interception and light utilization. Species able to allocate resources to the uppermost waters can improve their light interception.	Bornette & Puijalon (2011); Baattrup-Pedersen & Göthe (2015); Willby et al., (2000)
	Decreased nutrient concentration		Growth form, root:shoot	+	Macrophytes	Less certain	Generally, lower nutrient levels promote higher macrophyte diversity. Specific traits responses to decreased nutrients, unrelated to increase of light, are relatively poorly understood. A decrease in unrooted, floating macrophytes and an increase in species able to invest in more extensive rooting	Bornette & Puijalon (2011); Grime, 2001; Lacoul & Freedman (2006)

							systems could be expected, as species will have to rely more on the nutrients in the sediment with decreasing nutrients in the water.	
					Macroinvertebrate	Uncertain	No known direct effect of nutrient reduction on macroinvertebrates.	
Bio-manipulation	Increased light	Decrease in phytoplankton (Chl a), Decrease of benthic feeding	Morphological index, Growth form	++	Macrophyte	Well established	Benthic-feeding fish suck up sediment and benthic fauna, to filter out the organisms and eject the sediment, clouding the water. Improved light conditions can thus be expected due to the decrease of phytoplankton and decrease of benthic feeding. Traits relate to light interception and light utilization. Species able to allocate resources to the uppermost waters can improve their light interception.	Bornette & Puijalon (2011); Baattrup-Pedersen & Göth (2015). Willby et al., (2000). Williams et al., (2002); Hansson (1998)
	Decrease of cyprinid fish	Reduction of herbivory	Palatability (N:phenolics, C:N, leaf tougness)	+	Macrophyte	Less certain	Direct effect of foraging cyprinids on macrophytes unclear. Macrophytes can be part of diet of cyprinids, but only if other food sources are unavailable. Also macrophytes can be negatively affected by plucking of leaves during the foraging for macroinvertebrates. More palatable plants could be more	Williams et al., (2002); Wood et al., (2016); Strand (1999)

							positively affected by decrease in herbivory. Palatability of a plant depends on physical properties and its nutritional value. High nitrogen concentration means greater nutrition for species and therefore greater herbivory can be expected. Phenolics and leave toughness make a plant less palatable.	
		Reduction of predation	Size	+ /-	Macroinverte brate	Less certain	Biomanipulation in general has a positive effect on macroinvertebrates, because of the release from predation by cyprinid fish and increase in macrophytes. This effect could be greater for larger macroinvertebrates, because they are generally subject of predation by omnivorous fish. Smaller macroinvertebrates could consequently be negatively affected by the increase of predation by larger macroinvertebrates.	Boll, (2010); Diehl (1992)
		Increased food availability	Foraging behaviour-predator	+	Macroinverte brate	Less certain	Decreased competition with benthic feeding fish can result in increased food availability for predaceous macroinvertebrates.	Diehl, (1992)

		Increase of macrophytes	Substrate preference-macrophytes, Feeding type-macrophytes	+	Macroinvertebrate	Well established	The increase in abundance of macrophytes generally following biomanipulation, has a positive effect on macroinvertebrates because they can seek shelter from predators. An additional positive effect can be expected for macro-invertebrates that feed on or are associated with macrophytes.	Boll, (2010)

Table 5 contains the effect traits that were identified from the review of 15 peer-reviewed publications. For the ecosystem functions nutrient and sediment retention, only macrophyte traits were found. Traits relating to the decomposability and palatability of plants were similar. Effect traits of macroinvertebrates for water purification related mostly to the foraging behaviour and could influence the function both positively and negatively.

Table 5 List of effect traits as result of the literature study.

Ecosystem function	Process	Effect traits	Effect	Species group	Certainty	Justification	Reference
Water purification	Promoting nutrient recycling	C:N aboveground, C:N belowground, Biomass belowground, Biomass aboveground, Root porosity	+	Macrophytes	Less certain	Higher quantities of soil C (higher C:N and biomass) provides substrate for denitrification and primes the soil in general for decomposition of organic material. Higher oxygen in soils can both inhibit and promote denitrification. Denitrification takes place in anoxic conditions, but O_2 can promote NO_3- production, which in turn can diffuse in to the anaerobic zone and promote denitrification. In an anaerobic environment (below 10% oxygen saturation), oxygen release from roots is more likely to facilitate denitrification.	McGill et al., (2010); Sutton-Grier et al., (2013)

		Foraging behaviour-active filterers (+), Locomotion-burrowing (-)	+/-	Macroinvertebrates	Less certain	Tube dwelling macroinvertebrates like chironomids have been found to promote nitrification and denitrification by oxygenating the sediment. However, bioturbation can also increase the release of ammonium and phosphorous of the sediment, thereby having a negative effect on the water quality. Filter feeders can remove great amount of particulates from the water column. Part of the filtered material is used for growth and reproduction, or excreted inorganically. Great parts are also translocated to the sediment, thereby having a positive effect on the water quality.	Vanni, (2002); Nalepa et al. (1991); Boll, (2010); Bergman & Hansson, (1999)
		Foraging behaviour-benthic	-	Fish	Less certain	Benthic feeding fish disturb the sediment and translocate nutrients stored in the sediment to the water column.	Persson, (1997); Bergman & Hansson, (1999)
	Nutrient retention	Growth form, Productivity (RGR, leaf area), root type, decomposability (-) (leaf toughness, lignin, leaf texture, C:N), Life span	+	Macrophytes	Less certain	Plants fix nutrients from water and/or the sediment (dependent on their growth form and root:shoot), thereby having a positive effect on nutrient retention in general. High productivity allows for the fast uptake of nutrient during the growing season, but trade-offs exist between fast growth and decomposability. Fast growing plants generally invest less in compounds that make the plant less decomposable (i.e. lignin). Fast growth therefore does not necessarily lead to increased stored nutrients.	De Bello et al. (2010); Freschet et al. (2012); García-Llorente, (2011); Moor et al. (2015)
	Sediment retention	Morphological index, body	+	Macrophytes	Well established	Morphological index ((Height + lateral spread)/2) is a measure of the species space occupancy/size high	De Bello et al. (2010);

		flexibility (-)				morphological index has a positive effect on sedimentation. Body flexibility expresses the amount of deformation under water flow pressure.	García-Llorente, (2011); Moor et al. (2015)
		Foraging behaviour-benthic	--	Fish	Well established	Benthic-feeding fish suck up sediment and benthic fauna, to filter out the organisms and eject the sediment, clouding the water.	Williams et al., (2002); Hansson (1998)
Food provision	Provision of food for larger animals	Palatability (phenolics (-), C:N (+), tissue toughness (-)), number of reproductive organs, Fruit size	+	Macrophytes	Well established	(Holds true for generalist herbivores) Palatability of a plant depends on physical properties and its nutritional value. High nitrogen concentration means greater nutrition for species and therefore greater herbivory can be expected. Phenolics and leave toughness make a plant less palatable.	Grutters, (2017); Strand (1999); Garcia-Llorente (2011); Elger,& Willby. (2003).
		Size	+	Macro-invertebrates	Less certain	Omnivorous fish generally predate on large predatory macroinvertebrates.	Diehl (1992)
Habitat provision			+	Macro-invertebrates		General positive effect of increased macrophytes	Boll, (2010)

Correlations between response traits and water quality

A significant positive correlation was found between LA 3 (“large” leaf area, 20-100 cm^2) ($p=0.0222$, $r=0.6776$) and MI 3 (morphological index between 6 and 7) ($p=0.0061$, $r=0.7651$; Figure 4; see appendix A for details) with the water quality variable Secchi depth. The growth forms “free floating, submerged leaves” ($p=0.0060$, $r=-0.7657$) and “anchored, submerged leaves” ($p=0.0344$, $r=-0.6386$) showed a significant negative correlation with the concentration of nitrogen in the water.

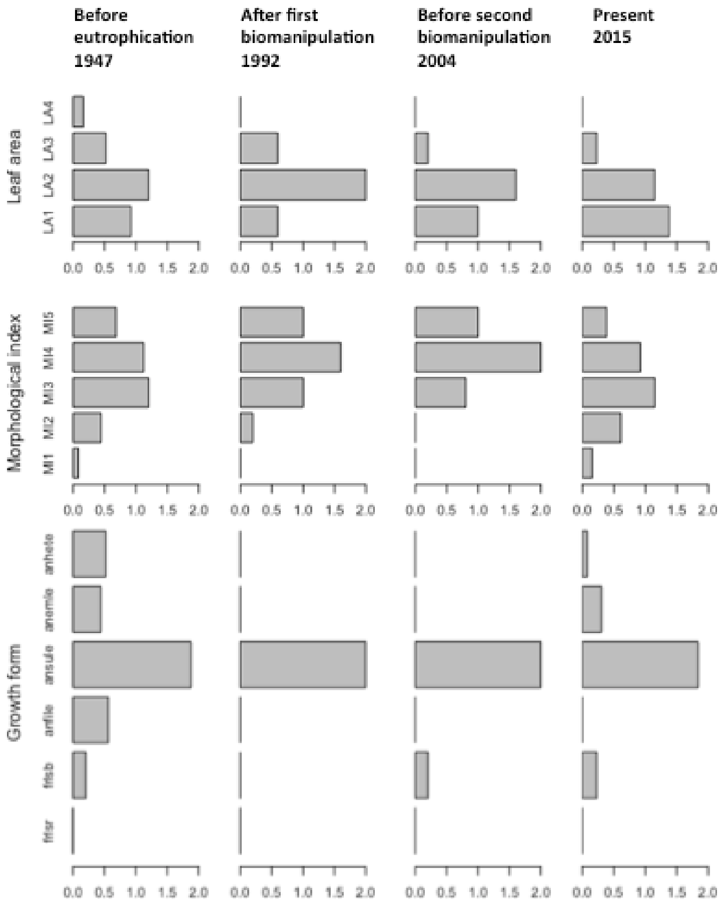


Figure 1 Mean trait value of the macrophyte community before the eutrophication (1947), after the first biomanipulation (1992), before the second biomanipulation (2005) and the most recent recording (2015). Only three traits are shown, the barplots of all macrophyte traits can be found in appendix B.

Macrophyte mean trait value over time

No significant changes in trait value of macrophytes over time were found (see appendix A for details). The pattern in mean trait value was similar for all traits before eutrophication (1947), after the first biomanipulation (1992), before the second biomanipulation (2005) and the most recent recording (2015). In the years in between the two biomanipulation attempts there was a lower number of macrophyte traits, 22 and 23 in 1996 and 2004 against 34 and 31 in 1947 and 2015, respectively. Also there are higher mean trait values of higher leaf area and morphological index classes (figure 4). The oldest (1947) and the most recent (2015) recordings of species seem most similar in terms mean trait value, although should be noted that 32 species were recorded in 1947 whereas only 17 species were found in 2015. The barplots of all macrophyte traits can be found in appendix B.

The weighted mean macrophyte trait abundance shows three different patterns over time (figure 5). First there are traits that increase in relative abundance in between the two biomanipulation attempts (1992-2005) and decrease again in the period of biomanipulation (MI 5, siapgr and LA 3) or

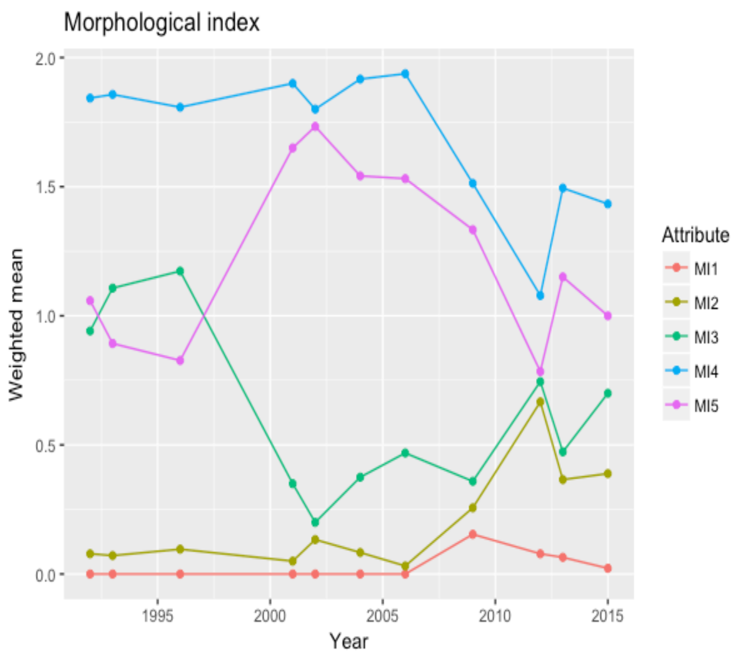


Figure 5 Weighted mean of the trait value of the morphological index over time. The line graphs of all macrophyte traits can be found in appendix C.

have the inverted response (MI 3). Second there are traits that have been dominant in the community since 1992 and decrease in relative abundance in recent years (ansule, muapgr, LA 2, MI4, nowaxy, soft, perrenn). Lastly there are traits that (re)appear in the community (frlsb, anemle, anhete, MI 1, siabgr, waxy, F1, BF 1, RO 1). Other traits seem to change little over time. In general, the macrophyte community seems to move towards a state where more traits are present in more similar amounts. The line graphs of all macrophyte traits can be found in appendix C.

Density of macroinvertebrates

Macroinvertebrate mean trait value does not significantly change in the period 2005-2014. However, macroinvertebrates do change in their density over the years (figure 6). The density of some species groups (e.g. *Pisidium* sp. and Ceratopogonidae) follow the same trend as that of the vegetation, with a decrease in the years in between the biomanipulation attempts and an increase again from 2005 onwards. The abundance of some macroinvertebrates seems more affected by the reduction in cyprinid (i.e. Chironomidae) (figure 7) and increase in the year with the highest reduction of cyprinids. Other groups like Oligochaeta are not affected by either biomanipulation events.

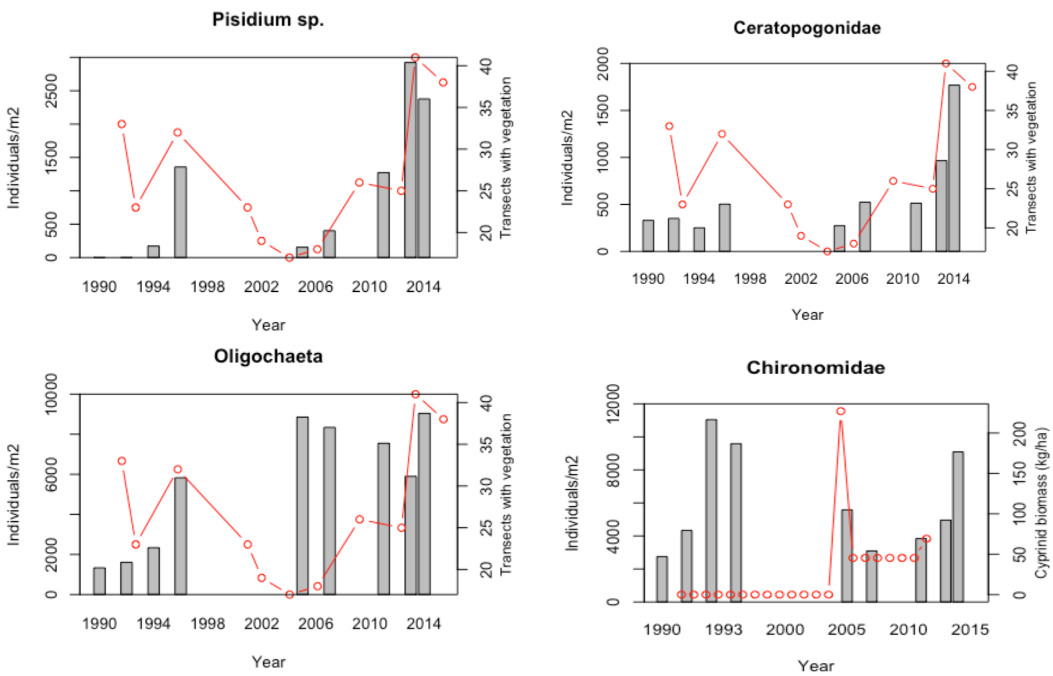


Figure 6 The density (ind/m^2) of four macroinvertebrate groups over time. Red line displays the number of transect vegetation was present or in case of the Chironomidae the biomass of cyprinids. Graphs of all macroinvertebrates can be found in appendix D.

Overlap between response and effect traits

The degree of overlap over time between leaf area (response trait for light) and three different effect traits for sediment retention, food provision and nutrient retention reaches values up to 0.5 (figure 8). A table of overlap between all traits can be found in appendix E.

Over time, overlap between leaf area attributes and leaf toughness stays low (between 0.1-0.3) and relatively constant (Figure 8c). A greater variation is found for the overlap between body flexibility and fruit size over time (figures 8a and 8b, respectively). In general, LA 3 seems to overlap little with any of the effect traits. On the other hand, the overlap between LA 1 and LA 2 and the effect traits is greater and varies more over time.

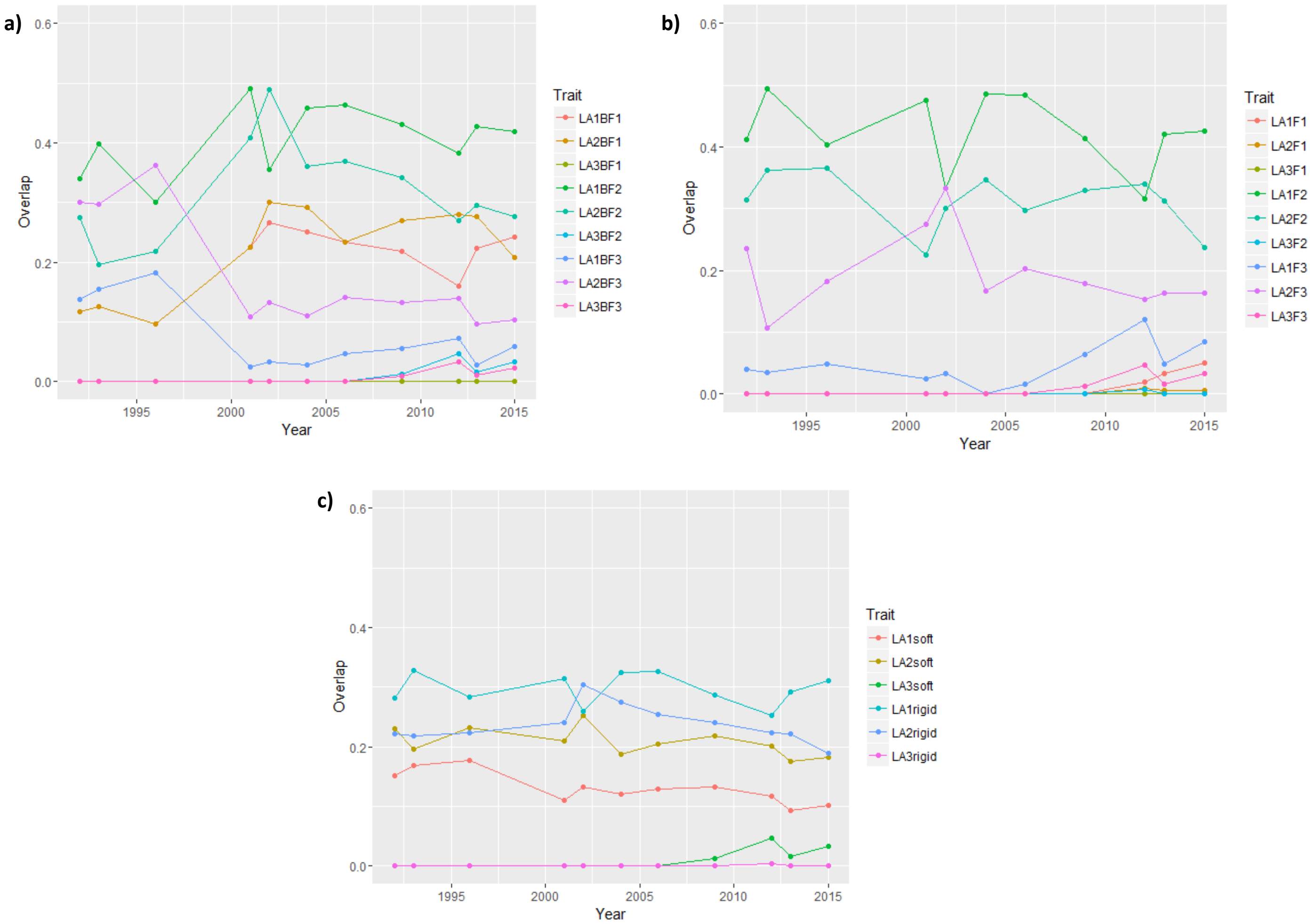


Figure 8 Overlap over time between leaf area and three different effect traits a) Body flexibility b) Fruit size and c) leaf toughness.

Discussion

The aim of this study was to test whether using a framework and effect traits could identify the effects of long-term management on the ecosystem functioning and ecosystem services potential of freshwater ecosystems. The literature review showed that there are several candidate traits with reported responses and effects that are be relevant to the case study of lake Ringsjön. Overall, the management actions taken in lake Ringsjön seem to have had a positive effect on species diversity and water quality. This was also visible in the traits, which became more similar to the period before the eutrophication. Furthermore, the analysis of overlap shows a partial overlap between response traits for light and some effect traits, suggesting ecosystem resilience. This is good news for Lake Ringsjön, and shows that the two management actions that were used to try and reduce the effects of eutrophication are giving positive results.

I found that the increase in macrophyte richness also resulted in the increase in the diversity of traits. After the second biomanipulation there is a decrease in the relative abundance of the most dominant traits and a (re)appearance of others. This would indicate that the community is becoming more functionally diverse. The tendency towards greater mean abundance of higher leaf area and morphological index classes in between the two biomanipulation attempts combined with the significant correlation found between Secchi depth and LA3 and MI3 argues for the use of these traits for predicting species response to light.

Fewer traits were available for predicting species response to nutrients, and the resulting correlations with the growth forms are counter-intuitive. It was expected that there would be an increase of species with roots that can obtain nutrients from the sediment and water. Instead the abundance of free-floating plants increased and anchored plants with submerged leaves decreased. The optimal growth form of plants is however subject to other factors, for instance light and water movement (Madsen et al., 2001). It is therefore debatable whether growth form is a valid trait for predicting species response to nutrients. A better trait could be root:shoot ratio (Bornette & Puijalon, 2011), although here this trait was not used because the limited data availability.

Both biomanipulation and the reduction of nutrient load affect the light conditions in the lake in a similar way, namely by decreasing the amount of phytoplankton. It is therefore difficult to disentangle the effects of both measures. However, the fact that the second biomanipulation resulted in higher macrophyte abundance suggests that the nutrient levels were too high for macrophyte reestablishment during the first biomanipulation. The removal of cyprinid fish could also have had a positive effect on the light availability by the decrease of benthic feeding. Benthic feeding fish, like adult cyprinid fish, disturb the sediment and cloud the water while foraging (Bergman & Hansson, 1999; Williams et al., 2002). The biomanipulation did not seem to affect macrophytes directly, as there were little observed differences palatability traits. It could be that the cyprinid fish did not feed on macrophytes in the first place, as omnivorous fish probably only feed on macrophytes if other food sources are not available (Williams et al., 2002). Also it is possible that leaf texture and evergreen leaves are not good indicators for the palatability of a plant. Biochemical traits, like C:N and C:phenolics ratio, could be more useful in this case, as palatability of a plant depends on physical properties and its nutritional value (Grutters et al., 2017). There is often a greater availability of traits that are easy to measure, while other (biochemical) traits can prove to be better predictors for a given process (Moor, 2016). Furthermore, traits of freshwater biodiversity is currently underrepresented in trait literature (Hevia et al. 2017). This put a limit on this study. For future studies on trait-driver and trait-ecosystem function relationships, there is a need for more standardized measurements of trait values of freshwater species.

The changes in macroinvertebrate abundances could be the result of both the increase in macrophytes and the decrease of cyprinid fish. However, it should be noted that measurements on the density of macroinvertebrates are only conducted in one transect, it is therefore difficult to say whether these trends are true for the whole lake. Most of the studied macroinvertebrates are associated with macrophytes, either because macrophytes are their preferred substrate or because it is a food source (Appendix F). Some macroinvertebrate groups, for instance *Pisidium* sp., increase with the increase in macrophyte abundance. The increase in *Pisidium* sp. abundance could positively affect water quality because *Pisidium* sp. actively filter water (Nalepa et al., 1991). Others macroinvertebrate groups are more likely to be influenced by the release from predation by cyprinid fish. This effect is most visible in the density of chironomids who increase in the year of the biomanipulation. This is in line with Boll (2010) who reported the same effect on chironomids after the biomanipulation of lake Vaeng.

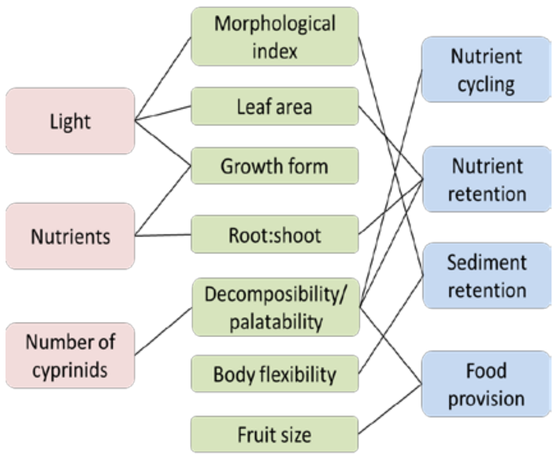


Figure 9 Functional traits of macrophytes (green) where a relationship with drivers (red) and /or ecosystem function has been found in literature.

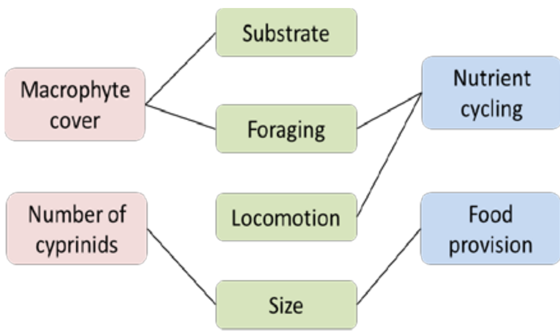


Figure 10 Functional traits of macroinvertebrates (green) where a relationship with drivers (red) and /or ecosystem function has been found in literature.

As yet there are few studies that tested the overlap between response and effect traits to provide an indicator of the relationship between drivers and ecosystem functions (Hevia et al., 2017). In this study I found that the some traits are the same for both driver and function. For instance, the morphological index of macrophytes is both a response trait for light and an effect trait for sediment retention (figure 9). This is likely because a greater space occupancy (i.e. a high morphological index) is both beneficial for light capture and sedimentation (Moor, 2016; Bornette & Puijalon, 2011). Identifying traits that are responsible for both the response to a driver as the effect on a function is important, as species possessing such a trait will always respond to the driver and affect the ecosystem function (Hevia et al., 2017). Overlap between response and effect traits can also result from species possessing traits for both response and effect. I found that the lower leaf area classes had a relatively high overlap with the lower body flexibility classes. This would imply that an increase in species with low leaf area classes leads to more sediment retention. In contrast, I also found that the higher leaf area class had little overlap with any effect traits. Implying that an increase in species possessing this trait would not have an effect on ecosystem function. Species with high leaf areas have a benefit over species with lower leaf areas in low light conditions, because they can capture more light (Bornette & Puijalon, 2011). These results would imply that if an increase in light availability is small, there would be no effect on ecosystem function. However, the competitive advantage of species with high leaf areas disappears when light conditions are sufficient to also support species with lower leaf areas. This was also happened in Ringsjön, with increasing light the relative abundance of the low leaf area class increased.

Whether the change in the relative abundance of traits also led to a change in ecosystem functioning of lake Ringsjön is difficult to extrapolate, as there have been no direct measurements of the functions. Some indication could however be given. For example, since the start of the biomanipulation the number of sightings of water birds increased, pointing to increased food availability for water birds in the lake. Also the increased water quality could be the result of the changes in species composition. This are however speculations and a relationship between the changes in species composition and ecosystem function cannot be established in this study. To accomplish this, more measurements of ecosystem functions are needed.

Another topic of future research could be into the relationship between ecosystem function and ecosystem service delivery. An ecosystem service potential does not necessarily lead to the provision of an ecosystem service. Ecosystem services usually need some human intervention for their production and are therefore not provided without human's needs for them (Haines-Young et al., 2010; Palomo et al., 2016). To examine the ecosystem service supply of an area indicators are needed. An example of such an indicator that is available for lake Ringsjön is the number of sold fishing licences. The increase in sold fishing licences in recent years (Ringsjön's Vatternrad, pers. comm.) could point to the increase of the ecosystem service "fishing". Although this is not necessarily the result of increased ecosystem functioning, it could be also be that the demand for the service increased (for instance due to an increase in the popularity of fishing) (Andersson et al., 2015).

Here I used functional traits to assess the effects of management on species composition and ecosystem function of lake Ringsjön during the period 1990-2015. The additive value of using traits in these kind of studies is that it gives a more detailed understanding of the changes in an ecosystem and helps to discover general trends across ecosystems (Moor, 2016). However, current trait-based ecology is limited by two factors: (i) the suitability of a trait to predict species' response to a driver or effect on a function. (ii) The availability and quality of data on trait values. The framework of response and effect traits I built in this study reports the current knowledge on trait-driver and trait-ecosystem function relationship in biomanipulated lakes and is useful to apply and add to in other studies. The framework showed to be effective to some extent in explaining the management effects on species composition of Ringsjön. Furthermore, as one in few studies

(Hevia et al., 2017), I used a measurement of overlap between response and effect traits in this framework to predict the response of ecosystem function to a driver. However, limited measurement on indicators of the ecosystem function of lake Ringsjön make it difficult to validate this method. Trait-based ecology developed considerably in recent years (Hevia et al., 2017) and this study provided an insight in the current status of trait-based ecology in freshwater ecosystem. Addressing the gaps of knowledge I found here would be greatly relevant to improve understanding of management effects on ecosystem function and inform decision-making for the management of ecosystems in benefit of human well-being.

References

General text

Algae be gone! (ABG) (2014). Restaurering av övergödda sjöar – Erfarenheten från EU-projektet Algae Be Gone!. Retrieved from: http://www.ringsjon.se/wp-content/uploads/2015/08/ABGbok_hela.pdf

Andersson, E., Nykvist, B., Malinga, R., Jaramillo, F., & Lindborg, R. (2015). A social-ecological analysis of ecosystem services in two different farming systems. *Ambio*, 44, 102–12.

Balvanera, P., Pfisterer, A.B., Buchmann, N, & He, J.S. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters, 9,* 1146-1156.

Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J., Bardgett, R., Berg, M., et al. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19(10), 2873–2893.

Bennett, E.M., Cramer, W, Begossi, A, & Cundill, G. (2015). Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability. *Current opinion in Environmental Sustainability,* 14, 76-85.

Campbell, A.J., Biesmeijer, J.C., & Varma, V. (2012). Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic and Applied Ecology.* 13, 363-370.

Durance, I., Bruford, M. W., Chalmers, R., Chappell, N. A., Christie, M., Cosby, B. J., ... & Woodward, G. (2016). Chapter Three-The Challenges of Linking Ecosystem Services to Biodiversity: Lessons from a Large-Scale Freshwater Study. *Advances in Ecological Research*, 54, 87-134.

Ekologgruppen (2015). Ronne å sammanfattning av vattenkontrollen 2015. Retrieved from: http://www.ringsjon.se/wp-content/uploads/2016/06/Ringrap15_web.pdf

Engelhardt, K. (2006). Relating effect and response traits in submersed aquatic macrophytes. *Ecological Applications*, 16(5), 1808-1820.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86(6), 902-910.

Grutters, B., Roijendijk, Y. O., Verberk, W. C., & Bakker, E. S. (2017). Plant traits and plant biogeography control the biotic resistance provided by generalist herbivores. *Functional Ecology*.

Haines-Young, R. & Potschin, M. (2010). The links between biodiversity, ecosystem services and human well-being. *Ecosystem Ecology: a new synthesis. 110-139.*

Hansson, L.A., Enell, M., Bergman, E. (1999). Lake Ringsjön: its catchment area, its history and its importance. *Hydrobiologia,* 404, 1-7.

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., Bello, F., & González, J. A. (2017). Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. *Ecology and Evolution.*

Kotschy, K., Biggs, R., Daw, T., Folke, C., & West, P. (2015). Principle 1—maintain diversity and redundancy. Principles for building resilience sustaining ecosystem services in social-ecological systems. Cambridge University Press, Cambridge, 50-79.

Lavorel, S, & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology,* 16, 545-556.

Leps, J., De Bello, F., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, 78(4), 481-501.

Madsen, J. D., Chambers, P. A., James, W. F., Koch, E. W., & Westlake, D. F. (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia*, 444(1), 71-84.

McGill, B.J., Enquist, B.J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in ecology and evolution,* 21(4), 178-185.

Millennium Ecosystem Assessment (2005). Ecosystems and Human well being: wetlands an water synthesis. Washington DC: World resource institute.

Nalepa, T. F., Gardner, W. S., & Malczyk, J. M. (1991). Phosphorus cycling by mussels (Unionidae : Bivalvia) in Lake St. Clair. *Hydrobiologia*, *219*(1), 239–250.

Palomo, I., Felipe-Lucia, M., Bennett, E., Martín-López, B., & Pascual, U. (2016). Chapter Six Disentangling the Pathways and Effects of Ecosystem Service Co-Production. *Advances in Ecological Research*, 54, 245–283.

Reyers, B, Biggs, R, & Cumming, G.S. (2013). Getting the measure of ecosystem services: a social–ecological approach. *Frontiers in Ecology and the Environment,* 11, 268-273.

Schmidt-Kloiber, A. & Hering D. (2015). www.freshwaterecology.info - an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators 53: 271-282.

Spangenberg, J. H., Haaren, C., & Settele, J. (2014). The ecosystem service cascade: Further developing the metaphor. Integrating societal processes to accommodate social processes and planning, and the case of bioenergy. *Ecological Economics*, 104, 22–32.

Steffen, W, Persson, Å., Deutsch, L, & Zalasiewicz, J. (2011). The Anthropocene: From global change to planetary stewardship. *Ambio*, 40, 739-761.

Søndergaard, M., & Jeppesen, E. (2007). Anthropogenic impacts on lake and stream ecosystems, and approaches to restoration. *Journal of Applied Ecology,* 44, 1089-1095.

Suding, K.N., Lavorel, S, & Chapin, F.S. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Chang Biology*, 14, 1125-1140.

TEEB (2010). *The economics of Ecosystems and Biodiversity (TEEB): Ecological and Economic Foundation*s. London:Earthscan.

Usseglio-Polatera, P, & Bournaud, M. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater biology,* 43, 175-205.

Villa, F., Bagstad, K. J., Voigt, B., Johnson, G. W., Portela, R., Honzák, M., & Batker, D. (2014). A methodology for adaptable and robust ecosystem services assessment. *PloS one*, *9*(3), 1-18.

Williams, A. E., Moss, B., & Eaton, J. (2002). Fish induced macrophyte loss in shallow lakes: top–down and bottom–up processes in mesocosm experiments. *Freshwater biology*, 47(11), 2216-2232.

World Bank (2014). *World development indicators 2015*. Washington, DC: World Bank.

<u>Traits</u>

Baattrup-Pedersen, A., Göthe, E., Larsen, S. E., O'Hare, M., Birk, S., Riis, T., & Friberg, N. (2015). Plant trait characteristics vary with size and eutrophication in European lowland streams. *Journal of Applied Ecology*, 52(6), 1617-1628.

Bergman, E, & Hansson, LA. (1999). Nutrient reduction and biomanipulation as tools to improve water quality: the Lake Ringsjön story.

Boll, T. (2010). *Response of macroinvertebrates in lakes to biomanipulation and climate change* (Doctoral dissertation, PhD Thesis. Aarhus University, Denmark).

Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences*, *73*(1), 1–14.

Diehl, S. (1992). Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology*, *73*(5), 1646-1661.

Elger, A., & Willby, N.J. (2003). Leaf dry matter content as an integrative expression of plant palatability: the case of freshwater macrophytes. *Functional Ecology*, 17(1), 58-65.

Freschet, G., Aerts, R., & Cornelissen, J. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology*, *26*(1), 56–65.

García-Llorente, M., Martín-López, B., Díaz, S., & Montes, C. (2011). Can ecosystem properties be fully translated into service values? An economic valuation of aquatic plant services.*Ecological Applications*, 21(8), 3083-3103.

Grutters, B., Roijendijk, Y. O., Verberk, W. C., & Bakker, E. S. (2017). Plant traits and plant biogeography control the biotic resistance provided by generalist herbivores. *Functional Ecology*.

Hansson, L. A., Annadotter, H., Bergman, E., Hamrin, S. F., Jeppesen, E., Kairesalo, T., Luokkanen, E., Nilsson, P.A., Søndergaard, M., Strand, J. (1998). Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. *Ecosystems*, 1(6), 558-574.

Lacoul, P., & Freedman, B. (2006). Environmental influences on aquatic plants in freshwater ecosystems. *Environmental Reviews*, *14*(2), 89–136.

McGill, B. M., Sutton-Grier, A. E., & Wright, J. P. (2010). Plant trait diversity buffers variability in denitrification potential over changes in season and soil conditions. *PLoS One*, 5(7).

Moor, H. (2016). *Function follows form: trait-based approaches to climate change effects on wetland vegetation and functioning*. (Doctoral dissertation, PhD Thesis. Stockholm University, Sweden).

Nalepa, T. F., Gardner, W. S., & Malczyk, J. M. (1991). Phosphorus cycling by mussels (Unionidae : Bivalvia) in Lake St. Clair. *Hydrobiologia*, *219*(1), 239–250.

Persson, A. (1997). Phosphorus release by fish in relation to external and internal load in a eutrophic lake. *Limnology and Oceanography*, *42*(3), 577-583.

Strand, J. A. (1999). The development of submerged macrophytes in Lake Ringsjön after biomanipulation. *Hydrobiologia*, *404*, 113-121.

Sutton-Grier, A. E., Wright, J. P., & Richardson, C. J. (2013). Different plant traits affect two pathways of riparian nitrogen removal in a restored freshwater wetland. *Plant and soil*, 365(1-2), 41-57.

Vanni, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, 33(1), 341-370.

Willby, N. J., Abernethy, V. J., & Demars, B. O. (2000). Attribute-based classification of European hydrophytes and its relationship to habitat utilization. *Freshwater Biology*, 43(1), 43-74.

Williams, A. E., Moss, B., & Eaton, J. (2002). Fish induced macrophyte loss in shallow lakes: top–down and bottom–up processes in mesocosm experiments. *Freshwater biology*, 47(11), 2216-2232.

Trait data

Bauernfeind, E., Moog, O. & Weichselbaumer, P. (1995).Ephemeroptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 1995. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.

Bauernfeind, E., Moog, O. & Weichselbaumer, P. (2002).Ephemeroptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 2002, Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Buffagni, A., Armanini, D.G., Cazzola, M., Alba-Tercedor, J., López-Rodríguez, M.J., Murphy, J., Sandin, L. & Schmidt-Kloiber, A. (2017).Dataset "Ephemeroptera". www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 6.0 (accessed on 20.03.2017).

Buffagni, A., Cazzola, M., López-Rodríguez, M.J., Alba-Tercedor, J. & Armanini, D.G. (2009).Distribution and Ecological Preferences of European Freshwater Organisms. Volume 3 - Ephemeroptera. Edited by Schmidt-Kloiber, A. & D. Hering. Pensoft Publishers (Sofia-Moscow). 254pp.

Car, M., Mohrig, W., Moog, O., Oosterbroek, P., Reusch, H., Wagner, R. & Zwick, P. (1995).Diptera (except Chironomidae) (authors depending on family). In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Eder, E., Hödl, W., Moog., O., Nesemann, H., Pöckl M. & Wittmann, K. (1995).Crustacea (authors depending on taxagroup). In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Graf, W., Grasser, U. & Waringer, J. (1995).Trichoptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 1995. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.

Graf, W., Grasser, U. & Waringer, J. (2002).Trichoptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 2002. Wasserwirtschaftskataster, Bundesministerium für Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Graf, W., Murphy, J., Dahl, J., Zamora-Muñoz, C. & López-Rodríguez, M.J. (2008).Distribution and Ecological Preferences of European Freshwater Organisms. Volume 1 - Trichoptera. Edited by Schmidt-Kloiber, A. & D. Hering. Pensoft Publishers (Sofia-Moscow). 388pp.

Graf, W., Murphy, J., Dahl, J., Zamora-Muñoz, C., López-Rodríguez M.J. & Schmidt-Kloiber., A. (2017).Dataset "Trichoptera". www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 6.0 (accessed on 20.03.2017).

Hörner, K., Moog, O. & Sporka, F. (1995).Oligochaeta. In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Nesemann, H. & Moog, O. (1995).Hirudinea. In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Nesemann, H. & Reischütz, P.L. (1995).Gastropoda. In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Schmedtje, U. & Colling, M. (1996).Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96, 543 pp.

Tachet, H., Bournaud, M., Richoux, P. & Usseglio-Polatera, P. (2010).Invertébrés d'eau douce - systématique, biologie, écologie. CNRS Editions, Paris, 600 p.

Zettel, H. (1995).Heteroptera. In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Websites

www.aquacross.eu
www.ringsjon.se
www.freshwaterecology.info

Appendix A: P values statistical test

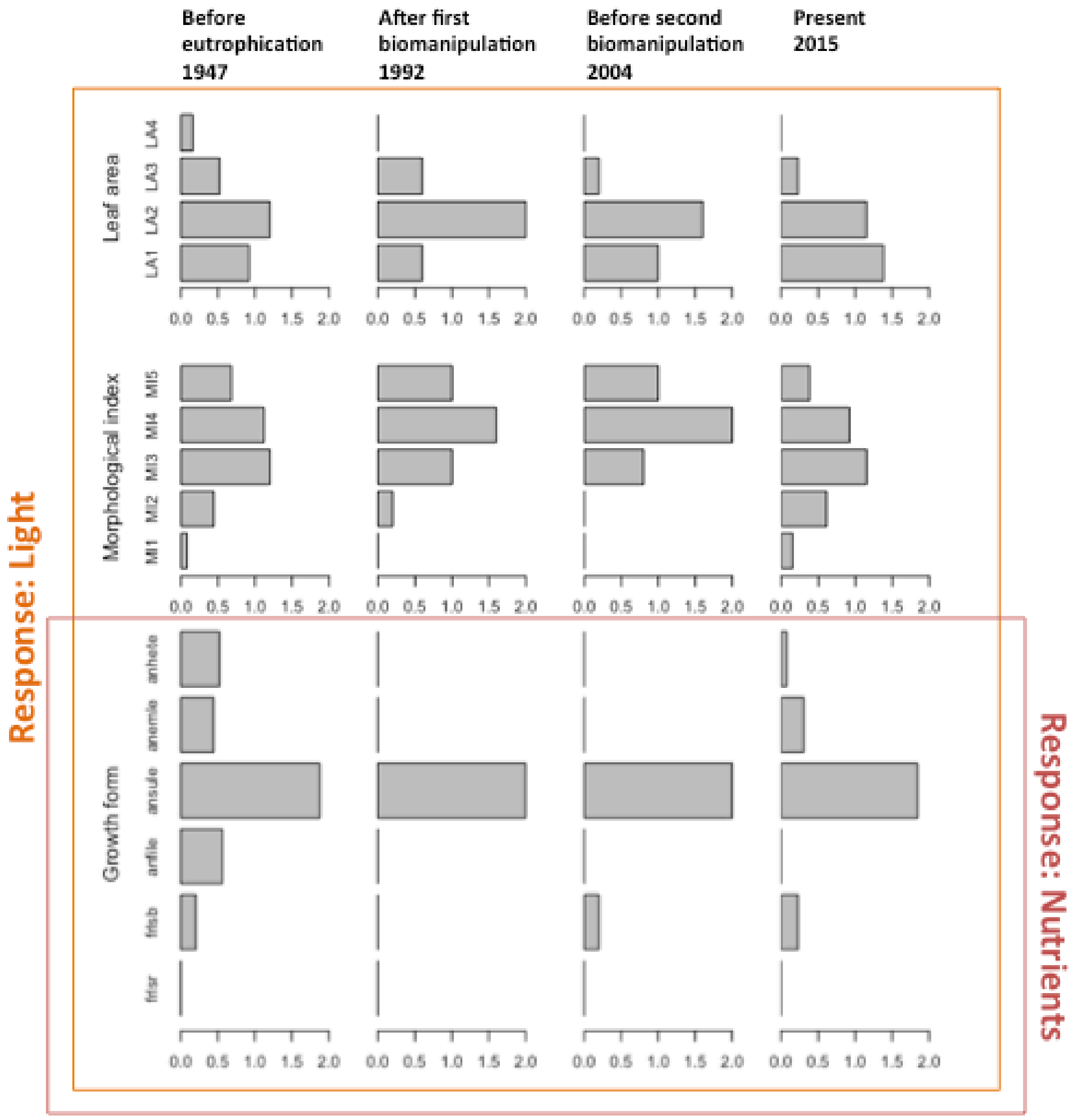
Table A1 Correlations between water quality variables and abundance of traits

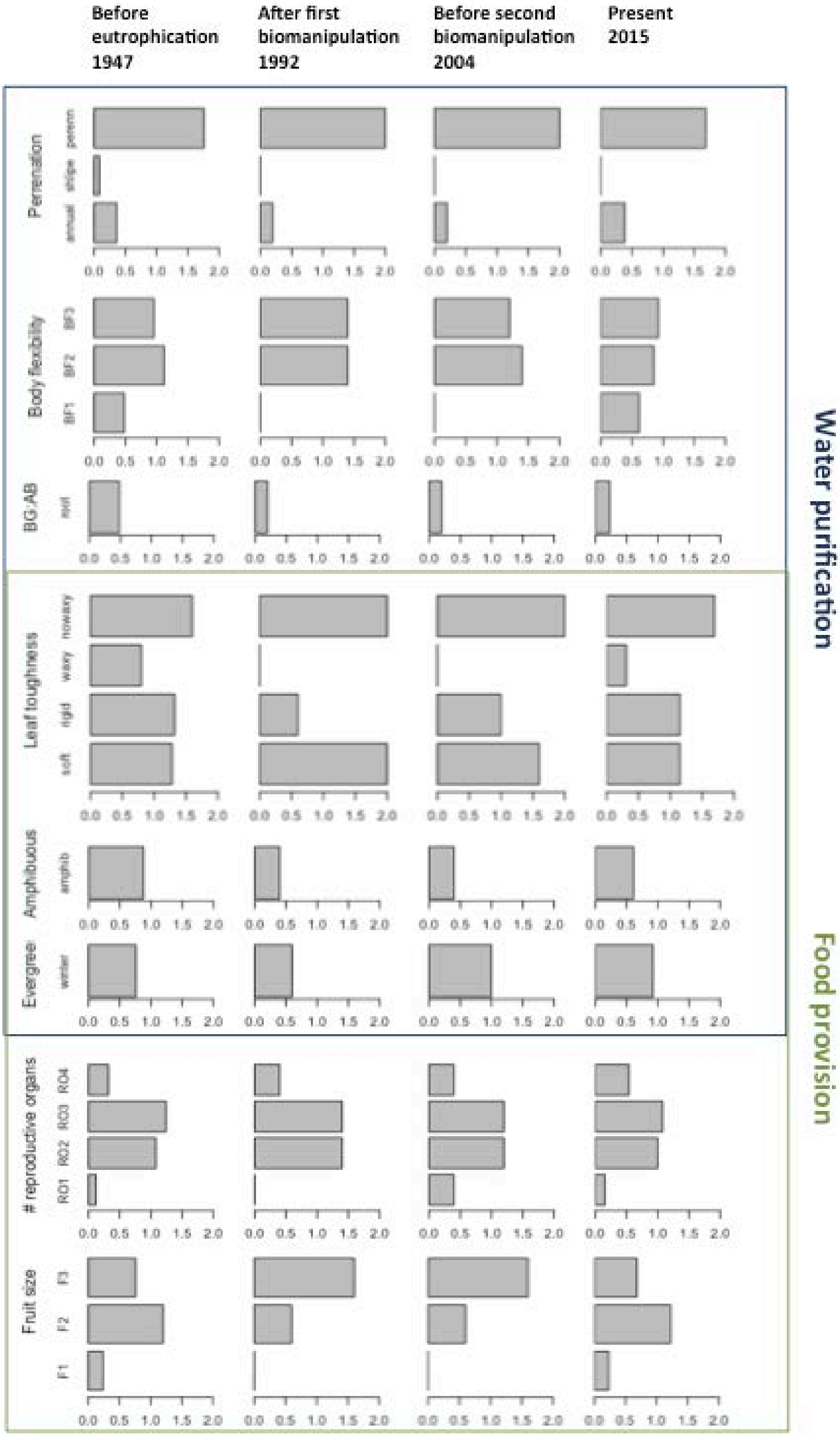
		p Secchi	r Secchi
Growth form	frlsb	0.8202	-0.0778
	anfile	0.9506	-0.0212
	ansule	0.3668	0.3019
	anhete	0.9506	-0.0212
Shoot architecture	siapgr	0.7158	-0.1243
	sibagr	0.8779	-0.0526
	muapgr	0.2583	0.3732
Leaf area	LA.1	0.7160	0.1242
	LA.2	0.2000	0.4187
	LA.3	0.0222*	0.6766
Morphological index	MI.1	0.9232	-0.0330
	MI.2	0.7223	-0.1213
	MI.3	0.0061**	0.7651
	MI.4	0.1862	0.4305
	MI.5	0.8731	-0.0547
		p Tot N	r Tot.N.ug.l
Growth form	frlsb	0.0060*	-0.7657
	anfile	0.1460	-0.4686
	ansule	0.0344*	-0.6386
	anhete	0.1460	-0.4686
		p Tot P	r Tot.P.ug.l
Growth form	frlsb	0.1727	-0.4427
	anfile	0.3130	-0.3356
	ansule	0.0717.	-0.5624
	anhete	0.3130	-0.3356

Table A2 Result of the Kruskal-Wallis test for macrophytes and macroinvertebrates

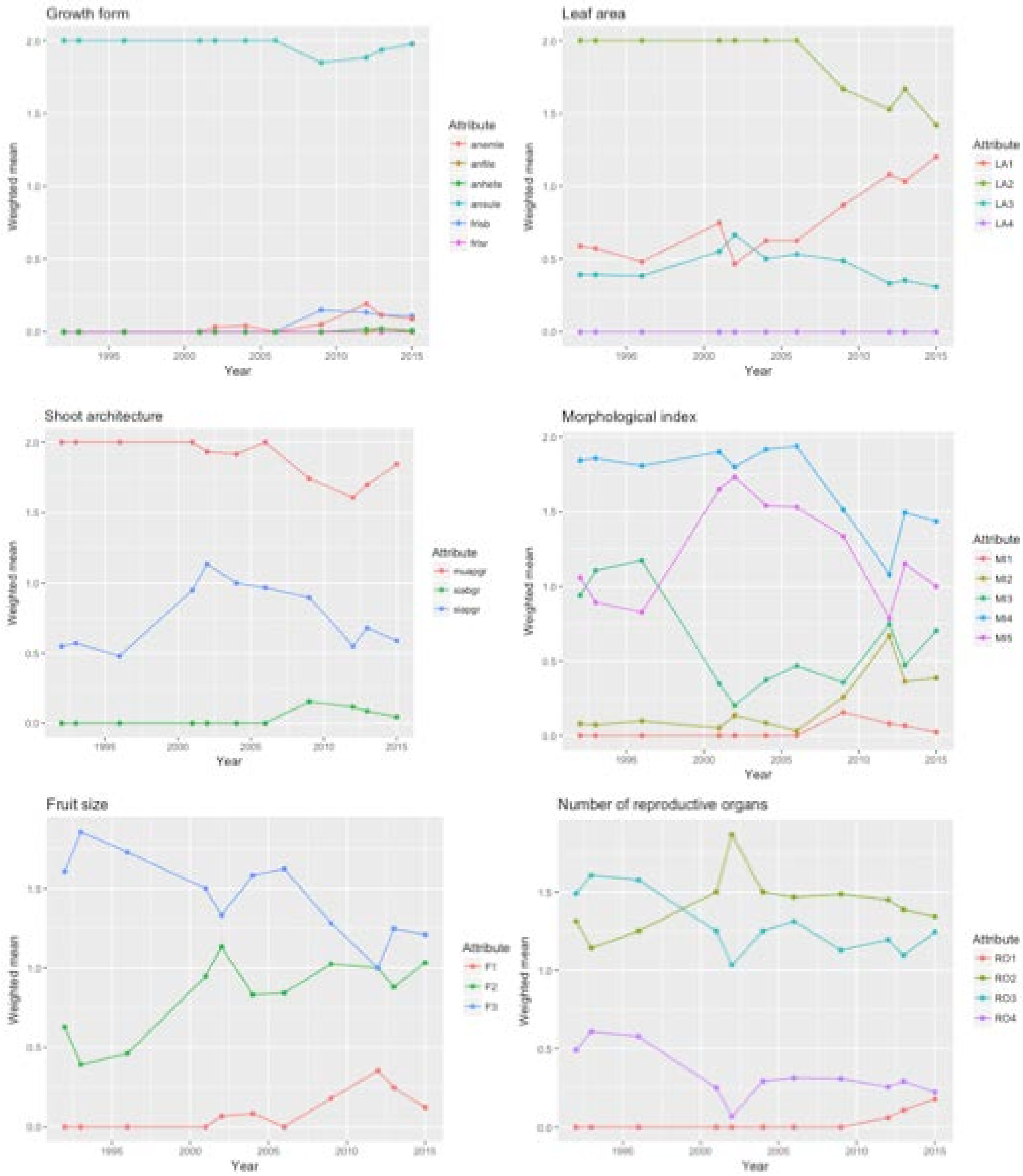
	p-value		p-value
LA1	0,32603027	gra	0,734518
LA2	0,24333904	min	0,9971313
LA3	0,66492345	shr	0,9766956
LA4	0,59768264	gat	0,9885126
MI1	0,84379536	aff	0,9616878
MI2	0,3783244	pre	0,9249517
MI3	0,7858096	par	0,9811398
MI4	0,09467222	oth	0,6304844
MI5	0,39857976	sws	0,9909144
frlsb	0,80895245	swd	0,9976451
anfile	0,0606573	bub	0,96939
ansule	0,84375258	spw	0,9817983
anemle	0,26015028	ses	0,9459854
anhete	0,15123234	oth.1	0,9984089
root	0,77768989	fbcp	0,8222535
RO1	0,70770792	grvl	0,9397518
RO2	0,83410159	sand	0,9766584
RO3	0,90779578	silt	0,9666677
RO4	0,79606063	macp	0,9377151
annual	0,98995406	micp	0,9686828
shlipe	0,82059886	twro	0,9302271
perenn	0,67284162	odil	0,9532882
winter	0,80229873	mud	0,9487758
amphib	0,52897601	X25	0,9830377
BF1	0,29038794	X225	0,9789228
BF2	0,60376552	X51	0,9932958
BF3	0,71786735	X12	0,9941671
soft	0,27702662	X24	0,952412
rigid	0,27883565	X48	0,9971313
waxy	0,07755047	X8	0,9971313
nowaxy	0,32824196		
F1	0,62324962		
F2	0,33351935		
F3	0,0993671		

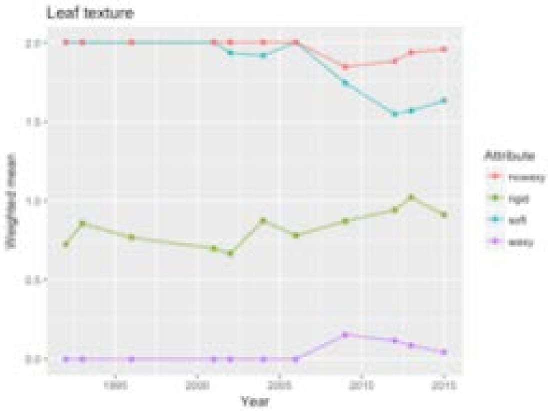
Appendix B: Comparison of mean trait value of the macrophyte community before and after the biomanipulation attempts

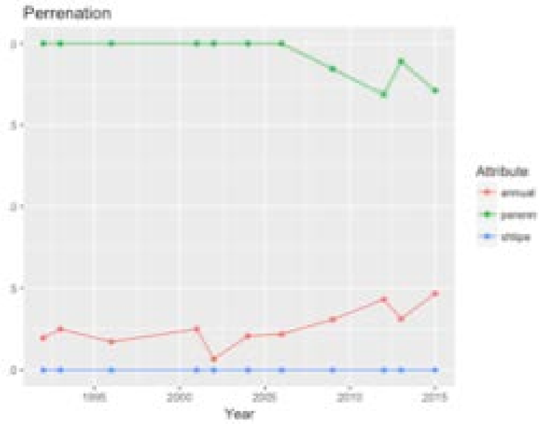


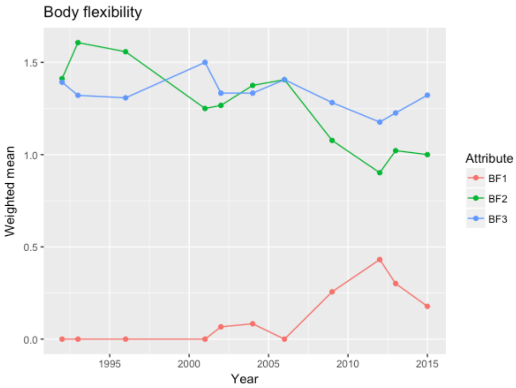

Before eutrophication 1947
After first biomanipulation 1992
Before second biomanipulation 2004
Present 2015
Perennation
annual
stipe
perenn
Body flexibility
BF1
BF2
BF3
BG:AB
Leaf toughness
soft
rigid
waxy
nowaxy
Amphibuous
amphib
Evergree
winter
reproductive organs
RO1
RO2
RO3
RO4
Fruit size
F1
F2
F3
0.0 0.5 1.0 1.5 2.0
Water purification
Food provision

Appendix C: Abundance weighted mean of the macrophyte community over time

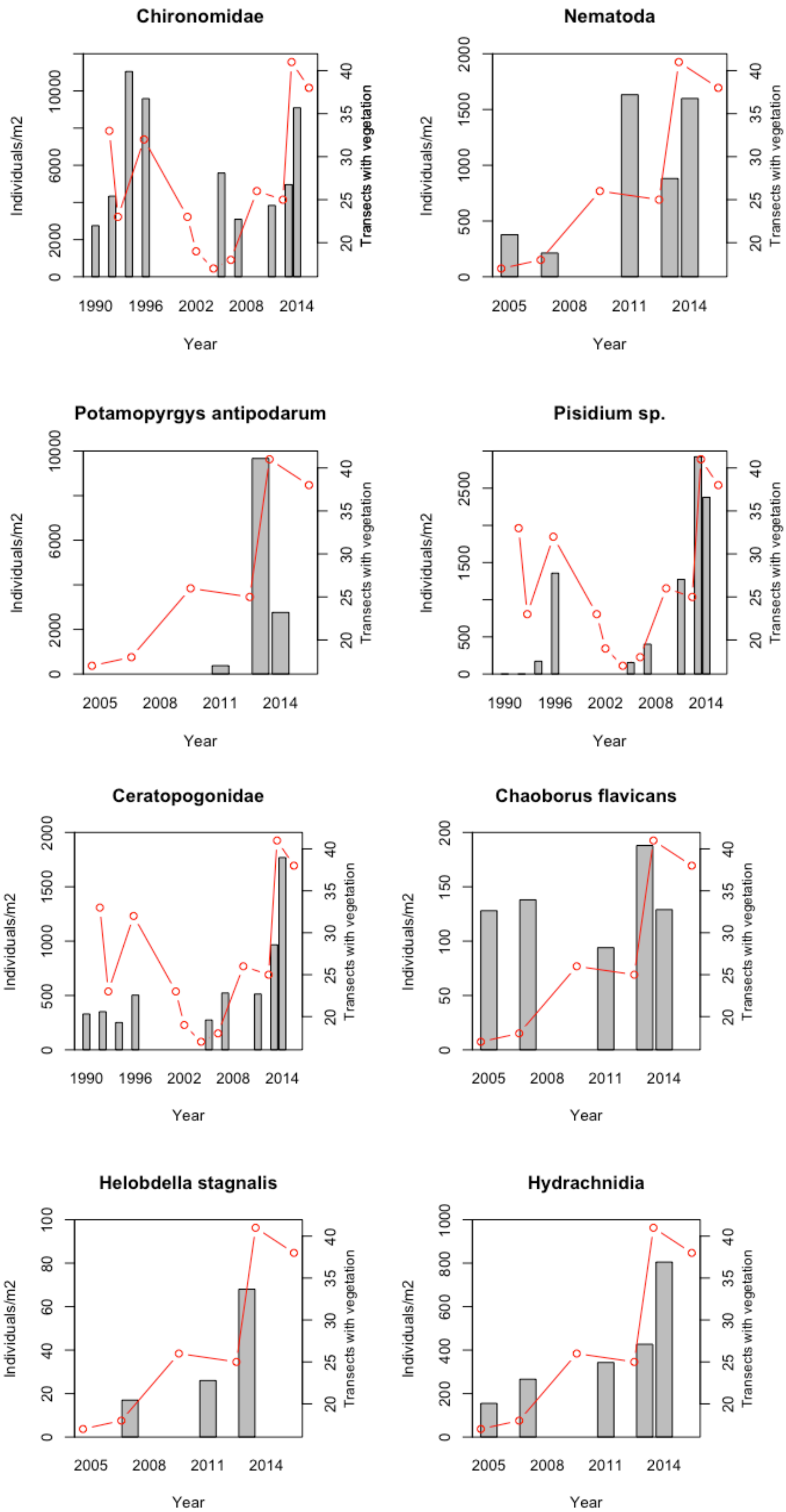


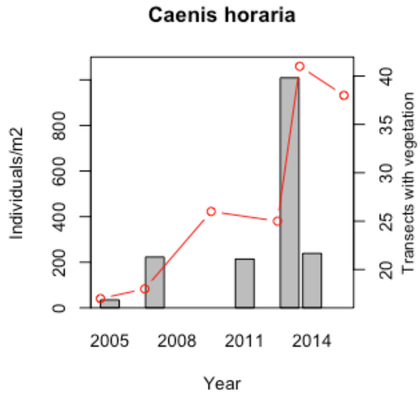

Leaf texture
Weighted mean
Attribute
Year
1995
2000
2005
2010
2015

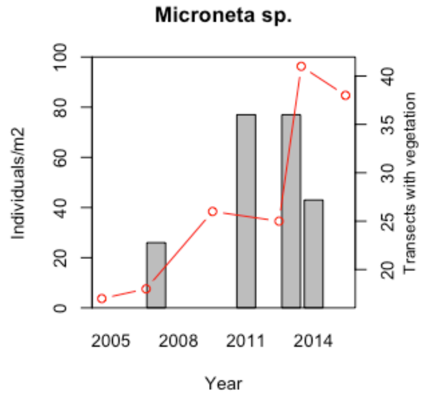

Perrenation
Attribute
annual
Year
1995
2000
2005
2010
2015

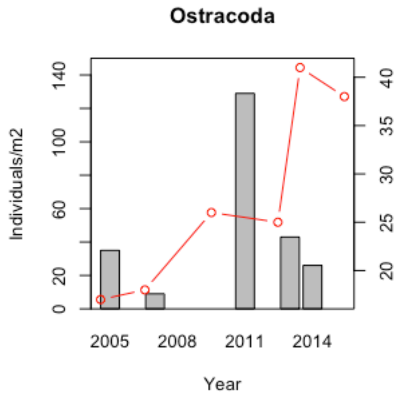

Body flexibility
Weighted mean
1.5
1.0
0.5
0.0
Attribute
BF1
BF2
BF3
Year
1995
2000
2005
2010
2015

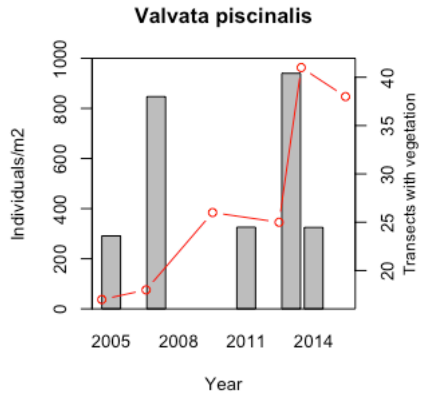
Appendix D: Density of macroinvertebrates over time

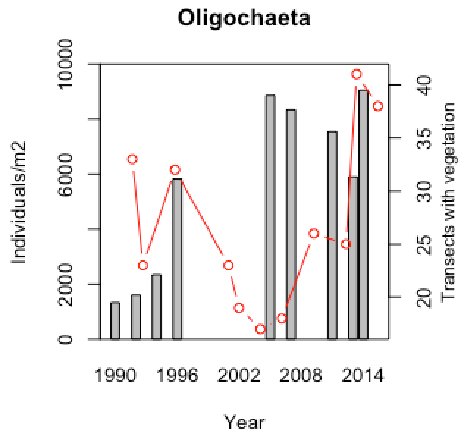



Caenis horaria
Individuals/m2
0 200 400 600 800
Transects with vegetation
20 25 30 35 40
2005 2008 2011 2014
Year


Microneta sp.
Individuals/m2
0 20 40 60 80 100
Transects with vegetation
20 25 30 35 40
2005 2008 2011 2014
Year


Ostracoda
Individuals/m2
0 20 60 100 140
Transects with vegetation
20 25 30 35 40
2005 2008 2011 2014
Year


Valvata piscinalis
Individuals/m2
0 200 400 600 800 1000
Transects with vegetation
20 25 30 35 40
2005 2008 2011 2014
Year


Oligochaeta
Individuals/m2
0 2000 6000 10000
Transects with vegetation
20 25 30 35 40
1990 1996 2002 2008 2014
Year

Appendix E Overlap between response and effect traits

		Light siapgr	muapgr	LA 1	LA 2	LA 3	MI 1	MI 2	MI 3	MI 4	MI 5
Nutrient retention	LA 1	0.0000	0.4020		0.1667	0.0000	0.0588	0.1078	0.2500	0.1765	0.0343
	LA 2	0.0490	0.3627	0.1667		0.0490	0.0000	0.1373	0.2598	0.1863	0.0735
	LA 3	0.0392	0.0490	0.0000	0.0490		0.0000	0.0196	0.0294	0.0196	0.0196
	root	0.0294	0.0294	0.0000	0.0980	0.0196	0.0000	0.0294	0.0294	0.0294	0.0294
	annual	0.0000	0.1961	0.1373	0.0784	0.0000	0.0000	0.0392	0.1127	0.0588	0.0147
	perenn	0.0490	0.5784	0.3627	0.4118	0.0490	0.0588	0.1569	0.3088	0.2255	0.0735
Food provision	winter	0.0000	0.3529	0.2745	0.2549	0.0000	0.0588	0.1176	0.1618	0.1471	0.0441
	amphib	0.0000	0.1765	0.1471	0.1471	0.0000	0.0588	0.0882	0.0686	0.0490	0.0294
	soft	0.0431	0.2971	0.1814	0.2343	0.0490	0.0000	0.0804	0.2255	0.1833	0.0676
	rigid	0.0118	0.1441	0.1696	0.1441	0.0118	0.0294	0.0941	0.1520	0.0990	0.0235
	waxy	0.0000	0.0382	0.0676	0.0382	0.0000	0.0294	0.0235	0.0382	0.0147	0.0000
	nowaxy	0.0431	0.3441	0.2480	0.2814	0.0490	0.0000	0.1275	0.2922	0.2324	0.0676
	RO 1	0.0000	0.0510	0.0510	0.0118	0.0000	0.0000	0.0000	0.0314	0.0510	0.0000
	RO 2	0.0490	0.3127	0.1902	0.2833	0.0490	0.0000	0.1471	0.2343	0.1755	0.0588
	RO 3	0.0392	0.4157	0.2882	0.2490	0.0392	0.0000	0.0980	0.3127	0.2000	0.0539
	RO 4	0.0000	0.0343	0.0784	0.0931	0.0000	0.0588	0.0294	0.0588	0.0343	0.0147
	F1	0.0000	0.0588	0.0784	0.0686	0.0000	0.0294	0.0588	0.0294	0.0294	0.0000
	F2	0.0196	0.4706	0.2941	0.2647	0.0196	0.0294	0.1176	0.2745	0.1275	0.0490
	F3	0.0490	0.2647	0.1078	0.1569	0.0490	0.0000	0.0392	0.1225	0.1275	0.0441
Sediment retention	MI 1	0.0000	0.0000	0.0588	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000

MI 2	0.0196	0.1078	0.1078	0.1373	0.0196	0.0000		0.1176	0.0000	0.0000
MI 3	0.0196	0.3775	0.2500	0.2598	0.0294	0.0000	0.1176		0.1716	0.0147
MI 4	0.0294	0.2647	0.1765	0.1863	0.0196	0.0000	0.0000	0.1716		0.0735
MI 5	0.0294	0.0735	0.0343	0.0735	0.0196	0.0000	0.0000	0.0147	0.0735	
BF1	0.0000	0.0294	0.1078	0.1275	0.0000	0.0588	0.1176	0.0588	0.0000	0.0000
BF2	0.0490	0.3529	0.1961	0.2255	0.0490	0.0000	0.0490	0.2402	0.1863	0.0441
BF3	0.0392	0.4314	0.2451	0.2255	0.0392	0.0000	0.0784	0.2304	0.1765	0.0637

		Nutrients		Fish					
		frlsb	root	winter	amphib	soft	rigid	waxy	nowaxy
Nutrient retention	LA 1	0.1078	0.0000	0.2745	0.1471	0.1814	0.1696	0.0676	0.2480
	LA 2	0.0294	0.0980	0.2549	0.1471	0.2343	0.1441	0.0382	0.2814
	LA 3	0.0000	0.0196	0.0000	0.0000	0.0490	0.0118	0.0000	0.0490
	root	0.0000		0.0588	0.0000	0.0235	0.0412	0.0000	0.0529
	annual	0.0000	0.0000	0.0196	0.0000	0.1078	0.0118	0.0000	0.1078
	perenn	0.1373	0.1176	0.5098	0.2941	0.2088	0.2324	0.0676	0.3147
	winter	0.0784	0.0588		0.2353	0.0882	0.1941	0.0529	0.1941
	amphib	0.0588	0.0000	0.2353		0.0559	0.0971	0.0676	0.0735
	soft	0.0294	0.0235	0.0882	0.0559		0.0735	0.0265	0.2853
	rigid	0.0490	0.0412	0.1941	0.0971	0.0735		0.0676	0.1794
	waxy	0.0294	0.0000	0.0529	0.0676	0.0265	0.0676		0.0147
	nowaxy	0.0490	0.0529	0.1941	0.0735	0.2853	0.1794	0.0147	
	RO 1	0.0314	0.0000	0.0392	0.0000	0.0118	0.0294	0.0000	0.0412
	RO 2	0.0431	0.0392	0.1520	0.1569	0.2353	0.1186	0.0343	0.2725
	RO 3	0.0235	0.0196	0.1863	0.0784	0.2676	0.1147	0.0382	0.2853
	RO 4	0.0588	0.0588	0.1520	0.0588	0.0343	0.0824	0.0294	0.0637

	F1	0.0882	0.0000	0.0882	0.0882	0.0294	0.0588	0.0294	0.0588
	F2	0.0294	0.0784	0.2647	0.2059	0.1873	0.1500	0.0676	0.2343
	F3	0.0196	0.0392	0.1765	0.0000	0.1196	0.0647	0.0000	0.1490
Sediment retention	MI 1	0.0588	0.0000	0.0588	0.0588	0.0000	0.0294	0.0294	0.0000
	MI 2	0.0000	0.0294	0.1176	0.0882	0.0804	0.0941	0.0235	0.1275
	MI 3	0.0490	0.0294	0.1618	0.0686	0.2255	0.1520	0.0382	0.2922
	MI 4	0.0490	0.0294	0.1471	0.0490	0.1833	0.0990	0.0147	0.2324
	MI 5	0.0000	0.0294	0.0441	0.0294	0.0676	0.0235	0.0000	0.0676
	BF1	0.0588	0.0588	0.2059	0.1471	0.0118	0.1118	0.0529	0.0588
	BF2	0.0588	0.0392	0.2059	0.0294	0.1667	0.1176	0.0235	0.2137
	BF3	0.0196	0.0196	0.1176	0.1176	0.2480	0.0618	0.0147	0.2480

Appendix F Trait values of macrophytes and macroinvertebrates

		Caenis horaria	Ceratopogonidae	Chaoborus flavicans	Chironomidae	Helobdella stagnalis	Hydrachnidia Gen. sp.	Micronecta sp.	Nematoda Gen. sp.	Oligochaeta Gen. sp.	Ostracoda Gen. sp.	Pisidium sp.	Potamopyrgus antipodarum	Valvata piscinalis
Feeding type	gra	0	0	0	1	0	0	0	0	0	0	0	1	0
	min	0	0	0	1	0	0	0	0	0	0	0	0	0
	xyl	0	0	0	0	0	0	0	0	0	0	0	0	0
	shr	0	0	0	0	0	0	0	1	0	1	0	1	0
	gat	5	0	0	2	0	0	5	2	5	4	0	2	5
	aff	0	0	0	1	0	0	0	0	0	0	5	0	0
	pff	0	0	0	0	0	0	0	0	0	0	0	0	0
	pre	0	5	5	1	5	4	0	2	0	0	0	0	0
	par	0	0	0	1	0	2	0	1	0	0	0	0	0
	oth	0	0	0	0	0	0	0	0	0	0	0	2	0
Locomotion	sws	0	0	3	0	0	2	0	0	0	0	0	0	0
	swd	0	4	3	1	0	0	4	3	0	0	0	0	0
	bub	0	0	0	0	0	0	0	0	4	0	1	0	0
	spw	0	0	0	1	5	2	0	3	1	0	2	5	5
	ses	0	0	0	2	0	2	0	0	1	0	3	0	0
	oth	5	2	0	2	0	1	2	0	0	0	0	0	0
Prefered substrate	fbcp	2	2	0	3	2	0	4	0	1	0	1	3	3
	grvl	2	3	1	1	0	0	2	0	2	0	1	2	2
	sand	3	4	1	3	0	0	2	0	3	0	4	1	1
	silt	3	1	1	2	0	0	1	0	0	0	4	1	1
	macp	4	3	1	4	5	0	4	0	0	0	3	3	5
	micp	0	3	0	0	0	0	0	0	0	0	0	3	2
	twro	2	3	0	2	0	0	0	0	1	0	1	0	3
	odil	3	1	0	1	3	0	2	0	1	0	3	0	1
	mud	5	4	4	3	0	0	3	0	3	0	4	4	4
Size	< 0.25	0	0	0	0	0	0	3	0	0	5	0	0	0
	0.25-0.5	2	0	0	1	0	0	1	0	0	0	3	3	2
	0.5-1	3	1	0	2	3	0	0	0	0	0	2	2	3
	1-2	0	3	3	3	1	0	0	0	1	0	1	0	0
	2-4	0	0	0	2	0	0	0	0	1	0	0	0	0
	4-8	0	0	0	0	0	0	0	0	3	0	0	0	0
	> 8	0	0	0	0	0	0	0	0	3	0	0	0	0

	Callitriche hermaphroditica	Eleocharis acicularis	Elodea canadensis	Lemna trisulca	Littorella uniflora	Myriophyllum spicatum	Potamogeton berchtoldii	Potamogeton crispus	Potamogeton filiformis	Potamogeton gramineus	Potamogeton lucens	Potamogeton obtusifolius	Potamogeton pectinatus	Potamogeton perfoliatus	Ranunculus circinatus	Ranunculus reptans	Utricularia vulgaris	Butomus umbellatus	Ceratophyllum demersum	Isoetes lacustris	Myriophyllum alterniflorum	Najas flexilis	Nuphar luteum	Polygonum amphibium	Potamogeton natans	Potamogeton friesii	Ranunculus peltatus	Scirpus lacustris
frlsb	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0
anfile	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	2	2	2	0	2	2
ansule	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	2	2	2	2	1	2	2	2	2
aneml e	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	1	1	0	0	1	2
anhete	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	2	0	0	0	0	2	0	2	0	2	2
siapgr	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0
sibagr	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	2	0	0	0	0	2
muapg r	2	0	2	0	0	2	2	2	2	2	2	2	2	2	2	2	2	0	2	0	2	2	0	2	1	2	2	0
LA 1	2	1	2	2	0	1	2	0	2	1	0	0	2	0	2	2	2	0	2	0	1	2	0	0	0	0	1	0
LA 2	0	2	0	0	2	2	0	2	1	2	2	2	2	2	0	2	2	0	0	2	2	0	0	1	2	2	2	0
LA 3	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	2	0	0	0	0	0	2	2	0	2	2
LA 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
MI 1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI 2	2	2	0	0	2	0	0	0	1	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	1	0
MI 3	1	0	1	0	2	0	2	2	2	2	2	2	1	0	2	2	2	0	1	2	1	2	0	1	2	2	2	0
MI 4	0	0	2	0	0	2	1	2	0	1	0	1	2	2	1	0	2	2	2	0	2	0	0	2	2	1	2	1

MI 5	0	0	0	0	0	2	0	0	0	0	0	0	1	2	0	0	0	2	1	0	2	0	2	2	1	0	0	2
RO 1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
RO 2	2	2	1	0	0	2	1	1	1	2	2	1	0	2	0	1	2	1	2	1	2	2	1	0	0	1	0	2
RO 3	2	0	0	0	0	1	2	2	2	1	1	2	2	1	2	2	2	2	0	2	0	1	2	2	2	2	2	1
RO 4	0	0	0	2	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
annual	2	0	0	0	0	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	0	2	0	0	0	2	2	0
shlipe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
perenn	0	2	2	2	2	2	0	2	2	2	2	0	2	2	2	2	2	2	2	2	2	0	2	2	2	0	2	2
winter	0	2	2	2	1	1	0	1	0	0	0	0	1	0	2	1	0	0	0	2	0	0	1	0	1	0	2	0
amphib	0	2	0	2	0	2	0	0	0	1	0	0	0	0	0	2	0	2	0	0	2	0	2	2	1	0	2	2
BF1	0	2	0	2	2	0	0	0	0	0	0	0	0	0	0	2	0	1	0	2	0	0	0	0	0	0	0	1
BF2	0	0	2	0	0	0	0	2	0	0	2	2	1	2	2	2	2	2	2	0	0	2	2	2	0	2	1	2
BF3	2	0	0	0	0	2	2	1	2	2	1	1	2	1	0	0	1	2	0	0	2	0	0	0	2	1	2	2
soft	2	0	0	0	0	2	2	2	2	2	2	2	2	2	0	1	2	2	0	0	2	2	2	0	1	2	2	2
rigid	0	2	2	2	2	0	0	1	1	2	0	0	1	1	2	2	0	2	2	2	0	0	2	2	2	0	1	2
waxy	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	2	0	2	0	2	0	0	2	2	2	0	2	2
nowaxy	2	2	2	0	2	2	2	2	2	2	2	2	2	2	2	0	2	1	2	1	2	2	2	0	1	2	2	1
F1	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	2	0	0	0	0	0	0	0	0
F2	2	0	0	1	2	2	2	0	2	2	0	2	0	1	2	2	0	2	0	0	2	2	0	2	0	2	2	2
F3	1	0	2	0	0	0	0	2	0	0	2	0	2	2	0	0	0	0	2	0	0	1	2	0	2	0	0	1